

Climate Change Reconsidered II

Biological Impacts

NIPCC

NONGOVERNMENTAL INTERNATIONAL PANEL
ON CLIMATE CHANGE

Climate Change Reconsidered II

Biological Impacts

Lead Authors/Editors

Craig D. Idso (USA), Sherwood B. Idso (USA), Robert M. Carter (Australia), S. Fred Singer (USA)

Contributing Authors and Reviewers

David J. Barnes (Australia), Raymond A. Cloyd (USA), Susan Crockford (Canada), Weihong Cui (China), Kees DeGroot (The Netherlands), Robert G. Dillon (USA), John Dale Dunn (USA), Ole Henrik Ellestad (Norway), Fred Goldberg (Sweden), Barry Goldman (Australia), H. Dickson Hoese (USA), Morten Jørdal (Norway), Madhav Khandekar (Canada), Miroslav Kutilek (Czech Republic), Steven W. Leavitt (USA), Howard Maccabee (USA), Jennifer Marohasy (Australia), Cliff Ollier (Australia), Jim Petch (United Kingdom), Robert J. Reginato (USA), Paul Reiter (France), Tom Segalstad (Norway), Gary Sharp (USA), Walter Starck (Australia), David Stockwell (Australia), Mitchell Taylor (Canada), Gerd Weber (Germany), Bastow Wilson (New Zealand), Raphael Wust (Australia)

Several additional reviewers wish to remain anonymous.

Editors

Diane Carol Bast (USA), S.T. Karnick (USA)

NIPCC

NONGOVERNMENTAL INTERNATIONAL PANEL
ON CLIMATE CHANGE

Reviews of *Climate Change Reconsidered II: Physical Science*

"I fully support the efforts of the Nongovernmental International Panel on Climate Change (NIPCC) and publication of its latest report, *Climate Change Reconsidered II: Physical Science*, to help the general public to understand the reality of global climate change."

Kumar Raina, Former Deputy Director General
Geological Survey of India

"*Climate Change Reconsidered II* fulfills an important role in countering the IPCC part by part, highlighting crucial things they ignore such as the Little Ice Age and the recovery (warming) which began in 1800–1850. In contrast to the IPCC, which often ignores evidence of past changes, the authors of the NIPCC report recognize that climatology requires studying past changes to infer future changes."

Syun-Ichi Akasofu, Founding Director & Professor of Physics Emeritus
International Arctic Research Center, University of Alaska Fairbanks

"The work of the NIPCC to present the evidence for natural climate warming and climate change is an essential counter-balance to the biased reporting of the IPCC. They have brought to focus a range of peer-reviewed publications showing that natural forces have in the past and continue today to dominate the climate signal."

Ian Clark, Department of Earth Sciences
University of Ottawa, Canada

"The CCR-II report correctly explains that most of the reports on global warming and its impacts on sea-level rise, ice melts, glacial retreats, impact on crop production, extreme weather events, rainfall changes, etc. have not properly considered factors such as physical impacts of human activities, natural variability in climate, lopsided models used in the prediction of production estimates, etc. There is a need to look into these phenomena at local and regional scales before sensationalization of global warming-related studies."

S. Jeevananda Reddy, Former Chief Technical Advisor
United Nations World Meteorological Organization

"Library shelves are cluttered with books on global warming. The problem is identifying which ones are worth reading. The NIPCC's CCR-II report is one of these. Its coverage of the topic is comprehensive without being superficial. It sorts through conflicting claims made by scientists and highlights mounting evidence that climate sensitivity to carbon dioxide increase is lower than climate models have until now assumed."

Chris de Freitas, School of Environment
The University of Auckland, New Zealand

"Rather than coming from a pre-determined politicized position that is typical of the IPCC, the NIPCC constrains itself to the scientific process so as to provide objective information. If we (scientists) are honest, we understand that the study of atmospheric processes/dynamics is in its infancy. Consequently, the work of the NIPCC and its most recent report is very important."

Bruce Borders, Professor of Forest Biometrics
Warnell School of Forestry and Natural Resources, University of Georgia

"I support [the work of the NIPCC] because I am convinced that the whole field of climate and climate change urgently needs an open debate between several 'schools of thought,' in science as well as other disciplines, many of which jumped on the IPCC bandwagon far too readily. Climate, and even more so impacts and responses, are far too complex and important to be left to an official body like the IPCC."

Sonja A. Boehmer-Christiansen
Reader Emeritus, Department of Geography, Hull University
Editor, *Energy & Environment*

Climate Change Reconsidered II

Biological Impacts

© 2014, Center for the Study of Carbon Dioxide and Global Change and Science and Environmental Policy Project

Published by THE HEARTLAND INSTITUTE
One South Wacker Drive #2740
Chicago, Illinois 60606 U.S.A.
phone +1 (312) 377-4000
fax +1 (312) 377-5000
www.heartland.org

All rights reserved, including the right to reproduce this book or portions thereof in any form. Opinions expressed are solely those of the authors. Nothing in this report should be construed as reflecting the views of the Center for the Study of Carbon Dioxide and Global Change, Science and Environmental Policy Project, or The Heartland Institute, or as an attempt to influence pending legislation. Additional copies of this book are available from The Heartland Institute at the following prices (plus shipping and handling):

1-10 copies	\$154 per copy
11-50 copies	\$123 per copy
51-100 copies	\$98 per copy
101 or more	\$79 per copy

Please use the following citation for this report:

Idso, C.D, Idso, S.B., Carter, R.M., and Singer, S.F. (Eds.) 2014. *Climate Change Reconsidered II: Biological Impacts*. Chicago, IL: The Heartland Institute.

This print version is black and white. A color version is available for free online at www.climatechangereconsidered.org.

ISBN-13 – 978-1-934791-43-1
ISBN-10 – 1-934791-43-1

2014

1 2 3 4 5 6

Foreword

For the past five years, The Heartland Institute has been proud to partner with the Center for the Study of Carbon Dioxide and Global Change and the Science and Environmental Policy Project (SEPP) to produce authoritative and independent assessments of the latest science concerning climate change. The present volume in the *Climate Change Reconsidered* series focuses on the biological impacts of rising temperatures and atmospheric carbon dioxide (CO₂) levels.

The United Nations' Intergovernmental Panel on Climate Change (IPCC) insists that rising temperatures and CO₂ levels have harmful effects on Earth's plant and animal life. But as this report demonstrates, IPCC's claims are at odds with literally thousands of real-world observations, model-based projections, and laboratory and in-the-field experiments. The reality is that the world is getting greener over time as plants, animals, and humans benefit from higher temperatures and CO₂-enriched air.

NIPCC: A Brief History

The Nongovernmental International Panel on Climate Change, or NIPCC, is an international panel of scientists and scholars who came together to understand the causes and consequences of climate change. NIPCC has no formal attachment to or sponsorship from any government or government agency.

NIPCC seeks to objectively analyze and interpret data and facts without conforming to any specific agenda. This organizational structure and purpose stand in contrast to those of IPCC, which is government-sponsored, politically motivated, and predisposed to believing that climate change is a problem in need of a U.N. solution.

NIPCC traces its beginnings to an informal meeting held in Milan, Italy in 2003 organized by Dr. S. Fred Singer and the Science and Environmental Policy Project (SEPP). The purpose was to produce an independent evaluation of the available scientific evidence on the subject of carbon dioxide-induced global warming in anticipation of the release of IPCC's *Fourth Assessment Report* (AR4). NIPCC scientists concluded IPCC was biased with respect to making future projections of climate change, discerning a significant human-induced influence on current and past climatic trends, and evaluating the impacts of potential carbon dioxide-induced environmental changes on Earth's biosphere.

To highlight such deficiencies in IPCC's AR4, in 2008 SEPP partnered with The Heartland Institute to produce *Nature, Not Human Activity, Rules the Climate*. In 2009, the Center for the Study of Carbon Dioxide and Global Change joined the original two sponsors to produce *Climate Change Reconsidered: The 2009 Report of the Nongovernmental International Panel on Climate Change (NIPCC)*, the first comprehensive alternative to the alarmist reports of IPCC.

In 2010, a Web site (www.nipccreport.org) was created to highlight scientific studies NIPCC scientists believed likely would be downplayed or ignored by IPCC during preparation of its next assessment report. In 2011, the three sponsoring organizations produced *Climate Change Reconsidered: The 2011 Interim Report of the Nongovernmental International Panel on Climate Change (NIPCC)*.

In 2013, a division of the Chinese Academy of Sciences translated and published an abridged edition of the 2009 and 2011 NIPCC reports in a single volume. Also in 2013, NIPCC released *Climate Change Reconsidered II: Physical Science*, the first of

Climate Change Reconsidered II: Biological Impacts

three volumes bringing the original 2009 report up-to-date with research from the 2011 *Interim Report* plus research as current as the third quarter of 2013. A new Web site was created (www.ClimateChangeReconsidered.org) to feature the new report and future volumes, including the current one, and news about their release.

The current volume is the second volume in the Climate Change Reconsidered II series, subtitled *Biological Impacts*. A third and final volume, subtitled *Human Welfare, Energy, and Policies*, is also being released in 2014.

CCR II: Biological Impacts

In this new report, Lead Authors/Editors Craig D. Idso, Robert M. Carter, and S. Fred Singer have been joined by a fourth author, Sherwood B. Idso, one of the world's most distinguished soil scientists and authorities on the impact of CO₂ on plants. Together, they worked with a team of more than 30 scientists from 13 countries to produce a report that is comprehensive, objective, and faithful to the scientific method. The sheer size of this volume—more than 1,000 pages and containing references to thousands of peer-reviewed articles and books—suggests what an extraordinary research, writing, and editing endeavor this turned out to be.

As they did for previous volumes in the Climate Change Reconsidered series, NIPCC authors paid special attention to peer-reviewed articles that were either overlooked by IPCC or that contain data, discussion, or implications arguing against IPCC's claim that "human interference" in the global climate has "dangerous" consequences for the natural world and human populations. They found a large body of evidence produced by thousands of scientists over the

course of many years that directly challenges IPCC's narrative. Study after study reveals that warming produces more benefits than harms for a wide range of plants and animals and, not insignificantly, humans as well. So plentiful is the research and so clear are the conclusions that one can only wonder how IPCC's authors overlooked them.

The Lead Authors/Editors briefly discuss their perspective and findings in the Preface, followed by an Executive Summary beginning on page 1 summarizing the volume's principal findings. Most notably, its authors say IPCC has exaggerated the negative impacts of global warming and rising atmospheric CO₂ levels: "We find no net harm to the global environment or to human health, and often find the opposite: net benefits to plants, including important food crops, and to animals and human health."

Acknowledgements

As we did in the forewords of previous volumes in the Climate Change Reconsidered series, we extend our sincere thanks and appreciation to the scientists and other experts who helped write this report and its precursors, to those who conducted the original research that is summarized and cited, and to those who participated in the peer-review process. Editors could not hope to work for a team of wiser, more distinguished, or more patient writers.

Funding for this effort once again came from three family foundations, none of them having any commercial interest in the topic. We thank them for their generosity. No government or corporate funds were solicited or received to support this project.

**Diane Carol Bast**

Executive Editor

The Heartland Institute

**S.T. Karnick**

Research Director

The Heartland Institute

Preface

Climate Change Reconsidered II: Biological Impacts (CCR-IIb) is produced by the Nongovernmental International Panel on Climate Change (NIPCC), a collaboration of three organizations—the Center for the Study of Carbon Dioxide and Global Change, Science and Environmental Policy Project (SEPP), and The Heartland Institute. The four Lead Authors/Editors—Craig D. Idso, Sherwood B. Idso, Robert M. Carter, and S. Fred Singer—assembled and worked closely with more than 30 contributors and reviewers from 13 countries. This report was subjected to the common standards of peer review. Reviewers who agreed to be identified are listed on the title page.

CCR-IIb is the second of three volumes in the Climate Change Reconsidered II series. The first volume, *Climate Change Reconsidered II: Physical Science* (CCR-IIa) was published in September 2013. It examined the theory, models, and evidence regarding the science of climate change and concluded the human impact on global climate is small and any warming that may occur as a result of human carbon dioxide (CO₂) and other greenhouse gas emissions is likely to have little effect on global temperatures, the cryosphere (ice-covered areas), hydrosphere (oceans, lakes, and rivers), or weather. (See Figure 1.) The current volume focuses on scientific research on the impacts of rising temperatures and atmospheric CO₂ levels on the biological world. It finds no net harm to the global environment or to human health and often finds the opposite: net benefits to plants, including important food crops, and to animals and human health.

CCR-IIb broadly tracks and critiques the work of IPCC's Working Group II, which is expected to release its report on the impacts of climate change around the same time as this report is presented. It

appears IPCC is continuing its pattern of selectively reporting data to present an alarmist view of the impacts of climate change. A draft of Working Group II's forthcoming *Summary for Policymakers* identifies eight "key risks":

- i. Risk of death, injury, and disrupted livelihoods in low-lying coastal zones and small island developing states, due to sea-level rise, coastal flooding, and storm surges.
- ii. Risk of food insecurity linked to warming, drought, and precipitation variability, particularly for poorer populations.
- iii. Risk of severe harm for large urban populations due to inland flooding.
- iv. Risk of loss of rural livelihoods and income due to insufficient access to drinking and irrigation water and reduced agricultural productivity, particularly for farmers and pastoralists with minimal capital in semi-arid regions.
- v. Systemic risks due to extreme events leading to breakdown of infrastructure networks and critical services.
- vi. Risk of loss of marine ecosystems and the services they provide for coastal livelihoods, especially for fishing communities in the tropics and the Arctic.
- vii. Risk of loss of terrestrial ecosystems and the services they provide for terrestrial livelihoods.
- viii. Risk of mortality, morbidity, and other harms during periods of extreme heat, particularly for vulnerable urban populations.

**Figure 1.
Physical Science Summary**

- Global climate models are unable to make accurate projections of climate even 10 years ahead, let alone the 100-year period that has been adopted by policy planners. The output of such models should therefore not be used to guide public policy formulation.
- Neither the rate nor the magnitude of the reported late twentieth century surface warming (1979–2000) lay outside the range of normal natural variability, nor were they in any way unusual compared to earlier episodes in Earth's climatic history.
- Solar forcing of temperature change is likely more important than is currently recognized.
- No unambiguous evidence exists of dangerous interference in the global climate caused by human-related CO₂ emissions. In particular, the cryosphere is not melting at an enhanced rate; sea-level rise is not accelerating; and no systematic changes have been documented in evaporation or rainfall or in the magnitude or intensity of extreme meteorological events.
- Any human global climate signal is so small as to be nearly indiscernible against the background variability of the natural climate system. Climate change is always occurring.
- A phase of temperature stasis or cooling has succeeded the mild warming of the twentieth century. Similar periods of warming and cooling due to natural variability are certain to occur in the future irrespective of human emissions of greenhouse gases.
- *Source:* Idso, C.D., Carter, R.M., and Singer, S.F. (Eds.) 2013. *Climate Change Reconsidered II: Physical Science*. Chicago, IL: The Heartland Institute.

The research summarized in CCR-IIb effectively refutes five of these apocalyptic forecasts. The remaining three “key risks”—the harm coastal and inland flooding will do to people and to

infrastructure—are addressed in the first and third volumes of the Climate Change Reconsidered II series.

A careful reading of the chapters below reveals thousands of peer-reviewed scientific journal articles do not support and often contradict IPCC's alarmist narrative. NIPCC scientists have worked hard to remain true to the facts in their representations of the studies cited in this work. The research is usually quoted directly and at some length, along with a description of the methodology used and qualifications that accompanied the stated conclusions. Editorial commentary is generally limited to introductions and sometimes brief conclusions at the end of sections.

Whether the subject is the likely effects of warming on crops, trees, weeds, birds, butterflies, or polar bears, it seems IPCC invariably picks the studies and models that paint global warming in the darkest possible hues. IPCC sees “death, injury, and disrupted livelihoods”—to borrow a phrase from Working Group II—everywhere it looks.

Oftentimes, IPCC's pessimistic forecasts fly in the face of scientific observations. The global ecosystem is not suffering from the rising temperatures and atmospheric CO₂ levels IPCC has called “unprecedented,” despite all the models and hypotheses IPCC's authors marshal to make that case. Real-world data show conclusively that most plants flourish when exposed to higher temperatures and higher levels of CO₂ and that the planet's terrestrial biosphere is undergoing a great post-Industrial Revolution greening that is causing deserts to retreat and forests to expand, enlarging habitat for wildlife. Essentially the same story can be told of global warming's impact on terrestrial animals, aquatic life, and human health.

Why are these research findings and this perspective missing from IPCC's reports? NIPCC has been publishing volumes containing this research for five years—long enough, one would think, for the authors of IPCC's reports to have taken notice, if only to disagree. But the draft of the Working Group II contribution to IPCC's *Fifth Assessment Report* suggests otherwise. Either IPCC's authors purposely ignore this research because it runs counter to their thesis that any human impact on climate must be bad and therefore stopped at any cost, or they are inept and have failed to conduct a proper and full scientific investigation of the pertinent literature. Either way,

Preface

IPCC is misleading the scientific community, policymakers, and the general public. Because the stakes are high, this is a grave disservice.

We are not alone in questioning the accuracy or reliability of IPCC reports. In 2010, the InterAcademy Council, an international organization representing the world's leading national academies of science, produced an audit of IPCC procedures. In its report, *Climate Change Assessments: Review of the Processes & Procedures of the IPCC*, the IAC decried the lack of independent review, reliance on unpublished and non-peer-reviewed sources, refusal by some of the lead authors to share their data with critics, and political interference in the selection of authors and contributors.

How CO₂ enrichment has affected global food production and biospheric productivity is a matter of fact, not opinion. The evidence is overwhelming that it has and will continue to help plants thrive, leading to greater biodiversity, shrinking deserts, expanded habitat for wildlife, and more food for a growing human population. In sharp contrast to IPCC's pessimistic forecast of declining food production, NIPCC's authors say a future warming of the climate coupled with rising atmospheric CO₂ levels will boost global agricultural production and help meet the food needs of the planet's growing population. They find

the positive direct effects of CO₂ on crop yields tend to overcome any negative effects associated with changed weather conditions. Journalists, policymakers, and the interested public should demand to know why IPCC either hides or is silent about these truths.

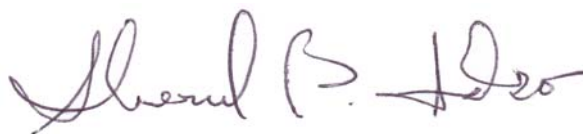
We acknowledge, as we did in the prefaces to previous volumes in this series, that not every scientist whose work we cite disagrees with IPCC positions even though their research points in different directions. We recognize there may be some among the thousands of scientists we quote who are dismayed to see their work cited in a book written by "skeptics." We ask them to read this book with an open mind and ask themselves how much of what they think they know to be true is based on trust, perhaps misplaced, in claims propagated by IPCC. Even scientists need to be reminded sometimes that skepticism, not conformity, is the higher value in the pursuit of knowledge.

We thank all those who participated in the writing, reviewing, editing, and proofreading of this volume. This was a huge undertaking that involved thousands of hours and scores of people over the course of several years. The result exceeded our hopes, and we trust it meets your expectations.

**Craig D. Idso, Ph.D.**

Chairman

Center for the Study of Carbon Dioxide and Global Change

**Sherwood B. Idso, Ph.D.**

President

Center for the Study of Carbon Dioxide and Global Change

**Robert M. Carter, Ph.D.**

Emeritus Fellow

Institute of Public Affairs (Australia)

**S. Fred Singer, Ph.D.**

President

Science and Environmental Policy Project

Table of Contents

Foreword	iii
Preface	vii
Executive Summary.....	1
1. CO₂, Plants, and Soils	11
Key Findings	11
Introduction	12
1.1 Plant Responses to Atmospheric CO ₂ Enrichment.....	13
1.2 Ecosystem Responses to CO ₂ Enrichment	45
2. Plant Characteristics.....	163
Key Findings	164
Introduction	166
2.1 Acclimation	167
2.2 Antioxidants	185
2.3 Chlorophyll.....	186
2.4 Early Spring Growth	187
2.5 Flowers	190
2.6 Fluctuating Asymmetry	194
2.7 Hormones	195
2.8 Glomalin.....	197
2.9 Isoprene.....	199
2.10 Leaves	200
2.11 Lignin	204
2.12 Lipids	206
2.13 Low Temperature	208
2.14 Monoterpenes.....	214
2.15 Nectar	215
2.16 Nitrogen Fixation	217
2.17 Nitrogen Use Efficiency	220
2.18 Nutrient Acquisition.....	221
2.19 Phenolics	225
2.20 Phenology.....	228
2.21 Protein	230
2.22 Respiration.....	235
2.23 Roots	243
2.24 Rubisco.....	254

Climate Change Reconsidered II: Biological Impacts

2.25 Seeds.....	258
2.26 Starch	265
2.27 Stomatal Density.....	266
2.28 Sugars	268
2.29 Tannins	269
2.30 Thylakoid Membranes	276
2.31 Transpiration.....	279
2.32 Vegetative Storage Proteins.....	287
2.33 Water Use Efficiency	288
2.34 Wood Density	309
3. Plants Under Stress	313
Key Findings	313
Introduction	315
3.1 Competition.....	316
3.2 Disease.....	321
3.3 Heavy Metal Toxicity	330
3.4 Herbivory	333
3.5 Iron Stress	352
3.6 Light Stress.....	353
3.7 Nitrogen Insufficiency	356
3.8 Ozone Pollution	367
3.9 Non-Ozone Air Pollutants	391
3.10 Phosphorus Insufficiency.....	395
3.11 The Progressive Nitrogen Limitation Hypothesis	397
3.12 Salinity Stress	411
3.13 Temperature Stress.....	417
3.14 UV-B Radiation Stress.....	440
3.15 Water Stress	443
3.16 Weeds.....	464
4. Earth's Vegetative Future	473
Key Findings	473
Introduction	475
4.1 Agricultural and Food Production	476
4.2 Biospheric Productivity: The Greening of the Earth	493
4.3 Biodiversity	566
4.4 Extinction	569
4.5 Evolution	581
5. Terrestrial Animals	597
Key Findings	597
Introduction	598
5.1 The Extinction Hypothesis	600
5.2 Amphibians	617
5.3 Arthropods	625
5.4 Birds.....	626
5.5 Insects	651
5.6 Mammals	700
5.7 Parasites and Other Diseases	705
5.8 Polar Bears	710
5.9 Reptiles	730
5.10 Worms	737

Table of Contents

6. Aquatic Life	743
Key Findings	743
Introduction	744
6.1 Ocean Warming	745
6.2 Freshwater Warming	817
6.3 Ocean “Acidification”	822
6.4 Freshwater “Acidification”	919
6.5 Simultaneous Ocean Warming and “Acidification”	926
 7. Human Health.....	 955
Key Findings	955
Introduction	956
7.1 Hot vs. Cold Weather	957
7.2 Cardiovascular Disease.....	976
7.3 Respiratory Disease	987
7.4 Stroke Occurrence.....	993
7.5 Malaria	995
7.6 Dengue Fever	1004
7.7 Tick-Borne Diseases	1009
7.8 Effects of CO ₂	1011
 APPENDIX 1: Acronyms	 1039
 APPENDIX 2: Authors, Contributors, and Reviewers	 1043
 APPENDIX 3: Plant Dry Weight (Biomass) Responses to Atmospheric CO₂ Enrichment.....	 1045
 APPENDIX 4: Plant Photosynthesis (Net CO₂ Exchange Rate) Responses to Atmospheric CO₂ Enrichment	 1055

Executive Summary

This report is produced by the Nongovernmental International Panel on Climate Change (NIPCC), a joint project of three organizations: Center for the Study of Carbon Dioxide and Global Change, Science and Environmental Policy Project (SEPP), and The Heartland Institute. Four Lead Authors/Editors—Craig D. Idso, Sherwood B. Idso, Robert M. Carter, and S. Fred Singer—assembled and worked closely with more than 30 authors, contributors, and reviewers. This volume was subjected to the common standards of peer review.

This work provides the scientific balance that is missing from the overly alarmist reports of the United Nations' Intergovernmental Panel on Climate Change (IPCC), which are highly selective in their review of climate science and controversial with regard to their projections of future climate change. Although IPCC claims to be unbiased and to have based its assessment on the best available science, we have found this not to be the case. In many instances conclusions have been seriously exaggerated, relevant facts have been distorted, and key scientific studies have been ignored.

1. Impact on Plants and Soil

Carbon dioxide (CO₂) is the basis of nearly all life on Earth. It is the primary raw material utilized by most plants to produce the organic matter from which they construct their tissues. Not surprisingly, thousands of laboratory and field experiments conducted over the past 200 years demonstrate that plant productivity and growth both rise as the CO₂ concentration of the air increases.

As early as 1804, de Saussure showed that peas exposed to high CO₂ concentrations grew better than

control plants in ambient air, and work conducted in the early 1900s significantly increased the number of species in which a growth-enhancing effect of atmospheric CO₂ enrichment was observed to occur (Demoussy, 1902–1904; Cummings and Jones, 1918). By the time a group of scientists convened at Duke University in 1977 for a workshop on Anticipated Plant Responses to Global Carbon Dioxide Enrichment, an annotated bibliography of 590 scientific studies dealing with CO₂ effects on vegetation had been prepared (Strain, 1978). This body of research demonstrated increased levels of atmospheric CO₂ generally produce increases in plant photosynthesis, decreases in plant water loss by transpiration, increases in leaf area, and increases in plant branch and fruit numbers, to name but a few of the most commonly reported benefits. (See Figure 1.)

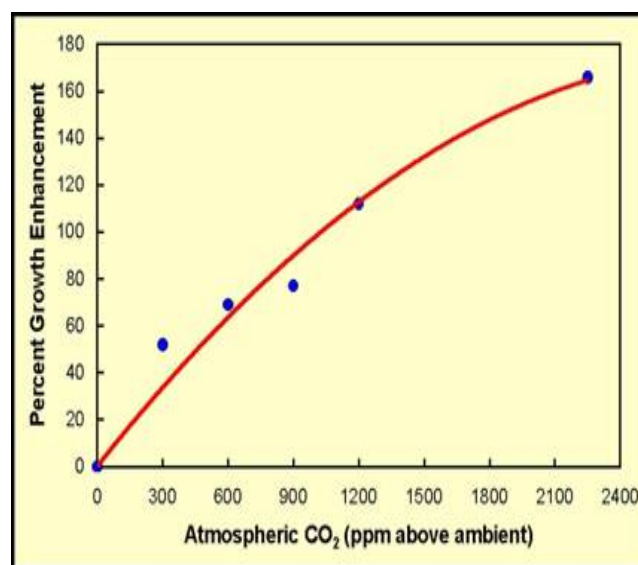


Figure 1. Positive Impact of CO₂ on Plants and Trees. Adapted from Idso, K.E. (1992).

Five years later, at the International Conference on Rising Atmospheric Carbon Dioxide and Plant Productivity, it was concluded a doubling of the air's CO₂ concentration likely would lead to a 50% increase in photosynthesis in C₃ plants, a doubling of water use efficiency in both C₃ and C₄ plants, significant increases in biological nitrogen fixation in almost all biological systems, and an increase in the ability of plants to adapt to a variety of environmental stresses (Lemon, 1983). In the years since, many other studies have been conducted on hundreds of different plant species, repeatedly confirming the growth-enhancing, water-saving, and stress-alleviating advantages that elevated atmospheric CO₂ concentrations bestow upon Earth's plants and soils (Idso and Singer, 2009; Idso and Idso, 2011).

Chapter 1 focuses on basic plant productivity responses to elevated CO₂ and includes in two appendices tabular presentations of more than 5,500 individual plant photosynthetic and biomass responses to CO₂-enriched air, finding nearly all plants experience increases in these two parameters at higher levels of CO₂. Chapter 1 also examines the effect of elevated CO₂ on ecosystems including forests, grasslands, peatlands, wetlands, and soils. This review of the literature reveals elevated CO₂ improves the productivity of ecosystems both in plant tissues aboveground and in the soils beneath them.

2. Impact on Plant Characteristics

There are two principal methods researchers utilize to ascertain how Earth's terrestrial plants will be affected by a continuation of the historical rise in the atmosphere's CO₂ concentration. One way is to grow plants in CO₂-enriched air to levels expected to be experienced in the decades and centuries to come. In the case of long-lived trees, growth over prior decades and centuries as the CO₂ concentration has risen can be derived from studying the yearly growth rings produced over those time periods and that now comprise the living or dead trees' trunks.

The primary information sought in these studies are rates of photosynthesis and biomass production and the efficiency with which the various plants and trees utilize water. There are a host of other effects of significance, including substances produced in the growth process that impact how well it proceeds, substances deposited in the parts of agricultural crops that are harvested for human and animal consump-

tion, and substances that determine whether insect pests find the foliage or fruit of a certain crop or tree to be to their liking. Finally, there is the question of whether forest soils will have sufficient nitrogen to sustain the long-term CO₂-enhanced growth rates of long-lived trees.

Chapter 2 examines these and other effects of atmospheric CO₂ enrichment on plant characteristics. Extensive research finds those effects are overwhelmingly positive. For example, rising CO₂ levels promote plant growth by increasing the concentrations of plant hormones that stimulate cell division, cell elongation, and protein synthesis; by enabling plants to produce more and larger flowers; by increasing the production of glomalin, an important protein created by fungi living in symbiotic association with the roots of most vascular plants; and by affecting leaf characteristics of agricultural plants that lead to higher rates and efficiencies of photosynthesis and growth as well as increased resistance to herbivory and pathogen attack.

3. Impact on Plants Under Stress

According to IPCC, a warmer future will introduce new sources of stress on the biological world, including increases in forest fires, droughts, and extreme heat events. IPCC fails to ask whether the higher levels of atmospheric CO₂ its models also predict will aid or hinder the ability of plants to cope with these challenges. Had it looked, IPCC would have discovered an extensive body of research showing how atmospheric CO₂ enrichment ameliorates the negative effects of a number of environmental plant stresses. The relative percentage growth enhancement produced by an increase in the air's CO₂ concentration is generally greater under stressful and resource-limited conditions than when growing conditions are ideal.

Chapter 3 reports research on the effects of rising CO₂ levels on the ability of plants to cope with pathogenic invaders, drought, rising temperatures, the deleterious effects of heavy metals in soil, herbivory by insects and animals, and shortages of essential nutrients in soil such as nitrogen. Rising CO₂ typically reduces and can completely override the negative effects of ozone pollution on the photosynthesis, growth, and yield of nearly all agricultural crops and trees that have been experimentally evaluated. Rising CO₂ also can help plants overcome

stresses imposed by the buildup of soil salinity from repeated irrigation.

4. Likely Future Impacts on Plants

Chapter 4 analyzes how atmospheric CO₂ enrichment has boosted global food production and biospheric productivity since the beginning of the Industrial Revolution. It also reports how rising CO₂ helps plants avoid temperature-induced extinctions, which many models predict could occur if global temperatures rise significantly in the future. Whereas IPCC forecasts severe food shortages, the preponderance of evidence suggests the many yield-enhancing benefits of rising atmospheric CO₂ will help ensure more food is grown to meet the needs of the planet's growing population.

Chapter 4 also reports on the current health of the terrestrial biosphere, analyzing the productivity of the globe as a whole followed by regional analyses on continental and sub-continental scales. According to IPCC, the productivity of the terrestrial biosphere should be declining because of rising temperatures and other perceived negative climatic changes. In contrast, empirical data show it to be increasing, in large measure due to the aerial fertilization effect of rising atmospheric CO₂.

Chapter 4 concludes with an examination of topics pertaining to biodiversity, plant extinctions, and plant evolution, which represent three important topics in assessing the future of Earth's terrestrial biosphere.

5. Impact on Terrestrial Animals

IPCC's *Fourth Assessment Report* claimed "new evidence suggests that climate-driven extinctions and range retractions are already widespread" and the "projected impacts on biodiversity are significant and of key relevance, since global losses in biodiversity are irreversible (*very high confidence*)" (IPCC, 2007). However, as shown in the first volume of the Climate Change Reconsidered II series, *Physical Science*, there is a growing divide between IPCC's climate model simulations and real-world observations of global warmth. The species-modeling research IPCC almost exclusively relies on to make these predictions depends on climate models known to exaggerate future global warming and extreme weather events.

Even assuming IPCC climate models were unbiased and reasonably accurate at regional scales, the "climate envelope" models used by IPCC are deeply flawed due to assumptions about the immobility of species that are routinely contradicted by real-world observations. IPCC also improperly characterizes the adaptive responses (e.g., range shifts, phenotypic or genetic adaptations) of many species as supporting their model-based extinction claims, when in reality such adaptive responses provide documentary evidence of species resilience.

Chapter 5 begins with a review and analysis of IPCC-based species extinction claims, highlighting many of the problems inherent in the models on which such claims are based. The model projections are then evaluated against real-world observations of various animal species and their response to what IPCC has called the unprecedented rise in temperature and atmospheric CO₂ levels of the twentieth and twenty-first centuries. Results of that evaluation reveal that although there likely will be some changes in species population dynamics, few if any species likely will be driven even close to extinction. In a number of instances, real-world data indicate warmer temperatures and higher atmospheric CO₂ concentrations will be highly beneficial, favoring a proliferation of species. IPCC continues to ignore such positive externalities of rising temperature and atmospheric CO₂.

6. Impact on Aquatic Life

IPCC postulates that human interference in the climate will significantly harm aquatic life by causing temperatures of the world's water bodies to rise and through the absorption of CO₂ from the atmosphere into water, thereby lowering the pH of freshwater and ocean water (a process referred to as "acidification"). In both scenarios, IPCC projects marine and freshwater species will be negatively impacted and will experience future declines, which in some instances may be so severe as to cause species extinctions.

In contrast, the material presented in Chapter 6, representing the findings of hundreds of peer-reviewed research analyses, suggests a much better future is in store for Earth's aquatic life. Many laboratory and field studies demonstrate growth and developmental improvements in response to higher temperatures and reduced water pH levels. Other

research illustrates the capability of coral and other marine and freshwater species to tolerate and adapt to the rising temperature (see Figure 2) and pH decline of the planet's water bodies. When these observations are considered, the pessimistic projections of IPCC give way to considerable optimism with respect to the future of the planet's marine life.

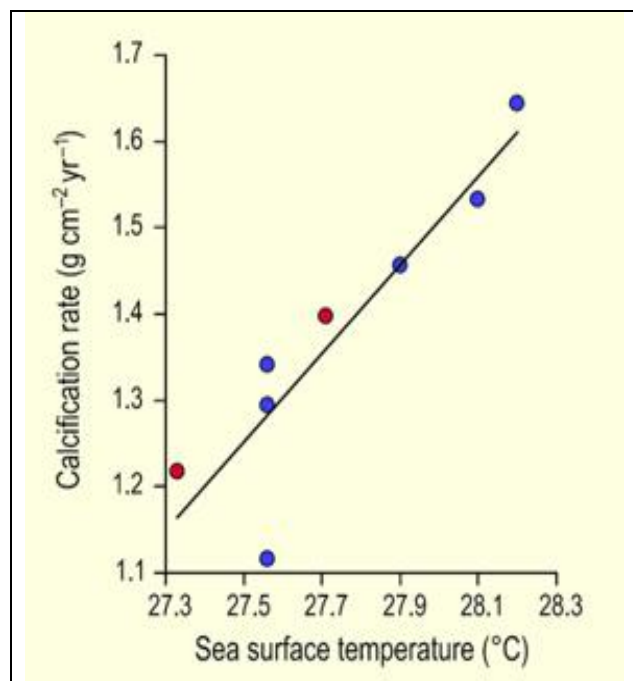


Figure 2. Coral calcification rates rise with seawater temperature. Adapted from Carricart-Ganivet and Gonzalez-Diaz (2009).

7. Impact on Human Health

Carbon dioxide is invisible, odorless, nontoxic, and does not seriously affect human health until the CO₂ content of the air reaches approximately 15,000 ppm, more than 37 times greater than the current concentration of atmospheric CO₂ (Luft *et al.*, 1974). There is no reason to be concerned about any direct adverse human health consequences of the ongoing rise in the air's CO₂ content now or in the future, as even extreme model projections do not indicate anthropogenic activities will raise the air's CO₂ concentration above 1,000 to 2,000 ppm. Nevertheless, IPCC contends rising CO₂ concentrations are causing several indirect threats to human health, which they project will worsen as the air's CO₂ concentration rises in the future.

In a draft Technical Summary of its upcoming report, Working Group II claims, "The health of human populations is sensitive to shifts in weather patterns and other aspects of climate change [*very high confidence*] and "There is emerging evidence of non-linearities in response (such as greater-than-expected mortality due to heat waves) as climates become more extreme" (IPCC, 2013, p. 16; *italics in original, bold removed*).

Research reviewed in CCR-IIb, however, shows IPCC's view of the impacts of rising temperatures and atmospheric CO₂ on human health is simply wrong. Numerous peer-reviewed studies demonstrate a warmer planet is beneficial to humanity, as warmer temperatures in all parts of the world lead to decreases in temperature-related mortality. The medical literature shows warmer temperatures and a smaller difference between daily high and low temperatures, as occurred during the twentieth and early twenty-first centuries, reduce mortality rates due to cardiovascular and respiratory disease and stroke occurrence.

Similarly, the research is quite clear that climate has exerted only a minimal influence on recent trends in vector-borne diseases such as malaria, dengue fever, and tick-borne diseases. Other factors, many of them related to economic and technological setbacks or progress and not to weather, are far more important in determining the transmission and prevalence of such diseases.

Finally, and perhaps surprisingly, IPCC entirely overlooks the positive effects of rising levels of atmospheric CO₂ on human health. Carbon dioxide fertilization has been shown to enhance certain health-promoting substances in plants, such as antioxidants, vitamin C, and fatty acids, and promote the growth of plants such as St. John's wort used for the treatment of a variety of illnesses. In this way, global warming portends great health benefits for humans. IPCC makes no mention of these benefits.

The remainder of this executive summary consists of key findings organized by chapter.

Key Findings by Chapter**Chapter 1. CO₂, Plants, and Soils**

- Results obtained under 3,586 separate sets of experimental conditions conducted on 549 plant species reveal nearly all plants experience increases in dry weight or biomass in response to atmospheric CO₂ enrichment (henceforth referred to as “rising CO₂”). Additional results obtained under 2,094 separate experimental conditions conducted on 472 plant species reveal nearly all plants experience increases in their rates of photosynthesis in response to rising CO₂.
- Long-term CO₂ enrichment studies confirm the findings of shorter-term experiments, demonstrating that the growth-enhancing, water-conserving, and stress-alleviating effects of rising CO₂ likely persist throughout plant lifetimes.
- Forest productivity and growth rates around the world have increased gradually since the Industrial Revolution in concert with, and in response to, the historical increase in the air’s CO₂ concentration. Therefore, as CO₂ continues to rise, forests likely will respond by exhibiting significant increases in biomass production and they likely will grow more robustly and significantly expand their ranges.
- Modest increases in air temperature tend to increase carbon storage in forests and their soils. Thus, old-growth forests can be significant carbon sinks and their capacity to sequester carbon in the future will be enhanced as CO₂ continues to rise.
- As CO₂ continues to rise, the productivity of grassland species will increase even under unfavorable growing conditions characterized by less-than-adequate soil moisture, inadequate soil nutrition, elevated air temperature, and physical stress imposed by herbivory.
- The thawing of permafrost caused by increases in air temperature likely will not transform peatlands from carbon sinks to carbon sources. Instead, rapid terrestrialization likely will act to intensify carbon-sink conditions.

- Rising CO₂ likely will enhance the productivity and carbon sequestering ability of Earth’s wetlands. In addition, rising CO₂ may help some coastal wetlands counterbalance the negative impacts of rising seas.
- Rising CO₂ likely will allow greater numbers of beneficial bacteria (that help sequester carbon and nitrogen) to exist within soils and anaerobic water environments, thereby benefitting both terrestrial and aquatic ecosystems.
- The aerial fertilization effect of rising CO₂ likely will result in greater soil carbon stores due to increased carbon input to soils, even in nutrient-poor soils and in spite of predicted increases in temperature. The carbon-sequestering capability of Earth’s vegetation likely will act as a significant brake on the rate-of-rise of the air’s CO₂ content and thereby help to mute the magnitude of any CO₂-induced global warming.
- Rising CO₂ has significantly reduced the erosion of valuable topsoil over the past several decades; the continuing increase in atmospheric CO₂ can maintain this trend and perhaps even accelerate it for the foreseeable future.

Chapter 2. Plant Characteristics

- Rising CO₂ enhances plant growth, development, and ultimate yield (in the case of agricultural crops) by increasing the concentrations of plant hormones that stimulate cell division, cell elongation, and protein synthesis.
- Rising CO₂ enables plants to produce more and larger flowers, as well as other flower-related changes having significant implications for plant productivity and survival, almost all of which are positive.
- Rising CO₂ increases the production of glomalin, a protein created by fungi living in symbiotic association with the roots of 80 percent of the planet’s vascular plants, where it is having a huge positive impact on the biosphere.
- Rising CO₂ likely will affect many leaf characteristics of agricultural plants, with the

majority of the changes leading to higher rates and efficiencies of photosynthesis and growth as well as increased resistance to herbivory and pathogen attack.

- Rising CO₂ stimulates photosynthesis in nearly all plants, enabling them to produce more nonstructural carbohydrates that can be used to create important carbon-based secondary compounds, one of which is lignin.
- Rising CO₂ leads to enhanced plant fitness, flower pollination, and nectar production, leading to increases in fruit, grain, and vegetable yields of agricultural crops as well as productivity increases in natural vegetation.
- As rising CO₂ causes many plants to increase biomass, the larger plants likely will develop more extensive root systems enabling them to extract greater amounts of mineral nutrients from the soil.
- Rising CO₂ causes plants to sequentially reduce the openness of their stomata, thus restricting unnecessary water loss via excessive transpiration, while some plants also reduce the density (number per area) of stomata on their leaves.
- Rising CO₂ significantly enhances the condensed tannin concentrations of the vast majority of trees and grasses, providing them with stronger defenses against various herbivores both above and below ground. This in turn reduces the amount of methane, a potent greenhouse gas, released to the atmosphere by ruminants browsing on tree leaves and grass.
- As the air's CO₂ content rises, many plant species may not experience photosynthetic acclimation even under conditions of low soil nitrogen. In the event that a plant cannot balance its carbohydrate sources and sinks, CO₂-induced acclimation provides a way of achieving that balance by shifting resources away from the site of photosynthesis to enhance sink development or other important plant processes.

Chapter 3. Plants Under Stress

- Rising CO₂ exerts a greater positive influence on diseased as opposed to healthy plants because it significantly ameliorates the negative effects of stresses imposed on plants by pathogenic invaders.
- Rising CO₂ helps many plants use water more efficiently, helping them overcome stressful conditions imposed by drought or other less-than-optimum soil moisture conditions.
- Enhanced rates of plant photosynthesis and biomass production from rising CO₂ will not be diminished by any global warming that might accompany it in the future. In fact, if ambient air temperatures rise concurrently, the growth-promoting effects of atmospheric CO₂ enrichment will likely rise even more.
- Although rising CO₂ increases the growth of many weeds, the fraction helped is not as large as that experienced by non-weeds. Thus, CO₂ enrichment of the air may provide non-weeds with greater protection against weed-induced decreases in productivity.
- Rising CO₂ improves plants' abilities to withstand the deleterious effects of heavy metals where they are present in soils at toxic levels.
- Rising CO₂ reduces the frequency and severity of herbivory against crops and trees by increasing production of natural substances that repel insects, leading to the production of more symmetrical leaves that are less susceptible to attacks by herbivores, and making trees more capable of surviving severe defoliation.
- Rising CO₂ increases net photosynthesis and biomass production by many agricultural crops, grasses, and grassland species even when soil nitrogen concentrations tend to limit their growth. Additional CO₂-induced carbon input to the soil stimulates microbial decomposition and thus leads to more available soil nitrogen, thereby conclusively disproving the progressive nitrogen limitation hypothesis.
- Rising CO₂ typically reduces and can completely override the negative effects of ozone pollution on

Executive Summary

the photosynthesis, growth, and yield of nearly all agricultural crops and trees that have been experimentally evaluated.

- Rising CO₂ can help plants overcome stresses imposed by the buildup of soil salinity from repeated irrigation.
- Rising CO₂ is a powerful antidote for the deleterious biological impacts that might be caused by an increase in the flux of UV-B radiation at the surface of Earth due to depletion of the planet's stratospheric ozone layer.

Chapter 4. Earth's Vegetative Future

- The vigor of Earth's terrestrial biosphere has been increasing with time, revealing a great post-Industrial Revolution greening of the Earth that extends across the entire globe. Over the past 50 years global carbon uptake has doubled from 2.4 ± 0.8 billion tons in 1960 to 5.0 ± 0.9 billion tons in 2010.
- The atmosphere's rising CO₂ content, which IPCC considers to be the chief culprit behind all of its "reasons for concern" about the future of the biosphere, is most likely the primary cause of the observed greening trend.
- The observed greening of the Earth has occurred in spite of all the many real and imagined assaults on Earth's vegetation, including fires, disease, pest outbreaks, air pollution, deforestation, and climatic change. Rising CO₂ is making the biosphere more resilient to stress even as it becomes more lush and productive.
- Agricultural productivity in the United States and across the globe dramatically increased over the last three decades of the twentieth century, a phenomenon partly due to new cultivation techniques but also due partly to warmer temperatures and higher CO₂ levels.
- A future warming of the climate coupled with rising CO₂ will further boost global agricultural production and help meet the food needs of the planet's growing population.
- The positive direct effects of higher levels of atmospheric CO₂ on future crop yields are likely to dominate any hypothetical negative effects associated with changing weather conditions, just as they have during the twentieth and early twenty-first centuries.
- Plants can adjust their physiology to accommodate a warming of both the magnitude and rate-of-rise typically predicted by climate models, should such a warming actually occur.
- Evidence continues to accumulate for substantial heritable variation of ecologically important plant traits, including root allocation, drought tolerance, and nutrient plasticity, which suggests rapid evolution is likely to occur based on epigenetic variation alone. Rising CO₂ will exert significant selection pressure on plants, which can be expected to improve their performance in the face of various environmental stressors via the process of micro-evolution.
- As good as things currently are for world agriculture, natural selection and bioengineering could bring about additional beneficial effects. For example, highly CO₂-responsive genotypes of a wide variety of plants could be selected to take advantage of their genetic ability to optimize their growth in response to rising CO₂.

Chapter 5. Terrestrial Animals

- IPCC's forecast of future species extinction relies on a narrow view of the literature that is highly selective and based almost entirely on model projections as opposed to real-world observations; the latter often contradict the former.
- Numerous shortcomings are inherent in the models utilized in predicting the impact of climate on the health and distributions of animal species. Assumptions and limitations make them unreliable.
- Research suggests amphibian populations will suffer little, if any, harm from projected CO₂-induced global warming, and they may even benefit from it.

- Although some changes in bird populations and their habitat areas have been documented in the literature, linking such changes to CO₂-induced global warming remains elusive. Also, when there have been changes, they often are positive, as many species have adapted and are thriving in response to rising temperatures of the modern era.
- Polar bears have survived historic changes in climate that have exceeded those of the twentieth century or are forecast by computer models to occur in the future. In addition, some populations of polar bears appear to be stable despite rising temperatures and summer sea ice declines. The biggest threat they face is not from global warming but hunting by humans, which historically has taken a huge toll on polar bear populations.
- The net effect of climate change on the spread of parasitic and vector-borne diseases is complex and at this time appears difficult to predict. Rising temperatures increase the mortality rates as well as the development rates of many parasites of veterinary importance, and temperature is only one of many variables that influence the range of viruses and other sources of diseases.
- Existing published research indicates rising temperatures likely will not increase, and may decrease, plant damage from leaf-eating herbivores, as rising atmospheric CO₂ boosts the production of certain defensive compounds in plants that are detrimental to animal pests.
- Empirical data on many animal species, including butterflies, other insects, reptiles, and mammals, indicate global warming and its myriad ecological effects tend to foster the expansion and proliferation of animal habitats, ranges, and populations, or otherwise have no observable impacts one way or the other.
- Multiple lines of evidence indicate animal species are adapting, and in some cases evolving, to cope with climate change of the modern era, as expected by Darwinian evolution and well-established ecological concepts.

Chapter 6. Aquatic Life

- Multiple studies from multiple ocean regions confirm ocean productivity tends to increase with temperature. Subjects of this research include phytoplankton and macroalgae, corals, crustaceans, and fish.
- Aquatic life has survived decadal, centennial, and millennial-scale climate oscillations that have persisted for millions of years. Evidence indicates they are well-equipped to adapt to forecasted increases in temperature, if necessary.
- Many aquatic species demonstrate the capability to adjust their individual critical thermal maximum (the upper temperature at which the onset of behavioral incapacitation occurs) upwards in response to temperature increases forecast by IPCC.
- The decline in ocean pH levels in the year 2100 (as compared to preindustrial times) may only be half the 0.4 value IPCC has calculated.
- The natural variability in ocean pH levels often is much greater than the change in pH levels forecast by IPCC.
- Natural fluctuations in pH may have a large impact on the development of resilience in marine populations, as heterogeneity in the environment with regard to pH and pCO₂ exposure may result in populations that are acclimatized to variable pH or extremes in pH.
- Caution should be applied when interpreting results from laboratory-based studies of lower seawater pH levels. Such studies often are incapable, or fall far short, of mimicking conditions in the real world, and thus they frequently yield results quite different than what is observed in nature.
- Rising temperatures and atmospheric CO₂ levels do not pose a significant threat to aquatic life. Many aquatic species have shown considerable tolerance to temperatures and CO₂ values predicted for the next few centuries, and many have demonstrated a likelihood of positive responses in empirical studies.

Executive Summary

- Rising seawater temperature is conducive to enhanced coral calcification, leading some experts to forecast coral calcification will increase by about 35% beyond pre-industrial levels by 2100, and no extinction of coral reefs will occur in the future.
- For those species showing negative responses, there are adequate reasons to conclude such responses will be largely mitigated through phenotypic adaptation or evolution during the many decades to centuries the pH concentration is projected to fall. A similar assessment can be made with respect to the impact of rising temperatures or a combination of rising temperature and marine/freshwater “acidification.”
- cardiovascular diseases associated with high temperatures and summer heat waves.
- Extensive scientific examination and research contradict the claim that malaria will expand across the globe and intensify as a result of CO₂-induced warming.
- Concerns over large increases in vector-borne diseases such as dengue as a result of rising temperatures are unfounded and unsupported by the scientific literature, as climatic indices are poor predictors for dengue disease.
- Although temperature and climate largely determine the geographical distribution of ticks, they are not among the significant factors determining the incidence of tick-borne diseases.

Chapter 7. Human Health

- Warmer temperatures lead to a decrease in temperature-related mortality, including deaths associated with cardiovascular disease, respiratory disease, and strokes. The evidence of this benefit comes from research conducted in every major country of the world.
- In the United States the average person who died because of cold temperature exposure lost in excess of 10 years of potential life, whereas the average person who died because of hot temperature exposure likely lost no more than a few days or weeks of life.
- In the United States, some 4,600 deaths are delayed each year as people move from cold northeastern states to warm southwestern states. Between 3 and 7% of the gain in longevity experienced over the past three decades was due simply to people moving to warmer states.
- Cold-related deaths are far more numerous than heat-related deaths in the United States, Europe, and almost all countries outside the tropics. Coronary and cerebral thrombosis account for about half of all cold-related mortality.
- Global warming is reducing the incidence of cardiovascular diseases related to low temperatures and wintry weather by a much greater degree than it increases the incidence of
- Rising CO₂ is not only raising the productivity of Earth’s common food plants but also significantly increasing the quantity and potency of the many health-promoting substances found in their tissues, which are the ultimate sources of sustenance for essentially all animals and humans.
- Rising CO₂ positively impacts the production of numerous health-promoting substances found in medicinal or “health food” plants, and this phenomenon may have contributed to the increase in human life span that has occurred over the past century or so.
- There is little reason to expect any significant CO₂-induced increases in human-health-harming substances produced by plants as atmospheric CO₂ levels continue to rise.

References

- Carricart-Ganivet, J.P. and Gonzalez-Diaz, P. 2009. Growth characteristics of skeletons of *Montastraea annularis* (Cnidaria: Scleractinia) from the northwest coast of Cuba. *Ciencias Marinas* 35: 237–243.
- Idso, C.D. and Idso, S.B. 2011. *The Many Benefits of Atmospheric CO₂ Enrichment*. Vales Lake Publishing, LLC, Pueblo West, Colorado, USA.
- Idso, C.D. and Singer, S.F. 2009. *Climate Change Reconsidered: 2009 Report of the Nongovernmental*

Climate Change Reconsidered II: Biological Impacts

International Panel on Climate Change (NIPCC). The Heartland Institute, Chicago, Illinois, USA.

Idso, K.E. 1992. Plant responses to rising levels of atmospheric carbon dioxide. *Climatological Publications Scientific Paper* No. 23, Office of Climatology, Arizona State University, Tempe, Arizona.

IPCC. 2007. *Climate Change 2007: Impacts, Adaptation and Vulnerability*. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., and Hanson, C.D. (Eds.) Cambridge University Press, Cambridge, UK.

IPCC. 2013. Technical Summary. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability*. Contribution of Working Group II to the Fifth Assessment Report of the

Intergovernmental Panel on Climate Change, draft dated October 28, 2013.

Lemon, E.R. (Ed.) 1983. *CO₂ and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide*. Westview Press, Boulder, CO.

Luft, U.C., Finkelstein, S., and Elliot, J.C. 1974. Respiratory gas exchange, acid-base balance, and electrolytes during and after maximal work breathing 15 mm Hg PICO₂. In: Nahas, G. and Schaefer, K.E. (Eds.) *Carbon Dioxide and Metabolic Regulations*. Springer-Verlag, New York, NY, pp. 273–281.

Strain, B.R. 1978. *Report of the Workshop on Anticipated Plant Responses to Global Carbon Dioxide Enrichment*. Department of Botany, Duke University, Durham, NC.

1

CO₂, Plants, and Soils

Key Findings

Introduction

1.1 Plant Responses to Atmospheric CO₂ Enrichment

- 1.1.1 Dry Weight (Biomass)
- 1.1.2 Plant Photosynthesis (Net CO₂ Exchange Rate)
- 1.1.3 Long-Term Studies
- 1.1.4 Lifetime Exposure to Elevated CO₂
- 1.1.5 Growth Responses to Very High CO₂ Concentrations

1.2 Ecosystem Responses to CO₂ Enrichment

- 1.2.1 Forests
 - 1.2.2 Grasslands
 - 1.2.3 Peatlands
 - 1.2.4 Wetlands
 - 1.2.5 Soils
-

Key Findings

The key findings of the present chapter are listed below.

- Results from 3,586 separate experimental conditions conducted on 549 plant species reveal nearly all plants will experience increases in dry weight or biomass in response to atmospheric CO₂ enrichment. Results from an additional 2,094 separate experimental conditions conducted on 472 plant species reveal nearly all plants will experience increases in photosynthesis in response to atmospheric CO₂ enrichment.
- Long-term CO₂ enrichment studies confirm the findings of shorter-term experiments, demonstrating the effects of elevated atmospheric CO₂ likely persist across plant lifetimes.
- Several studies indicate plants are not harmed by super-elevated atmospheric CO₂ concentrations an

order of magnitude or more greater than the globe's current mean. Instead, positive growth responses are reported, some of which are particularly large. Most plants will display enhanced rates of photosynthesis and biomass production as the atmosphere's CO₂ concentration rises.

- Forest growth rates throughout the world have increased over the years in concert with, and in response to, the historical increase in the air's CO₂ concentration. As the atmosphere's CO₂ concentration continues to rise, forests likely will respond by exhibiting significant increases in biomass production, and thus they likely will grow more robustly and significantly expand their ranges, as is already being documented in many parts of the world.
- Where tropical forests have not been decimated by the targeted and direct destructive actions of

Climate Change Reconsidered II: Biological Impacts

people, such as the felling and burning of trees, forest productivity has been growing with the passing of time, rising with the increasing CO₂ content of the air. It has been doing so despite changes in atmospheric, soil, and water chemistry, including twentieth century global warming, which IPCC claims to have been unprecedented over the past one to two millennia.

- In contrast to frequently stated assumptions, old-growth forests can be significant carbon sinks, and their capacity to sequester carbon in the future will be enhanced as the atmospheric CO₂ content rises.
- Future increases in air temperature likely will have a positive effect on carbon storage in forests and their associated soils.
- As the air's CO₂ concentration increases, the productivity of grassland species will increase, even under unfavorable growing conditions characterized by less-than-adequate soil moisture, inadequate soil nutrition, elevated air temperature, and physical stress imposed by herbivory.
- In contrast to IPCC projections, the thawing of permafrost caused by increases in air temperature and CO₂ will not likely transform peatlands from carbon-sink to carbon-source ecosystems. Instead, as permafrost thaws, plants and trees can begin to grow again on these lands and in so doing, they sequester carbon.
- Rising atmospheric CO₂ likely will enhance the productivity and carbon sequestering ability of wetlands. In addition, elevated CO₂ may assist some coastal wetlands in counterbalancing the negative impacts of rising seas.
- Rising atmospheric CO₂ concentrations likely will allow greater numbers of beneficial bacteria, which help sequester carbon and nitrogen, to exist within soils and anaerobic water environments, a two-pronged phenomenon benefiting both terrestrial and aquatic ecosystems.
- The aerial fertilization effect of atmospheric CO₂ enrichment likely will result in greater soil carbon stores due to increased carbon-input into soils, even in nutrient-poor soils and in spite of predicted increases in temperature. In addition, the soil-carbon-sequestering capability of Earth's vegetation likely will act as a significant brake on

the rate-of-rise of the air's CO₂ content and thereby help to mute the magnitude of any CO₂-induced global warming.

- The historical increase in the atmosphere's CO₂ concentration has significantly reduced erosion of valuable topsoil over the past several decades, and the continuing increase in atmospheric CO₂ can maintain this trend, and perhaps even accelerate it, throughout the foreseeable future.

Introduction

The United Nations' Intergovernmental International Panel on Climate Change (IPCC) insists that rising CO₂ levels, accompanied by even modest warming, will have harmful effects on plant life. In a draft of its Summary for Policymakers (SPM) to accompany its 2014 report, Working Group II says, "Without adaptation, local temperature increases of 1°C or more above preindustrial levels are projected to negatively impact yields for the major crops (wheat, rice, maize) in tropical and temperate regions, although individual locations may benefit (*medium confidence*). With or without adaptation, climate change will reduce median yields by 0 to 2% per decade for the rest of the century, as compared to a baseline without climate change" (IPCC 2014, p. 10).

These claims are at odds with the preponderance of research in this area dating as far back as the early 1900s (Demoussy, 1902–1904; Cummings and Jones, 1918) and as recent as 2013 (Isbell et al., 2013; Zhou et al., 2013). Two previous volumes in the *Climate Change Reconsidered* series (Idso and Singer, 2009; Idso, Carter, and Singer, 2011) contained extensive literature reviews that also contradict IPCC's conclusions, suggesting once again IPCC is ignoring research appearing in peer-reviewed journals that contradicts its preferred narrative.

The current chapter begins with an analysis, in Section 1.1, of basic plant productivity responses to elevated CO₂. It references a tabular presentation of more than 5,000 individual plant photosynthetic and biomass responses appearing in Appendices 3 and 4. Section 1.2 surveys the literature on the effects of CO₂ on various eco-systems including forests, grasslands, peatlands, wetlands, and soils, finding in each case the beneficial effects of rising atmospheric concentrations of CO₂ more than offset any negative effects.

References

Cummings, M.B. and Jones, C.H. 1918. *The Aerial Fertilization of Plants with Carbon Dioxide*. Vermont Agricultural Station Bulletin No. 211.

Demoussy, E. 1902–1904. Sur la vegetation dans des atmospheres riches en acide carbonique. *Comptes Rendus Academy of Science Paris* **136**: 325–328; **138**: 291–293; **139**: 883–885.

Idso, C.D. and Singer, S.F. 2009. *Climate Change Reconsidered: 2009 Report of the Nongovernmental International Panel on Climate Change (NIPCC)*. The Heartland Institute, Chicago, Illinois, USA.

Idso, C.D., Carter, R.M., and Singer, S.F. 2011. *Climate Change Reconsidered: 2011 Interim Report of the Nongovernmental International Panel on Climate Change (NIPCC)*. The Heartland Institute, Chicago, Illinois, USA.

IPCC. 2014. Summary for Policymakers. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* Draft dated October 28, 2013.

Isbell, F., Reich, P.B., Tilman, D., Hobbie, S.E., Polasky, S., and Binder, S. 2013. Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proceedings of the National Academy of Sciences USA* **110**: 11,911–11,916.

Zhou, X., Chen, C., Wang, Y., Smaill, S., and Clinton, P. 2013. Warming rather than increased precipitation increases soil recalcitrant organic carbon in a semiarid grassland after 6 years of treatments. *PLOS ONE* **8**: e53761.

1.1 Plant Responses to Atmospheric CO₂ Enrichment

1.1.1 Dry Weight (Biomass)

- Results from 3,586 separate experimental conditions conducted on 549 plant species reveal nearly all plants will experience increases in dry weight or biomass in response to atmospheric CO₂ enrichment.

Perhaps the best-known consequence of an increase in the air's CO₂ content is its stimulation of plant productivity (dry matter content or biomass). This growth enhancement occurs because carbon dioxide is the primary raw material utilized by plants to produce the organic matter out of which they construct their tissues. Consequently, the more CO₂

there is in the air, the bigger and better plants grow.

Table 1.1.1 in Appendix 3 reports the results of hundreds of peer-reviewed scientific studies indicating the biomass growth response of plants to a standardized 300 ppm increase in atmospheric CO₂ concentration. Plants are listed by common and/or scientific names, followed by the number of experimental studies conducted on each plant, the mean biomass response to a 300 ppm increase in the air's CO₂ content, and the standard error of that mean. Whenever the CO₂ increase for a given study was not exactly 300 ppm, a linear adjustment was computed. For example, if the CO₂ increase was 350 ppm and the growth response was a 60% enhancement, the adjusted 300 ppm CO₂ growth response was calculated as (300/350) x 60% = 51%.

The data in the table are printed by permission of the Center for the Study of Carbon Dioxide and Global Change and were taken from its Plant Growth database on 1 January 2014. The table summarizes CO₂ enrichment results from 3,586 separate experimental conditions conducted on 549 plant species. The responses are overwhelmingly positive. New data are added to the database at approximately weekly intervals and can be accessed free of charge at the center's website at http://www.co2science.org/data/plant_growth/dry/dry_subject.php. This online database also archives information pertaining to the experimental conditions under which each plant growth experiment was conducted, as well as the complete reference to the journal article from which the experimental results were obtained. The center's online database also lists percent increases in plant biomass for 600 and/or 900 ppm increases in the air's CO₂ concentration.

1.1.2 Plant Photosynthesis (Net CO₂ Exchange Rate)

- Results from 2,094 separate experimental conditions conducted on 472 plant species reveal nearly all plants will experience increases in photosynthesis in response to atmospheric CO₂ enrichment.

Table 1.1.2 in Appendix 4 reports the results of peer-reviewed scientific studies measuring the photosynthetic growth response of plants to a 300 ppm increase in atmospheric CO₂ concentration. Plants are listed by common and/or scientific names, followed by the number of experimental studies conducted on each plant, the mean photosynthetic

response to a 300 ppm increase in the air's CO₂ content, and the standard error of that mean. Whenever the CO₂ increase for a given study was not exactly 300 ppm, a linear adjustment was computed. For example, if the CO₂ increase was 350 ppm and the growth response was a 60% enhancement, the adjusted 300 ppm CO₂ growth response was calculated as $(300/350) \times 60\% = 51\%$.

The data in the table appear by permission of the Center for the Study of Carbon Dioxide and Global Change and were taken from its Plant Growth database on 1 January 2014. In all, the table summarizes CO₂ enrichment results from 2,094 separate experimental conditions conducted on 472 plant species. The responses are overwhelmingly positive.

New data are added to the database at approximately weekly intervals and can be accessed free of charge at the center's website at http://www.co2science.org/data/plant_growth/dry/dry_subject.php. This online database also archives information pertaining to the experimental conditions under which each plant growth experiment was conducted, as well as the complete reference to the journal article from which the experimental results were obtained. The center's online database also lists percent increases in plant photosynthetic rate for 600 and/or 900 ppm increases in the air's CO₂ concentration.

1.1.3 Long-Term Studies

One of the more commonly voiced concerns about atmospheric CO₂ enrichment is whether the plant growth enhancements observed in short-term laboratory and field studies will persist over the lifespan of plants. The subsections below investigate this topic with respect to both woody and non-woody plants, leaving no doubt as to the sustained response of plants to elevated atmospheric CO₂.

1.1.3.1 Non-Woody Plants

- Several long-term studies of various non-woody plants reveal sustained beneficial responses to elevated concentrations of atmospheric CO₂ over periods of many years.

In Switzerland, Niklaus *et al.* (2001) exposed a species-rich but nutrient-poor and water-limited, calcareous grassland dominated by *Bromus erectus* (which accounted for approximately half of the ecosystem's aboveground vegetative biomass) to

atmospheric CO₂ concentrations of approximately 360 and 600 ppm for six years, using screen-aided CO₂ control (SACC) technology. CO₂-induced increases in biomass production in years one through six of the experiment were, respectively, 5%, 20%, 22%, 27%, 31%, and 18%, for an average of 23.6% over the last five years of the study (Niklaus and Körner, 2004). This biomass increase ultimately increased carbon stocks in plant shoots and roots by 17 and 24%, respectively, and enhanced carbon stocks in vegetative litter by 34%. The net effect of these increases was an initial air-to-soil carbon flux of 210 g C m⁻² year⁻¹. After six years of treatment, however, the CO₂-enriched soils held only about 44% of the carbon expected from this influx rate, due to the low soil residence time of the newly input carbon. Nevertheless, the study showed atmospheric CO₂ enrichment can in fact enhance plant growth and carbon sequestration in low-nutrient and water-limited soils.

In Italy, Bettarini *et al.* (1998) measured the stomatal densities and conductances of the leaves of 17 species of plants growing in the vicinity of a natural CO₂-emitting spring that has produced twice-ambient atmospheric CO₂ concentrations for at least two centuries, while making similar measurements on plants of the same species located further from the spring, where normal CO₂ concentrations prevail. The elevated CO₂ decreased leaf stomatal conductances in all but one of the species by 19 to 73%. These reductions, however, were not accompanied by decreases in stomatal density, which remained unaffected by long-term atmospheric CO₂ enrichment in all but three species. Consequently, life-long exposure to elevated CO₂ reduced plant water use primarily by controlling leaf stomatal function, not by changing leaf anatomical features (i.e., the number of stomata per unit leaf area).

These findings are encouraging, but it has been suggested they cannot persist indefinitely in all situations. The productivity of Earth's temperate grasslands, for example, is often limited by the availability of soil nitrogen (Vitousek and Howarth, 1991), and both empirical and modeling studies have suggested the magnitude and duration of grassland growth responses to rising levels of atmospheric CO₂ may be constrained by inadequate supplies of soil nitrogen (Rastetter *et al.*, 1997; Luo and Reynolds, 1999; Thornley and Cannell, 2000).

In light of this mix of real-world observations and theoretical calculations, it would seem only natural to hypothesize, as Richter *et al.* (2003) do, "that increased below-ground translocation of photo-

assimilates at elevated $p\text{CO}_2$ would lead to an increase in immobilization of N due to an excess supply of energy to the roots and rhizosphere,” and that this phenomenon would lead ultimately to a reduction in the size of the growth-promoting effect of elevated atmospheric CO₂ that is manifest in short-term CO₂ enrichment experiments and at the start of long-term studies.

To test this hypothesis, Richter *et al.* (2003) measured gross rates of N mineralization, NH₄⁺ consumption, and N immobilization in soils on which monocultures of *Lolium perenne* and *Trifolium repens* had been exposed to ambient (360 ppm) and elevated (600 ppm) concentrations of atmospheric CO₂ at high and low rates of soil nitrogen addition for seven years in the Swiss free-air CO₂ enrichment (FACE) study conducted near Zurich. After seven years of treatment, they report, “gross mineralization, NH₄⁺ consumption and N immobilization in both the *L. perenne* and the *T. repens* swards did not show significant differences.” In addition, the size of the microbial N pool and immobilization of applied mineral ¹⁵N were not significantly affected by the elevated CO₂.

Richter *et al.* note the results of their study “did not support the initial hypothesis and indicate that below-ground turnover of N, as well as N availability, measured in short-term experiments are not strongly affected by long-term exposure to elevated CO₂.” They conclude “differences in plant N demand and not changes in soil N mineralization/immobilization are the driving factors for N dynamics in these meadow grassland systems.”

Thus, as also found in the woody plant studies of Finzi and Schlesinger (2003) and Schafer *et al.* (2003) conducted in the Duke Forest FACE experiment, Richter *et al.*’s work provides no evidence the growth responses of Earth’s grasslands to atmospheric CO₂ enrichment will ever be significantly reduced from what is suggested by moderate-term studies of a few to several years’ duration.

In a study of the same *L. perenne* and *T. repens* ecosystems that helps to explain some of these observations, Gamper *et al.* (2004) analyzed the effects of elevated CO₂ and N fertilization (14 vs. 56 g N m⁻²) on arbuscular mycorrhizal fungi. They report, “at elevated CO₂ and under both N treatments, AMF root colonization of both host plant species was increased” and “colonization levels of all three measured intraradical AMF structures (hyphae, arbuscules and vesicles) tended to be higher.” In addition, they found an increase in non-AMF root colonization under elevated CO₂. As a result, they

“hypothesize that AMF provide non-P-nutritional benefits under the phosphorus-rich soil conditions of our field experiment” and these benefits “may include improved N nutrition and increased protection against pathogens and/or herbivores.”

In another long-term study conducted in Switzerland, Ainsworth *et al.* (2003b) analyzed data from what has become the longest-running FACE experiment ever conducted anywhere in the world. The impetus for their analysis was the speculation that, in their words, “elevated CO₂ may partition resources away from leaves and, through increased production, sequester nutrients into organic matter causing deficiencies which indirectly cause decreased photosynthetic capacity.” In this regard, they cite the theoretical study of these considerations conducted by Luo and Reynolds (1999), who “predicted that the initial stimulation of photosynthetic production in grasslands would be lost within nine years of a step increase in CO₂, as imposed in FACE experiments.”

With real-world data obtained over nearly a decade of experimentation with white clover (*Trifolium repens*) grown in monoculture in the Swiss FACE array, Ainsworth *et al.* (2003b) characterized the photosynthetic responses of the plants to the extra 240 ppm of CO₂ delivered to them in the spring and autumn of the eighth year of the experiment. They determined there was no acclimation or down-regulation of photosynthetic capacity in the spring of the year. In the autumn, however, there was a down-regulation of approximately 20%, but it occurred “late in the growing season, when the 24-hour mean temperature had dropped below 10°C, and nightly frosts were occurring,” under which conditions “shoot growth is limited and the sink for carbohydrate is small, and acclimation of photosynthesis to elevated CO₂ would be expected.”

In spite of that acclimation and the stress of those cold conditions, the average photosynthetic rate of the CO₂-enriched plants at that time of year was still 37% greater than the ambient-treatment plants. Therefore, the five scientists conclude their results “do not support the prediction that the response of grassland species to elevated CO₂ will be short-lived as the demand for nutrients increases.” This conclusion clearly contradicts the claim of Luo and Reynolds and others’ similar claims, for as Ainsworth *et al.* reiterate in the concluding sentence of their paper, “contrary to the belief that the response of grassland species to elevated CO₂ will be short-lived, stimulation of photosynthesis in *T. repens* remained after eight years of exposure to elevated CO₂.”

In another report on this longest FACE study ever

conducted on a grassland species, Ainsworth *et al.* (2003a) note “photosynthesis is commonly stimulated in grasslands with experimental increases in atmospheric CO₂ concentration, a physiological response that could significantly alter the future carbon cycle if it persists in the long term.” However, they also note “an acclimation of photosynthetic capacity suggested by theoretical models and short-term experiments could completely remove this effect of CO₂.” This suggests, in their words, “perennial systems will respond to elevated CO₂ in the short term, but the response for grasslands will be short-lived (Roumet *et al.*, 2000),” and they cite Luo and Reynolds (1999) as suggesting an effective CO₂-induced stimulatory period of less than 10 years for both high- and low-productivity grasslands.

The only way to resolve the issue is to conduct a long-term experiment—such as the sour orange tree study of Idso and Kimball (2001)—which is exactly what the eight-member Ainsworth *et al.* (2003a) team of American, British, Italian, and Swiss scientists did in its ten-year study of perennial ryegrass (*Lolium perenne*).

The study was conducted in Switzerland within three replicate blocks of two 18-m-diameter FACE rings maintained at either 360 or 600 ppm CO₂ throughout each growing season of the entire 10-year period. The experimental plots, established in 1993 on a field of perennial ryegrass planted in August 1992, were further subdivided into low and high nitrogen fertilization treatments, and the plants grown within them were periodically harvested several times a year. In addition, the authors write, “more than 3,000 measurements characterized the response of leaf photosynthesis and stomatal conductance to elevated CO₂ across each growing season for the duration of the experiment.”

Ainsworth *et al.* (2003a) report, “over the 10 years as a whole, growth at elevated CO₂ resulted in a 43% higher rate of light-saturated leaf photosynthesis and a 36% increase in daily integral of leaf CO₂ uptake.” The 36% increase in daily CO₂ uptake was, in their words, “almost identical to the 38% increase seen on the first day of measurements in August 1993 and the 39% stimulation on the last day of measurements in May 2002.”

The researchers also reported a seasonal trend in the CO₂-induced increase in the daily integral of CO₂ fixation, which ranged from 25% in the spring to 41% in the summer and 48% in the fall. The scientists say this finding “is consistent with theoretical expectation, where because of the differing sensitivities of Rubisco oxygenase and carboxylase activity, the

proportionate stimulation of photosynthesis by a given increase in CO₂ will rise with temperature (Long, 1991).” This phenomenon has also been observed in a number of other plants.

Ainsworth *et al.* (2003a) additionally note “the percentage increase in photosynthetic carbon uptake in the first 20 days following a harvest (45%) was nearly double the percentage increase later in the regrowth cycle (23%).” This finding indicates CO₂-induced growth stimulation is greatest when the plant source:sink ratio is small; i.e., when there are few photosynthesizing leaves and many photosynthate-storing roots, so the CO₂-induced enhancement of photosynthesis need not immediately decline for lack of a sufficient repository to deposit the fruits of its labors, so to speak.

Summing up, the international team of scientists says the CO₂-induced photosynthetic stimulation “was maximal following harvest, at the warmest times of year and with a high supply of nitrogen.” They concluded, “this open-air field experiment provides no support for the prediction that stimulation of photosynthesis under elevated CO₂ is a transient phenomenon,” or as they phrase it in the abstract of their paper, “in contrast with theoretical expectations and the results of shorter duration experiments, the present results provide no [evidence of] significant change in photosynthetic stimulation across a 10-year period, nor greater acclimation ... in the latter years in either nitrogen treatment.”

The ultimate plant response is biomass production, which was studied in the same experiment by Schneider *et al.* (2004), who state, “in 1993, the CO₂ response of harvested biomass was 7.2%, increasing to 32% in 2002.” At low N, they report the CO₂ response “varied annually.” Nevertheless, it too exhibited a slowly increasing (though non-significant) trend, suggesting, given enough time, it might have gained statistical significance as well.

In addition, Schneider *et al.* report, “at high N supply, more N was mobilized from the soil after long-term exposure to elevated CO₂ than after ambient CO₂,” in contrast to the suggestion of Hungate *et al.* (2003) that just the opposite likely would occur. At low N, the Swiss team writes, “the reduced availability of N constantly limited the harvestable biomass to elevated CO₂ throughout the experiment,” more in harmony with Hungate *et al.*’s suggestion. This limitation may have been slightly reduced over the course of the 10-year study, and a still longer experiment may be needed to resolve the issue in the case of low-N soils.

Rasse *et al.* (2005) evaluated the long-term effects of atmospheric CO₂ enrichment on the net CO₂ exchange, shoot density, and shoot biomass of the wetland sedge, *Scirpus olneyi*, in a long-term *in situ* elevated CO₂ experiment at the Smithsonian Environmental Research Center on the USA's Chesapeake Bay. They found, in every one of the 17 years of the experiment's duration to the time of their analysis, the net CO₂ exchange rate and shoot biomass and density of the plants growing in the CO₂-enriched (ambient +340 ppm) air were all greater than among the plants growing in ambient air. The extra CO₂ boosted the net CO₂ exchange rate by 80% in the first year of the study, but the enhancement declined to about 35% by the end of the third year and remained relatively constant at that value over the following 15 years.

Shoot biomass and density also increased, but whereas the CO₂-induced stimulation of the net CO₂ exchange rate remained essentially constant over the past 15 years, the CO₂-induced stimulations of shoot biomass and density increased over time. After five years of a nearly constant stimulation of 16%, for example, shoot density increased in near-linear fashion to a value 128% above the ambient-air value at the end of year 17. The response of shoot biomass to CO₂ enrichment was also nearly linear, reaching a value approximately 70% above ambient at year 17. The trends in shoot density and biomass do not appear to be leveling off.

Net CO₂ exchange, shoot density, and shoot biomass were closely correlated with bay water salinity in this study: the higher the salinity, the more detrimental were its effects on these variables. Nevertheless, even at the highest levels of salinity reported, atmospheric CO₂ enrichment was able to produce a positive, albeit reduced, stimulatory effect on net CO₂ exchange. For shoot biomass and density, the responses were better still: Not only did atmospheric CO₂ enrichment essentially eradicate the detrimental effects of salinity, there was, Rasse *et al.* note, "circumstantial evidence suggesting that salinity stress increased the stimulation of shoot density by elevated atmospheric CO₂ concentration."

This experiment demonstrated several important findings. First, as the researchers state, their results "leave no doubt as to the sustained response of the salt marsh sedge to elevated atmospheric CO₂ concentration." Second, since the initial responses of the three growth variables declined or remained low during the first few years of the study, but leveled out or increased thereafter, much more long-term research needs to be carried out in order to ascertain the full

and correct impacts of atmospheric CO₂ enrichment on plants. In the case of the wetland sedge of this study, for example, it took ten years before an increasing trend in the shoot density could be recognized clearly. Finally, there is the authors' "most important finding": "that a species response to elevated atmospheric CO₂ concentration can continually increase when [it] is under stress and declining in its natural environment."

Gifford (2004) describes the findings of an international FACE workshop on *Short- and Long-Term Effects of Elevated Atmospheric CO₂ on Managed Ecosystems*, concentrating on a few key aspects of the aerial fertilization effect of atmospheric CO₂ enrichment and how it likely will be expressed in the real world as the air's CO₂ content rises.

He begins by noting Kimball *et al.* (2002) compared what was learned about elevated CO₂ effects on 11 different crops from recent FACE experiments with what had been learned from prior chamber studies, including open-top chambers. He reports Kimball *et al.* determined the FACE experiments confirmed, under longer-term field conditions and with but a couple exceptions, "all the prior quantitative chamber findings on crops grown and measured in elevated CO₂ concentration compared with ambient CO₂ concentration."

Next, Gifford notes the subsequent study of Long *et al.* (2004) confirms, "with greater statistical rigor and for a much wider range of species including crops, pasture species and trees, most of the conclusions of the evaluation by Kimball *et al.* (2002)." He reports Long presented an elegant exposition of how plants optimize "the deployment of N from photosynthetic machinery to growth organs such that a balance between C-source and C-sinks is maintained in the plant under elevated CO₂ concentration—a response that generally increases nitrogen use efficiency (Wolfe *et al.*, 1998)." In addition, he reports, several FACE studies demonstrate an increased abundance of legumes in CO₂-enriched plots, and this observation "is supportive of the notion that, in the long run, elevated CO₂ concentration may cause N-fixation to entrain more atmospheric N₂ into the ecosystem, leading ultimately to fuller expression of the increased growth and standing biomass potential that the elevated CO₂ provides (Gifford, 1992)."

Next, in an update of the analysis of Hendry *et al.* (1997), which focused on the effects of the rapidly fluctuating atmospheric CO₂ concentrations characteristic of FACE experiments, the technique's primary developer (George Hendry) concluded, according to

Climate Change Reconsidered II: Biological Impacts

Gifford, plant photosynthesis rates “can be decreased by 17% or more for the mean concentration reported when that mean is of large CO₂ fluctuations on the order of half the mean, and the deviations from the mean occur over a minute or longer.” In light of this finding, Gifford writes, “FACE technology might be systematically understating the effect of globally elevated CO₂ on ecosystem productivity.”

Gifford sums up the consensus of the participants at the FACE workshop with respect to “the CO₂ fertilizing effect,” stating, “the evidence for its existence in the real world continues to consolidate.”

References

- Ainsworth, E.A., Davey, P.A., Hymus, G.J., Osborne, C.P., Rogers, A., Blum, H., Nosberger, J., and Long, S.P. 2003a. Is stimulation of leaf photosynthesis by elevated carbon dioxide concentration maintained in the long term? A test with *Lolium perenne* grown for 10 years at two nitrogen fertilization levels under Free Air CO₂ Enrichment (FACE). *Plant, Cell and Environment* **26**: 705–714.
- Ainsworth, E.A., Rogers, A., Blum, H., Nosberger, J., and Long, S.P. 2003b. Variation in acclimation of photosynthesis in *Trifolium repens* after eight years of exposure to Free Air CO₂ Enrichment (FACE). *Journal of Experimental Botany* **54**: 2769–2774.
- Bettarini, I., Vaccari, F.P., and Miglietta, F. 1998. Elevated CO₂ concentrations and stomatal density: observations from 17 plant species growing in a CO₂ spring in central Italy. *Global Change Biology* **4**: 17–22.
- Finzi, A.C. and Schlesinger, W.H. 2003. Soil-nitrogen cycling in a pine forest exposed to 5 years of elevated carbon dioxide. *Ecosystems* **6**: 444–456.
- Gamper, H., Peter, M., Jansa, J., Luscher, A., Hartwig, U.A., and Leuann, A. 2004. Arbuscular mycorrhizal fungi benefit from 7 years of free air CO₂ enrichment in well-fertilized grass and legume monocultures. *Global Change Biology* **10**: 189–199.
- Gifford, R.M. 1992. Interaction of carbon dioxide with growth-limiting environmental factors in vegetation productivity: Implications for the global carbon cycle. *Advances in Bioclimatology* **1**: 25–58.
- Gifford, R.M. 2004. The CO₂ fertilising effect—does it occur in the real world? *New Phytologist* **163**: 221–225.
- Hendrey, G.R., Long, S.P., McKee, I.F., and Baker, N.R. 1997. Can photosynthesis respond to short term fluctuations in atmospheric carbon dioxide? *Photosynthesis Research* **51**: 170–184.
- Hungate, B.A., Dukes, J.S., Shaw, M.R., Luo, Y., and Field, C.B. 2003. Nitrogen and climate change. *Science* **302**: 1512–1513.
- Idso, S.B. and Kimball, B.A. 2001. CO₂ enrichment of sour orange trees: 13 years and counting. *Environmental and Experimental Botany* **46**: 147–153.
- Kimball, B.A., Kobayashi, K., and Bindi, M. 2002. Responses of agricultural crops to free-air CO₂ enrichment. *Advances in Agronomy* **77**: 293–368.
- Long, S.P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: has its importance been underestimated? *Plant, Cell and Environment* **14**: 729–739.
- Long, S.P., Ainsworth, E.A., Rogers, A., and Ort, D.R. 2004. Rising atmospheric carbon dioxide: Plants FACE the future. *Annual Review of Plant Biology* **55**: 591–628.
- Luo, Y. and Reynolds, J.F. 1999. Validity of extrapolating field CO₂ experiments to predict carbon sequestration in natural ecosystems. *Ecology* **80**: 1568–1583.
- Niklaus, P.A. and Körner, C. 2004. Synthesis of a six-year study of calcareous grassland responses to *in situ* CO₂ enrichment. *Ecological Monographs* **74**: 491–511.
- Niklaus, P.A., Wohlfender, M., Siegwolf, R., and Körner, C. 2001. Effects of six years atmospheric CO₂ enrichment on plant, soil, and soil microbial C of a calcareous grassland. *Plant and Soil* **233**: 189–202.
- Rasse, D.P., Peresta, G., and Drake, B.G. 2005. Seventeen years of elevated CO₂ exposure in a Chesapeake Bay Wetland: sustained but contrasting responses of plant growth and CO₂ uptake. *Global Change Biology* **11**: 369–377.
- Rastetter, E.B., Agren, G.I., and Shaver, G.R. 1997. Responses of N-limited ecosystems to increased CO₂: a balanced-nutrition, coupled-element-cycles model. *Ecological Applications* **7**: 444–460.
- Richter, M., Hartwig, U.A., Frossard, E., Nosberger, J., and Cadisch, G. 2003. Gross fluxes of nitrogen in grassland soil exposed to elevated atmospheric pCO₂ for seven years. *Soil Biology & Biochemistry* **35**: 1325–1335.
- Roumet, C., Garnier, E., Suzor, H., Salager, J.-L., and Roy, J. 2000. Short and long-term responses of whole-plant gas exchange to elevated CO₂ in four herbaceous species. *Environmental and Experimental Botany* **43**: 155–169.
- Schafer, K.V.R., Oren, R., Ellsworth, D.S., Lai, C.-T., Herrick, J.D., Finzi, A.C., Richter, D.D., and Katul, G.G. 2003. Exposure to an enriched CO₂ atmosphere alters carbon assimilation and allocation in a pine forest ecosystem. *Global Change Biology* **9**: 1378–1400.
- Schneider, M.K., Luscher, A., Richter, M., Aeschlimann, U., Hartwig, U.A., Blum, H., Frossard, E., and Nosberger,

J. 2004. Ten years of free-air CO₂ enrichment altered the mobilization of N from soil in *Lolium perenne* L. swards. *Global Change Biology* **10**: 1377–1388.

Thornley, J. and Cannell, M. 2000. Dynamics of mineral N availability in grassland ecosystems under increased [CO₂]: hypotheses evaluated using the Hurley Pasture Model. *Plant and Soil* **224**: 153–170.

Vitousek, P.M. and Howarth, R.W. 1991. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* **13**: 87–115.

Wolfe, D.W., Gifford, R.M., Hilbert, D., and Luo, Y. 1998. Integration of photosynthetic acclimation to CO₂ at the whole plant level. *Global Change Biology* **4**: 879–893.

1.1.3.2 Woody Plants

The aerial fertilization effect of atmospheric CO₂ enrichment will continue to benefit woody plants significantly.

1.1.3.2.1 Oak

- Multiple-year studies point to the likelihood oak trees of all species will grow ever more productively as the air's CO₂ content climbs higher, and they will be better able to withstand droughty conditions and more effectively sequester carbon in the years and decades ahead.

After burning to the ground a natural scrub-oak ecosystem comprised of *Quercus myrtifolia*, *Q. chapmanii*, and *Q. geminata*, located on an island just off the coast of central Florida, USA, Ainsworth *et al.* (2002) erected 16 open-top chambers on the site and fumigated them with air of either 380 or 700 ppm CO₂. In the third and fourth years of the experiment, they report, the extra CO₂ increased photosynthetic rates in regenerating *Q. myrtifolia* and *Q. chapmanii* trees by as much as 150% without inducing any degree of photosynthetic acclimation or down-regulation. *Q. geminata* did exhibit signs of acclimation, but after three years of exposure to elevated CO₂, the three species still exhibited an average increase of 53% in their combined mean rate of photosynthesis.

In a subsequent analysis of other data from the same experiment, Dijkstra *et al.* (2002) evaluated the effects of elevated CO₂ on the growth of the three oak species by means of allometric relationships between stem diameter and aboveground biomass (AGB), which they derived from destructive measurements

made on trees growing on an adjacent site. They found, in their words, “increased AGB in elevated CO₂ was apparent after eight months (44%), and the relative stimulation increased over time, from 55% at the end of 1997, 66% at the end of 1998, to 75% at the end of 1999.” They also report at the time of the last measurement, the AGB of the dominant *Q. myrtifolia* had increased by 73%, the AGB of the subdominant *Q. geminata* had increased by only 23%, and the AGB of the subdominant *Q. chapmanii* had risen by more than 150%. With respect to individual years, they note even though the mean increase in AGB during the drought year of 1998 was 51% lower than it was during 1997 and 54% lower than in 1999, “elevated CO₂ significantly increased annual increment in AGB by 122% during the drought year 1998, compared to a 65% increase in 1997 and a 116% increase in 1999.”

In another study of the Florida scrub-oak ecosystem, Hymus *et al.* (2003) report the extra CO₂ supplied to the CO₂-enriched chambers in their experiment increased maximum net ecosystem exchange of CO₂ (NEE) and the apparent quantum yield of NEE during the photoperiod. They also state the magnitude of the stimulation of maximum NEE, expressed per unit ground area, “was seasonal, rising from 50% in the winter to 180% in the summer,” in accord with what is known about the interactive effects of atmospheric CO₂ enrichment and daily, seasonal, and multiyear warming. Hymus *et al.* additionally note their study was the largest to show “the effects of elevated CO₂ on NEE measured *in situ*, and is the first to be carried out in a woody ecosystem,” where the beneficial effects of atmospheric CO₂ enrichment are “still evident after 6 years regeneration in the elevated CO₂.”

Another way of studying the long-term effects of atmospheric CO₂ enrichment on trees and shrubs was pioneered by researchers in Italy, where many natural springs emit copious quantities of CO₂ into the air, raising atmospheric CO₂ concentrations over modest tracts of land by various amounts. By measuring the air's CO₂ content at different places around these “CO₂ springs” over the course of long-term experiments conducted there, mean canopy-level atmospheric CO₂ concentrations can be determined, and woody plants growing at those locations are typically assumed to have lived their entire lives at the measured CO₂ concentrations.

In a study of *Quercus ilex* trees, some growing close to, and others distant from, certain of these CO₂ springs, Paoletti *et al.* (1998) found, in moving from an atmospheric CO₂ concentration of 350 ppm to 750

ppm, leaf stomatal frequency dropped by a factor of nearly 1.5, but there were no further reductions in this parameter as the air's CO₂ concentration rose as high as 2,600 ppm. They also note the amount of wax comprising the leaf cuticle increased nearly threefold between 750 and 2,600 ppm CO₂, but between 350 and 750 ppm CO₂ there was no difference in this leaf property. The net effect of these several responses was thus a continuous decline in water loss from the trees as the air's CO₂ content continuously rose, which led to a concomitant continuous increase in their water use efficiencies.

In another study conducted in Italy in the vicinity of natural CO₂ springs, Stylinski *et al.* (2000) worked with *Quercus pubescens* trees grown in ambient air and at an atmospheric CO₂ concentration of approximately 700 ppm throughout the entire 40 to 50 years of their existence. The CO₂-enriched trees exhibited photosynthetic rates 36–77% greater than those of the trees growing in ambient air; and the researchers did not detect signs of any photosynthetic down-regulation in the CO₂-enriched trees. In fact, they found no differences between the CO₂-enriched and ambient-treatment trees in terms of rubisco activity and content, total nitrogen content, chlorophyll content, and carotenoid content. As a result, they conclude “enhanced leaf photosynthetic rates at the CO₂ springs could increase carbon sequestering and productivity of whole tree canopies” and “higher carbon acquisition by *Q. pubescens* and other species could slow the rise in atmospheric CO₂.”

Blaschke *et al.* (2001) also studied gas exchange in mature *Q. pubescens* and *Q. ilex* trees exposed to atmospheric CO₂ concentrations of approximately 370 and 700 ppm for their entire lives. The average net photosynthetic rates of the CO₂-enriched trees were, respectively, 69% and 26% greater than those of the trees growing in ambient air. In addition, the stomatal conductances of the CO₂-enriched *Q. pubescens* trees were approximately 23% lower than those of trees of the same species growing in ambient air, and the CO₂-enriched *Q. ilex* trees displayed no stomatal response to elevated CO₂. Nevertheless, both species exhibited significant CO₂-induced increases in water use efficiency.

One less-than-ideal aspect of the Italian CO₂ springs is that they emit higher-than-normal concentrations of the phytotoxic air pollutants H₂S and SO₂ (Schulte *et al.*, 1999). This fact, however, makes the springs perfect settings in which to study the relative strengths of two competing phenomena: the growth-promoting effect of elevated CO₂ and the

growth-retarding effect of elevated H₂S and SO₂.

Grill *et al.* (2004) analyzed various properties of leaves and acorns produced on *Q. ilex* and *Q. pubescens* trees growing at double-to-triple normal atmospheric CO₂ concentrations near the CO₂ springs, as well as the same characteristics of leaves and acorns growing on similar trees located some distance away in ambient-CO₂ air. In addition, they analyzed several characteristics of seedlings they sprouted from acorns produced by the CO₂-enriched and ambient-treatment trees, and they used chromosome stress tests “to investigate whether alterations in sulphur-regime have negative consequences for seedlings.”

In reporting their findings, Grill *et al.* say “acorns from CO₂ springs contained significantly higher sulphur concentrations than controls (0.67 vs. 0.47 mg g⁻¹ dry weight in *Q. ilex* cotyledons and 1.10 vs. 0.80 in *Q. pubescens*),” indicating the trees were indeed affected by the H₂S and SO₂ contained in the air in the vicinity of the CO₂ springs. They also report *Q. ilex* seedlings grown from CO₂-spring acorns showed elevated rates of chromosomal aberrations in their root tips, suggesting the presence of a permanent pollution-induced stress. Nevertheless, as demonstrated by the results of several other studies conducted near the springs, the CO₂-enriched air—even in the presence of phytotoxic H₂S and SO₂—significantly enhanced the trees’ photosynthetic prowess: by 26–69% in the study of Blaschke *et al.* (2001), by 36–77% in the study of Stylinski *et al.* (2000), and by 175–510% in the study of Tognetti *et al.* (1998).

In a study in Italy that did not make use of natural CO₂ springs, Marek *et al.* (2001) constructed open-top chambers around 30-year-old *Q. ilex* trees growing in perennial evergreen stands and continuously exposed them to atmospheric CO₂ concentrations of 350 and 700 ppm for five more years. Throughout this period, the extra CO₂ increased rates of net photosynthesis in Sun and shade leaves by 68% and 59%, respectively, and photosynthetic acclimation was not apparent in any of the CO₂-enriched trees’ leaves. In addition, the light compensation point—the light intensity at which photosynthetic carbon uptake is equivalent to respiratory carbon loss—was 24% and 30% lower in the Sun and shade leaves of the CO₂-enriched trees than in the corresponding leaves of trees growing in ambient air. These findings suggest *Q. ilex* trees growing in CO₂-enriched air should exhibit net carbon gains earlier in the morning and maintain them later into the evening than trees exposed to ambient air. Together with the stimulatory effect of higher CO₂ concentrations on

photosynthesis, this observation further suggests carbon sequestration by this tree species will likely be much greater in a higher-CO₂ world of the future.

Although all of the reports described above imply the ongoing rise in the air's CO₂ content will do only good to the long-term growth and health of oak trees, Gartner *et al.* (2003) were concerned the wood of the trees might be more vulnerable to embolism in a CO₂-enriched atmosphere. They investigated this question with *Quercus ilex* seedlings grown for more than a year in climate-controlled greenhouses in either ambient air or air enriched to twice the ambient concentration of CO₂. Contrary to their hypothesis, they found the “plants grown in elevated CO₂ did not differ significantly in vulnerability to embolism or kS [specific conductivity] from plants grown in ambient CO₂.” In addition, they report “Tognetti *et al.* (1999) found no significant effect of elevated CO₂ on vulnerability to embolism or kS of branch samples from *Q. ilex* trees growing near CO₂ vents compared with trees growing at normal ambient CO₂.”

In one final study conducted under entirely natural, real-world conditions, Waterhouse *et al.* (2004) determined the intrinsic water use efficiency (IWUE) responses of three tree species growing across northern Europe—one of which was pedunculate oak (*Quercus robur*) growing at three sites in England and two sites in Finland—to the increase in atmospheric CO₂ concentration experienced between 1895 and 1994, using parameters derived from measurements of stable carbon isotope ratios of tree-ring cellulose. They report “all species at all the sites show a long-term increase in their values of IWUE during the past century,” noting “the main cause of this common behavior is likely to be the increase in atmospheric CO₂ concentration.”

Linearly extrapolating these responses (which occurred over a period of time when the air's CO₂ concentration rose by approximately 65 ppm) to what would be expected for the more common 300 ppm increase employed in the majority of atmospheric CO₂ enrichment experiments, the IWUE increase Waterhouse *et al.* observed for *Q. robur* amounted to 158 ± 14%, as best as can be determined from the graphs of their results. A response of this magnitude is probably not due to rising CO₂ alone, but instead to the positive synergism that occurs when atmospheric CO₂ and temperature rise together (see Section 3.13, Temperature Stress, in Chapter 3), as these parameters have done over the past century or so, clearly demonstrating high temperatures and high CO₂ concentrations benefit plants.

The findings of the several papers reviewed above point to the likelihood oak trees of all species will grow more productively as the air's CO₂ content climbs higher, will likely be better able to withstand droughty conditions, and will more effectively sequester carbon in the years and decades ahead.

References

- Ainsworth, E.A., Davey, P.A., Hymus, G.J., Drake, B.G., and Long, S.P. 2002. Long-term response of photosynthesis to elevated carbon dioxide in a Florida scrub-oak ecosystem. *Ecological Applications* **12**: 1267–1275.
- Blaschke, L., Schulte, M., Raschi, A., Slee, N., Rennenberg, H., and Polle, A. 2001. Photosynthesis, soluble and structural carbon compounds in two Mediterranean oak species (*Quercus pubescens* and *Q. ilex*) after lifetime growth at naturally elevated CO₂ concentrations. *Plant Biology* **3**: 288–297.
- Dijkstra, P., Hymus, G., Colavito, D., Vieglaiss, D.A., Cundari, C.M., Johnson, D.P., Hungate, B.A., Hinkle, C.R., and Drake, B.G. 2002. Elevated atmospheric CO₂ stimulates aboveground biomass in a fire-regenerated scrub-oak ecosystem. *Global Change Biology* **8**: 90–103.
- Gartner, B.L., Roy, J., and Huc, R. 2003. Effects of tension wood on specific conductivity and vulnerability to embolism of *Quercus ilex* seedlings grown at two atmospheric CO₂ concentrations. *Tree Physiology* **23**: 387–395.
- Grill, D., Muller, M., Tausz, M., Strnad, B., Wonisch, A., and Raschi, A. 2004. Effects of sulphurous gases in two CO₂ springs on total sulphur and thiols in acorns and oak seedlings. *Atmospheric Environment* **38**: 3775–3780.
- Hymus, G.J., Johnson, D.P., Dore, S., Anderson, H.P., Hinkle, C.R., and Drake, B.G. 2003. Effects of elevated atmospheric CO₂ on net ecosystem CO₂ exchange of a scrub-oak ecosystem. *Global Change Biology* **9**: 1802–1812.
- Marek, M.V., Sprtova, M., De Angelis, P., and Scarascia-Mugnozza, G. 2001. Spatial distribution of photosynthetic response to long-term influence of elevated CO₂ in a Mediterranean *macchia* mini-ecosystem. *Plant Science* **160**: 1125–1136.
- Paoletti, E., Nourrisson, G., Garrec, J.P., and Raschi, A. 1998. Modifications of the leaf surface structures of *Quercus ilex* L. in open, naturally CO₂-enriched environments. *Plant, Cell and Environment* **21**: 1071–1075.
- Schulte, M., Raiesi, F.G., Papke, H., Butterbach-Bahl, K., van Breemen, N., and Rennenberg, H. 1999. CO₂

concentration and atmospheric trace gas mixing ratio around natural CO₂ vents in different Mediterranean forests in central Italy. In: Raschi, A., Vaccori, F.P., and Miglietta, F. (Eds.). *Ecosystem Response to CO₂: The Maple Project Results*. European Communities, Brussels, Belgium, pp. 168–188.

Stylinski, C.D., Oechel, W.C., Gamon, J.A., Tissue, D.T., Miglietta, F., and Raschi, A. 2000. Effects of lifelong [CO₂] enrichment on carboxylation and light utilization of *Quercus pubescens* Willd. examined with gas exchange, biochemistry and optical techniques. *Plant, Cell and Environment* **23**: 1353–1362.

Tognetti, R., Johnson, J.D., Michelozzi, M., and Raschi, A. 1998. Response of foliar metabolism in mature trees of *Quercus pubescens* and *Quercus ilex* to long-term elevated CO₂. *Environmental and Experimental Botany* **39**: 233–245.

Tognetti, R., Longobucco, A., and Raschi, A. 1999. Seasonal embolism and xylem vulnerability in deciduous evergreen Mediterranean trees influenced by proximity to a carbon dioxide spring. *Tree Physiology* **19**: 271–277.

Waterhouse, J.S., Switsur, V.R., Barker, A.C., Carter, A.H.C., Hemming, D.L., Loader, N.J., and Robertson, I. 2004. Northern European trees show a progressively diminishing response to increasing atmospheric carbon dioxide concentrations. *Quaternary Science Reviews* **23**: 803–810.

1.1.3.2.2 Pine

It is important to know how Earth's trees will respond to the ongoing rise in the air's CO₂ content over the long-term; the only way to obtain such knowledge is to enrich the air in which they grow in long-term experiments. The following subsections review what has been learned in this regard with respect to various pine tree species.

1.1.3.2.2.1 Loblolly

- The “aerial fertilization effect” of atmospheric CO₂ enrichment will continue to significantly benefit Earth's loblolly pine forests as the atmosphere's CO₂ concentration rises.

In what was originally considered a long-term study, Tissue *et al.* (1997) grew loblolly pine seedlings for four years in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 650 ppm. Throughout the summers of this experiment, the seedlings in the CO₂-enriched chambers displayed photosynthetic rates 60 to 130% greater than those of

the seedlings growing in ambient air, and during the colder winter months, they exhibited photosynthetic rates 14 to 44% greater. These persistent increases in the rate of net carbon uptake increased biomass accumulation rates in the CO₂-enriched seedlings by fully 90%, prompting the scientists conducting the study to declare loblolly pines growing in a CO₂-enriched world of the future “could be a large sink for fossil fuel carbon emitted to the atmosphere.”

In another study of the same trees, Telewski *et al.* (1999) report elevated CO₂ did not significantly affect anatomical features of xylem cells, including their cell wall to cell interior ratio, resin canal area, and resin canal density, but it did significantly increase annual growth-ring widths by 93, 29, 15, and 37% during the four consecutive years of the study. Also, although not significantly so, the extra CO₂ increased average ring density in the same four years by 60, 4, 3, and 5%, leading the researchers to state, “projected increases in the atmospheric content of CO₂ may result in increased wood production without a loss in structural strength.” The tendency for wood density to increase in CO₂-enriched air portends the possibility of increased structural strength in the years ahead.

By far the longest study of loblolly pines was the free-air CO₂ enrichment (FACE) experiment conducted at Duke Forest in the Piedmont region of North Carolina, USA, where in August 1996 three 30m-diameter CO₂ delivery rings began to enrich the air around the 13-year-old trees they encircled to 200 ppm above the atmosphere's ambient CO₂ concentration, and three other FACE rings served as ambient-air control plots, as described by Hendrey *et al.* (1999).

In this study, LaDeau and Clark (2001) report, by the fall 1999 the CO₂-enriched trees “were twice as likely to be reproductively mature and produced three times more cones per tree.” Similarly, the trees growing in the CO₂-enriched air produced 2.4 times more cones in fall 2000. From August 1999 through July 2000, the two scientists also collected three times as many seeds in the CO₂-enriched FACE rings as they did in the ambient-air control rings.

LaDeau and Clark note naturally regenerated loblolly pine stands of the southeastern United States “are profoundly seed-limited for at least 25 years.” Thus, as the air's CO₂ content rises, the researchers state, “this period of seed limitation may be reduced,” which is more good news about this highly prized tree, in addition to the fact, according to William Schlesinger, codirector of the Duke project (Tangle, 2001), “trees in the high-CO₂ plots grew 25% faster than controls did during the first three growing

seasons of the experiment.”

One year later, Finzi *et al.* (2002) report over the first four years of differential CO₂ exposure in this study, the trees in the CO₂-enriched plots maintained average yearly rates of dry matter production 32% greater than the trees growing in ambient air. The average uptake of nitrogen from the soil was enhanced by 28% in the CO₂-enriched plots, and the CO₂-enriched trees displayed a 10% increase in nitrogen-use efficiency.

Several other papers dealing with various aspects of the experiment were published about the same time. As recounted by Luo *et al.* (2003), these analyses reveal the existence of a CO₂-induced “sustained photosynthetic stimulation at leaf and canopy levels [Myers *et al.*, 1999; Ellsworth, 2000; Luo *et al.*, 2001; Lai *et al.*, 2002], which resulted in sustained stimulation of wood biomass increment [Hamilton *et al.*, 2002] and a larger carbon accumulation in the forest floor at elevated CO₂ than at ambient CO₂ [Schlesinger and Lichter, 2001].” Based upon these findings and what they imply about rates of carbon removal from the atmosphere and its different residence times in plant, litter, and soil carbon pools, Luo *et al.* (2003) developed a model for studying the sustainability of carbon sequestration in forests. Applying this model to a situation where the atmospheric CO₂ concentration gradually rises from a value of 378 ppm in 2000 to a value of 710 ppm in 2100, they calculated the carbon sequestration rate of the Duke Forest would rise from an initial value of 69 g m⁻² yr⁻¹ to a final value of 201 g m⁻² yr⁻¹.

Schafer *et al.* (2003) linked a leaf-level CO₂ assimilation model (Katul *et al.*, 2000) with a light attenuation model (Campbell and Norman, 1998; Stenberg, 1998) and measurements of sap-flux-based canopy conductance (Kostner *et al.*, 1992; Ewers and Oren, 2000) to create what they call a canopy conductance-constrained CO₂ assimilation model, which they tested with measurements of net ecosystem exchange and net ecosystem production in the ambient and CO₂-enriched plots of the Duke Forest FACE study. They then used it to assess the effects of elevated CO₂ on carbon uptake and allocation to different components of the forest’s carbon budget under ambient and CO₂-enriched conditions. They report during the third and fourth years of the study, the extra 200 ppm of CO₂ supplied to the CO₂-enriched FACE plots increased the uptake of CO₂ by 39% in the dominant *Pinus taeda* L. trees.

These results were most impressive. However, many scientists at that time questioned whether the productivity gains associated with CO₂ enrichment

would persist in the long term. Even Schafer *et al.* suggested “if nutrient limitation imposes a constraint on future productivity,” as was widely believed would be the case, “it is likely that carbon allocation to the production of wood will decrease in favor of the allocation to fine root production, rhizodeposition, and mycorrhizal symbionts,” citing Norby *et al.* (1992, 2001). They further suggested this decrease could “result in a rapid return of fixed carbon to the atmosphere (Merbach *et al.*, 1999),” and thus, “high rates of carbon fixation under elevated CO₂ will result in an acceleration of the carbon cycle through the forest ecosystem with little of the carbon remaining in long-term storage pools.”

Indeed, it was well-accepted that the productivity of Earth’s temperate forests was limited by the availability of soil nitrogen (Vitousek and Howarth, 1991). This was especially believed to be the case in the southeastern United States, where pine-hardwood forests often remove so much nitrogen from the soils in which they grow that they induce what Finzi and Schlesinger (2003) describe as “a state of acute nutrient deficiency that can only be reversed with fertilization.” It would seem only natural, therefore, to presume (as they hypothesized in the early stages of the Duke Forest FACE study) “the increase in carbon fluxes to the microbial community under elevated CO₂ would increase the rate of nitrogen immobilization over mineralization,” which would ultimately lead to a decline in—and perhaps the total negation of—the significant CO₂-induced stimulation of forest net primary production that developed over the first two years of the experiment (DeLucia *et al.*, 1999; Hamilton *et al.*, 2002).

To test this hypothesis, Finzi and Schlesinger (2003) measured and analyzed the pool sizes and fluxes of inorganic and organic nitrogen in the forest floor and top 30 cm of mineral soil during the first five years of differential atmospheric CO₂ treatment in the Duke Forest FACE study, where half the plots were fumigated to maintain a mean CO₂ concentration 200 ppm above ambient. They report the extra CO₂ “significantly increased the input of carbon and nitrogen to the forest floor and the mineral soil.” Nevertheless, the researchers state “there was no statistically significant change in the cycling rate of nitrogen derived from soil organic matter under elevated CO₂.” Indeed, “neither the rate of net nitrogen mineralization nor gross ¹⁵NH₄⁺ dynamics were significantly altered by elevated CO₂.” In addition, they acknowledge “there was no statistically significant difference in the concentration or net flux of organic and inorganic nitrogen in the forest floor

and top 30-cm of mineral soil after five years of CO₂ fumigation,” concluding “microbial biomass was not a larger sink for nitrogen.”

On the basis of these results from the first five years of the Duke Forest FACE study, Finzi and Schlesinger rejected their original hypothesis that elevated levels of atmospheric CO₂ would significantly increase the rate of nitrogen immobilization by the microbial community, although they contend “elevated CO₂ will only increase the productivity of this forest during the initial stages of stand development, with nitrogen limitation constraining additional carbon sequestration under elevated CO₂ well before this stand reaches its equilibrium biomass.”

Crous and Ellsworth (2004) measured the photosynthetic rates of different-age needles at different crown positions on the loblolly pine trees at the Duke Forest FACE facility in the sixth year of the study, and then compared their results with the results of similar measurements made over the prior five years. Although they report there was “some evidence of moderate photosynthetic down-regulation ... in 1-year-old needles across the fifth to sixth year of CO₂ exposure,” the two researchers state “strong photosynthetic enhancement in response to elevated CO₂ (e.g., +60% across age classes and canopy locations) was observed across the years.”

Also at the conclusion of the sixth year of the study, Lichter *et al.* (2005) reviewed what had been learned about the effects of the extra CO₂ on the soil carbon dynamics of Duke Forest. Their work revealed, since the beginning of the study, organic carbon accumulated in the forest floor of the elevated CO₂ plots at a rate $52 \pm 16 \text{ g C m}^{-2} \text{ yr}^{-1}$ greater than expected during reforestation under ambient CO₂ conditions, as represented by the rate of carbon accumulation in the forest floor of the ambient CO₂ plots. This additional carbon sink, in the words of the researchers, “resulted from increased carbon inputs of $50 \pm 30 \text{ g C m}^{-2} \text{ yr}^{-1}$ to the forest floor in response to CO₂ enhancement of primary production.” And since there was “no evidence that the overall rate of decomposition of the forest floor decreased under the elevated CO₂ treatment,” they conclude “the additional carbon sink in the forest floor of the elevated CO₂ treatment ... is wholly dependent on the net primary production enhancement and increased carbon inputs,” which after a total of six years had increased the forest floor’s organic carbon content by approximately 27%, as best as can be determined from their plotted data. In addition, the data gave no indication this trend was on the verge of declining

anytime soon.

With respect to the underlying mineral soil, Lichter *et al.* said they could detect no statistically significant treatment effects on the carbon content of the bulk mineral soil or the intra-aggregate particulate organic matter and mineral-associated organic matter fractions after six years of CO₂ enrichment. Nevertheless, there was a nearly statistically significant ($P = 0.11$) increase of 18.5% in the free light fraction of the organic matter in the top 15 cm of the soil profile, as well as a 3.9% increase in the total intra-aggregate particulate organic matter there. The sum of the organic carbon in these two different categories plus the mineral-associated organic carbon was 11.5% greater in the CO₂-enriched plots than in the ambient treatment plots.

Although the scientists remained pessimistic and continued to assert “forest soils are unlikely to sequester significant additional quantities of atmospheric carbon associated with CO₂ fertilization because of the low rates of carbon input to refractory and protected soil organic matter pools,” the CO₂-enriched trees of their study continued to demonstrate a large and unabated growth advantage over the ambient-CO₂ trees. In addition, both the forest floor and the surface soil horizon beneath the CO₂-enriched trees continued to accumulate more organic carbon than the forest floor and surface soil horizon beneath the ambient-CO₂ trees.

LaDeau and Clark (2006) determined the reproductive responses (cone and seed production) of the loblolly pine trees at the Duke Forest FACE site to atmospheric CO₂ enrichment. They state, “carbon dioxide enrichment affected mean cone production both through early maturation and increased fecundity,” such that “trees in the elevated CO₂ plots produced twice as many cones between 1998 and 2004 as trees in the ambient plots.” They also report trees grown in elevated CO₂ “made the transition to reproductive maturation at smaller [trunk] diameters,” and they “not only reached reproductive maturation at smaller diameters, but also at younger ages.” By 2004, for example, “roughly 50% of ambient trees and 75% of fumigated trees [had] produced cones.” In addition, they observe, “22% of the trees in high CO₂ produced between 40 and 100 cones during the study, compared with only 9% of ambient trees.”

The two scientists say their findings indicate their previously documented “short-term responses indeed persist,” contradicting the opinions of those who downplay the biological benefits of atmospheric CO₂ enrichment. Furthermore, noting “*P. taeda* trees that produce large seed crops early in their life span tend

to continue to be prolific producers (Schultz, 1997),” they conclude “individual responses seen in this young forest may be sustained over their life span.”

At the eight-year point of the long-term FACE experiment, Moore *et al.* (2006) conducted a study that represented a turning point in most scientists’ thinking about what had come to be known as the Progressive Nitrogen Limitation hypothesis. They analyzed measurements of the basal areas of the trees’ trunks at approximately 1.4 m above ground level made at monthly intervals since the inception of the experiment. This work revealed, in response to the 50% increase in atmospheric CO₂ concentration employed in the Duke Forest FACE study, there was “a sustained increase in basal area increment over the first 8 years of the experiment” that varied between 13 and 27% with variations in weather and the timing of growth. In addition, the six scientists found “there was no evidence of a decline in the relative enhancement of tree growth by elevated CO₂ as might be expected if soil nutrients were becoming progressively more limiting,” which amazed many researchers (including several who were working on the experiment themselves), considering the low-fertility state of the soil in which the experiment was being conducted. Nevertheless, and despite many researchers’ presumptions the CO₂-induced growth stimulation of long-lived woody plants would gradually (and drastically) decline over time, there was no evidence that was occurring in the Duke Forest FACE study. The trees kept growing at a significantly elevated rate, even when nutrient limitations would have been expected to have kept them from doing so.

Two years later, Pritchard *et al.* (2008a) used minirhizotrons to characterize the fine root development of the trees from autumn 1998 through autumn 2004. Averaged over all six years of the study, they found the extra 200 ppm of CO₂ increased average fine-root standing crop by 23%, in good agreement with the stimulation of the forest’s net primary productivity of 18–24% observed over the period 1996–2002.

The nine researchers write, “the positive effects of CO₂ enrichment on fine root growth persisted 6 years following minirhizotron tube installation (8 years following initiation of the CO₂ fumigation),” providing once again no hint of progressive nitrogen limitation of the stimulatory effect of atmospheric CO₂ enrichment in a situation where one might have expected to have encountered it. In partial explanation of this finding, Pritchard *et al.* note the distal tips of fine roots are “the primary site for initiation of

mycorrhizal partnerships which are critical for resource acquisition and could also influence whether or not forests can sustain higher productivity in a CO₂-enriched world.” Nearly all evidence obtained to date suggests trees can indeed sustain a significant CO₂-induced increase in net primary productivity over the long term, and the reason they can do so may reside in the CO₂-induced stimulation of the growth of their important fine-root tips, as suggested by Pritchard *et al.*

In a related contemporaneous paper, Pritchard *et al.* (2008b) state data from long-term FACE experiments “have yet to provide convincing evidence in support of the progressive nitrogen limitation hypothesis.” They report exposure to elevated concentrations of atmospheric CO₂ had increased net primary productivity by 59%, 24%, 23%, and 30% at the Rhinelander, Wisconsin (USA), Oak Ridge National Laboratory (USA), Tuscania (Italy), and Duke, North Carolina (USA) FACE sites, respectively, “with little evidence to indicate a diminished response through time,” citing Finzi *et al.* (2007).

The leading hypothesis to explain these sustained high growth responses had been that atmospheric CO₂ enrichment leads to greater fine-root production and increased allocation of carbon to ectomycorrhizal fungi living in symbiotic association with plant roots, a dual phenomenon that leads to (1) the exploration of a greater volume of soil by plants in search of much-needed nitrogen, and (2) a more thorough search of each unit volume of soil. Consequently, Pritchard *et al.* (2008b) focused their attention on the role played by ectomycorrhizal fungi for five years in the Duke Forest FACE study.

Summed across all years of the study, the five researchers found the extra 200 ppm of CO₂ enjoyed by the trees in the high-CO₂ treatment did not influence mycorrhizal production in the top 15 cm of the forest soil, but it increased mycorrhizal root-tip production by 194% throughout the 15–30 cm depth interval. In addition, the production of soil rhizomorph length was 27% greater in CO₂-enriched plots than in the ambient-air plots.

In discussing their findings, Pritchard *et al.* note the CO₂-induced “stimulation of carbon flow into soil has increased the intensity of root and fungal foraging for nutrients” and “the shift in distribution of mycorrhizal fungi to deeper soils may enable perennial plant systems to acquire additional soil nitrogen to balance the increased availability of ecosystem carbohydrates in CO₂-enriched atmospheres.” This additional acquisition of nitrogen in the

CO₂-enriched plots of the Duke Forest study amounts to approximately 12 g N per m² per year and is well above estimated rates of N acquisition by the combined phenomena of N deposition, heterotrophic N fixation, and net N mineralization, which range from 3.4 to 6.0 g N per m² per year, as per Finzi *et al.* (2006, 2007), Hofmockel and Schlesinger (2007), and Hofmockel *et al.* (2007). Consequently, in concluding their commentary on the results of their work, Pritchard *et al.* write, “the notion that CO₂ enrichment expands the volume of soil effectively explored by roots and fungi, and that foraging in a given volume of soil also seems to intensify, provides compelling evidence to indicate that CO₂ enrichment has the potential to stimulate productivity (and carbon sequestration) in nitrogen-limited ecosystems more than previously expected.”

Jackson *et al.* (2009) describe belowground data they obtained at the Duke Forest FACE site, then present a synthesis of these and other results obtained for the years 1996 through 2008, to determine “which, if any, variables show evidence for a decrease in their response to atmospheric CO₂ during that time frame.” Their analyses indicate, among many other things, “on average, in elevated CO₂, fine-root biomass in the top 15 cm of soil increased by 24%,” and in recent years the fine-root biomass increase “grew stronger, averaging ~30% at high CO₂.” In terms of coarse roots having diameters greater than 2 mm and extending to a soil depth of 32 cm, they report biomass sampled in 2008 was “twice as great in elevated CO₂.” From the graphical representation of their results, it can be calculated the coarse-root biomass was fully 130% greater, which is astounding, particularly since the extra 200 ppm of CO₂ supplied to the air surrounding the CO₂-enriched trees represented an enhancement of only about 55% above ambient conditions. In the concluding sentence of their paper’s abstract, Jackson *et al.* state, “overall, the effect of elevated CO₂ belowground shows no sign of diminishing.”

In discussing their findings, the four researchers write, “if progressive nitrogen limitation were occurring in this system, we would expect differences in productivity to diminish for trees in the elevated vs. ambient CO₂ plots,” but “in fact there is little evidence from estimates of aboveground or total net primary productivity in the replicated Duke experiment that progressive nitrogen limitation is occurring there or at other forest FACE experiments,” even “after more than a decade of manipulation” of the air’s CO₂ content, citing—with respect to the latter portion of their statement—Finzi *et al.* (2007).

These most recent findings, plus all that preceded them, indicate there are many extremely well-documented observational—as opposed to theoretical—reasons to conclude the “aerial fertilization effect” of atmospheric CO₂ enrichment will significantly benefit Earth’s forests as the atmosphere’s CO₂ concentration rises.

References

- Campbell, G.S. and Norman, J.M. 1998. *An Introduction to Environmental Biophysics*. Second Edition. Springer Verlag, New York, NY.
- Crous, K.Y. and Ellsworth, D.S. 2004. Canopy position affects photosynthetic adjustments to long-term elevated CO₂ concentration (FACE) in aging needles in a mature *Pinus taeda* forest. *Tree Physiology* **24**: 961–970.
- DeLucia, E.H., Hamilton, J.G., Naidu, S.L., Thomas, R.B., Andrews, J.A., Finzi, A., Lavine, M., Matamala, R., Mohan, J.E., Hendrey, G.R., and Schlesinger, W.H. 1999. Net primary production of a forest ecosystem with experimental CO₂ enrichment. *Science* **284**: 1177–1179.
- Ellsworth, D.S. 2000. Seasonal CO₂ assimilation and stomatal limitations in a *Pinus taeda* canopy with varying climate. *Tree Physiology* **20**: 435–444.
- Ewers, B.E. and Oren, R. 2000. Analysis of assumptions and errors in the calculation of stomatal conductance from sap flux measurements. *Tree Physiology* **20**: 579–589.
- Finzi, A.C., DeLucia, E.H., Hamilton, J.G., Richter, D.D., and Schlesinger, W.H. 2002. The nitrogen budget of a pine forest under free air CO₂ enrichment. *Oecologia* **132**: 567–578.
- Finzi, A.C., Moore, D.J.P., DeLucia, E.H., Lichter, J., Hofmockel, K.S., Jackson, R.B., Kim, H.-S., Matamala, R., McCarthy, H.R., Oren, R., Phippen, J.S., and Schlesinger, W.H. 2006. Progressive nitrogen limitation of ecosystem processes under elevated CO₂ in a warm-temperate forest. *Ecology* **87**: 15–25.
- Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubes, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., and Ceulemans, R. 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂. *Proceedings of the National Academy of Sciences, USA* **104**: 14,014–14,019.
- Finzi, A.C. and Schlesinger, W.H. 2003. Soil-nitrogen cycling in a pine forest exposed to 5 years of elevated carbon dioxide. *Ecosystems* **6**: 444–456.
- Hamilton, J.G., DeLucia, E.H., George, K., Naidu, S.L.,

- Finzi, A.C., and Schlesinger, W.H. 2002. Forest carbon balance under elevated CO₂. *Oecologia* 10.1007/s00442-002-0884-x.
- Hendrey, G.R., Ellsworth, D.S., Lewin, K.F., and Nagy, J. 1999. A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO₂. *Global Change Biology* 5: 293–310.
- Hofmockel, K.S. and Schlesinger, W.H. 2007. Carbon dioxide effects on heterotrophic dinitrogen fixation in a temperate pine forest. *Soil Science Society of America Journal* 71: 140–144.
- Hofmockel, K.S., Schlesinger, W.H., and Jackson, R.B. 2007. Effects of elevated atmospheric CO₂ on amino acid and NH₄⁺-N cycling in a temperate pine ecosystem. *Global Change Biology* 13: 1950–1959.
- Jackson, R.B., Cook, C.W., Phippen, J.S., and Palmer, S.M. 2009. Increased belowground biomass and soil CO₂ fluxes after a decade of carbon dioxide enrichment in a warm-temperate forest. *Ecology* 90: 3352–3366.
- Katul, G.G., Ellsworth, D.S., and Lai, C.-T. 2000. Modeling assimilation and intercellular CO₂ from measured conductance: a synthesis of approaches. *Plant, Cell and Environment* 23: 347–353.
- Kostner, B.M.M., Schulze, E.-D., Kelliher, F.M., et al. 1992. Transpiration and canopy conductance in a pristine broad leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements. *Oecologia* 91: 350–359.
- LaDeau, S.L. and Clark, J.S. 2001. Rising CO₂ levels and the fecundity of forest trees. *Science* 292: 95–98.
- LaDeau, S.L. and Clark, J.S. 2006. Elevated CO₂ and tree fecundity: the role of tree size, interannual variability, and population heterogeneity. *Global Change Biology* 12: 822–833.
- Lai, C.T., Katul, G., Butnor, J., Ellsworth, D., and Oren, R. 2002. Modeling nighttime ecosystem respiration by a constrained source optimization method. *Global Change Biology* 8: 124–141.
- Lichter, J., Barron, S.H., Bevacqua, C.E., Finzi, A.C., Irving, K.F., Stemmler, E.A., and Schlesinger, W.H. 2005. Soil carbon sequestration and turnover in a pine forest after six years of atmospheric CO₂ enrichment. *Ecology* 86: 1835–1847.
- Luo, Y., Medlyn, B., Hui, D., Ellsworth, D., Reynolds, J., and Katul, G. 2001. Gross primary productivity in the Duke Forest: Modeling synthesis of the free-air CO₂ enrichment experiment and eddy-covariance measurements. *Ecological Applications* 11: 239–252.
- Luo, Y., White, L.W., Canadell, J.G., DeLucia, E.H., Ellsworth, D.S., Finzi, A., Lichter, J., and Schlesinger, W.H. 2003. Sustainability of terrestrial carbon sequestration: A case study in Duke Forest with inversion approach. *Global Biogeochemical Cycles* 17: 10.1029/2002GB001923.
- Merbach, W., Mirus, E., Knof, G., Remus, R., Ruppel, S., Russow, R., Gransee, A., and Schuize, J. 1999. Release of carbon and nitrogen compounds by plant roots and their possible ecological importance. *Zeitschrift für Pflanzenernährung und Bodenkunde* 162: 373–383.
- Moore, D.J.P., Aref, S., Ho, R.M., Phippen, J.S., Hamilton, J.G., and De Lucia, E.H. 2006. Annual basal area increment and growth duration of *Pinus taeda* in response to eight years of free-air carbon dioxide enrichment. *Global Change Biology* 12: 1367–1377.
- Myers, D.A., Thomas, R.B., and DeLucia, E.H. 1999. Photosynthetic capacity of loblolly pine (*Pinus taeda* L.) trees during the first year of carbon dioxide enrichment in a forest ecosystem. *Plant, Cell and Environment* 22: 473–481.
- Norby R.J., Gunderson, C.A., Wullschlegel, S.D., O'Neill, E.G., and McCracken, M.K. 1992. Productivity and compensatory response of yellow poplar trees in elevated CO₂. *Nature* 357: 322–324.
- Norby R.J., Todd, D.E., Fulps, J., and Johnson, D.W. 2001. Allometric determination of tree growth in CO₂ enriched sweetgum stand. *New Phytologist* 150: 477–487.
- Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., Finzi, A.C., Jackson, R.B., Matamala, R., Rogers, H.H., and Oren, R. 2008a. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO₂-enrichment: a six-year-minirhizotron study. *Global Change Biology* 14: 588–602.
- Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., and Oren, R. 2008b. Mycorrhizal and rhizomorph dynamics in a loblolly pine forest during 5 years of free-air-CO₂-enrichment. *Global Change Biology* 14: 1–13.
- Schafer, K.V.R., Oren, R., Ellsworth, D.S., Lai, C.-T., Herrick, J.D., Finzi, A.C., Richter, D.D., and Katul, G.G. 2003. Exposure to an enriched CO₂ atmosphere alters carbon assimilation and allocation in a pine forest ecosystem. *Global Change Biology* 9: 1378–1400.
- Schultz, R.P. 1997. *Loblolly Pine—The Ecology and Culture of Loblolly Pine (Pinus taeda L.)*. USDA Forest Service Agricultural Handbook 713. USDA Forest Service, Washington, DC, USA.
- Schlesinger, W.H. and Lichter, J. 2001. Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO₂. *Nature* 411: 466–469.
- Stenberg, P. 1998. Implications of shoot structure on the rate of photosynthesis at different levels in a coniferous

Climate Change Reconsidered II: Biological Impacts

canopy using a model incorporating grouping and penumbra. *Functional Ecology* **12**: 82–91.

Tangle, L. 2001. High CO₂ levels may give fast-growing trees an edge. *Science* **292**: 36–37.

Telewski, F.W., Swanson, R.T., Strain, B.R., and Burns, J.M. 1999. Wood properties and ring width responses to long-term atmospheric CO₂ enrichment in field-grown loblolly pine (*Pinus taeda* L.). *Plant, Cell and Environment* **22**: 213–219.

Tissue, D.T., Thomas, R.B., and Strain, B.R. 1997. Atmospheric CO₂ enrichment increases growth and photosynthesis of *Pinus taeda*: a 4-year experiment in the field. *Plant, Cell and Environment* **20**: 1123–1134.

Vitousek, P.M. and Howarth, R.W. 1991. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* **13**: 87–115.

1.1.3.2.2.2 Scots

- Evidence gleaned from multiyear studies suggests the historical rise in the atmosphere's CO₂ concentration has significantly enhanced the growth and well-being of Scots pine trees over the past century or more and will likely do the same for them in decades yet to come.

Researchers planted three-year-old pot-grown Scots pine (*Pinus sylvestris* L.) seedlings in the ground in four open-top chambers at the University of Antwerp in Belgium on 21 March 1996, and they continuously maintained them at atmospheric CO₂ concentrations of either 350 or 750 ppm, to determine the long-term effects of elevated CO₂ on various aspects of the growth and development of this important timber species, as described by Jach and Ceulemans (1999). To make the experimental results as representative as possible of the natural world, no nutrients or irrigation waters were applied to the soils during the entire period of the investigation.

During the second year of the study, Jach and Ceulemans (2000a) discovered the photosynthetic rates of current and one-year-old CO₂-enriched needles were 62 and 65% greater, respectively, than the photosynthetic rates of comparable needles on seedlings growing in ambient air. Simultaneously, Jach and Ceulemans (2000b) found dark respiration rates expressed on a needle-mass basis were 27 and 33% lower in current-year and one-year-old needles, respectively, on the CO₂-enriched trees than on the ambient-treatment trees. After three years of differential CO₂ exposure, Jach *et al.* (2000)

determined the extra CO₂ of the study had increased total seedling biomass production by 55%, even though the experimental soils were relatively nutrient-poor.

Possibly to compensate for this deficiency of nutrients, Jach *et al.* found the elevated CO₂ had increased root biomass by more than 150%, which would likely have enhanced the ability of the CO₂-enriched seedlings to explore a greater volume of soil for the nutrients they required to sustain their augmented growth and development. The three researchers conclude, “it is likely that on nutrient-poor forest sites valuable gains to the timber industry may be achieved under future climatic conditions, since increased root production may enhance both nutrient availability, and hence timber production, as well as increase wind stability.”

At the three-year point of the study, Gielen *et al.* (2000) determined elevated CO₂ did not significantly impact the photochemical quantum efficiency of photosystem II, nor did it affect any parameters associated with chlorophyll fluorescence, suggesting atmospheric CO₂ enrichment did not modify the light-dependent reactions of photosynthesis. They did find, however, elevated CO₂ reduced needle nitrogen and chlorophyll contents by 33 and 26%, respectively, although these reductions were statistically insignificant. Nonetheless, these latter observations suggest the light-independent reactions of photosynthesis were being modified by long-term exposure to elevated CO₂ in a manner indicating photosynthetic acclimation that allows for the redistribution of limiting resources, such as nitrogen, to other areas of the tree where they may be more needed.

At the four-year point of the study, Lin *et al.* (2001) found elevated CO₂ reduced needle stomatal density by an average of 7.4% while increasing needle thickness, mesophyll tissue area, and total cross-sectional area by 6.4, 5.7, and 10.4%, respectively. In addition, atmospheric CO₂ enrichment increased the average relative area occupied by phloem cells by 4.4%. The first of these observations suggests Scots pine trees will be better able to conserve water and cope with periods of drought in a future high-CO₂ world. In addition, the increase in mesophyll tissue portends an increase in photosynthetic rates, and the increase in phloem cell area suggests a greater capacity for transport of photosynthetic sugars from needles to actively growing sink tissues.

Finally, Waterhouse *et al.* (2004) determined the intrinsic water use efficiency response of Scots pines growing in South Bedfordshire in England to the

increase in the air's CO₂ content between 1895 and 1994, using parameters derived from measurements of stable carbon isotope ratios of tree-ring cellulose. The found there was a long-term increase in intrinsic water use efficiency during the prior century, and the main cause of this behavior was likely "the increase in atmospheric CO₂ concentration."

Linearly extrapolating the response (which occurred over a period of time when the air's CO₂ concentration rose by approximately 65 ppm) to what would be expected for a 300 ppm increase, the intrinsic water use efficiency increase they derived amounts to 195%, as best as can be determined from the graphs of their results. This substantial response is probably not due to the rising CO₂ alone but to the positive synergism that occurs when atmospheric CO₂ and temperature rise together.

The evidence gained from the last of these multiyear studies suggests the historical rise in the atmosphere's CO₂ concentration has significantly enhanced the growth and well-being of Earth's Scots pine trees over the past century or more, and the evidence of the other studies suggests the ongoing rise in atmospheric CO₂ (and possibly temperature as well) will likely do the same for decades yet to come.

References

- Gielen, B., Jach, M.E., and Ceulemans, R. 2000. Effects of season, needle age and elevated atmospheric CO₂ on chlorophyll fluorescence parameters and needle nitrogen concentration in (*Pinus sylvestris* L.). *Photosynthetica* **38**: 13–21.
- Jach, M.E. and Ceulemans, R. 1999. Effects of elevated atmospheric CO₂ on phenology, growth and crown structure of Scots pine (*Pinus sylvestris* L.) seedlings after two years of exposure in the field. *Tree Physiology* **19**:289–300.
- Jach, M.E. and Ceulemans, R. 2000a. Effects of season, needle age and elevated atmospheric CO₂ on photosynthesis in Scots pine (*Pinus sylvestris* L.). *Tree Physiology* **20**: 145–157.
- Jach, M.E. and Ceulemans, R. 2000b. Short- versus long-term effects of elevated CO₂ on night-time respiration of needles of Scots pine (*Pinus sylvestris* L.). *Photosynthetica* **38**: 57–67.
- Jach, M.E., Laureysens, I., and Ceulemans, R. 2000. Above- and below-ground production of young Scots pine (*Pinus sylvestris* L.) trees after three years of growth in the field under elevated CO₂. *Annals of Botany* **85**: 789–798.
- Lin, J., Jach, M.E., and Ceulemans, R. 2001. Stomatal density and needle anatomy of Scots pine (*Pinus sylvestris*) are affected by elevated CO₂. *New Phytologist* **150**: 665–674.
- Waterhouse, J.S., Switsur, V.R., Barker, A.C., Carter, A.H.C., Hemming, D.L., Loader, N.J., and Robertson, I. 2004. Northern European trees show a progressively diminishing response to increasing atmospheric carbon dioxide concentrations. *Quaternary Science Reviews* **23**: 803–810.
- 1.1.3.2.2.3 Other Pine Trees
- Aleppo and Shortleaf pines will likely experience greatly enhanced growth and development as the atmospheric CO₂ content continues its upward trajectory.
- Clues to how Earth's trees will respond to future increases in atmospheric CO₂ concentration may be obtained from studies of how they have responded to historical increases in the air's CO₂ content. This section reviews what has been learned for two less-analyzed species of pine tree: Aleppo pine (*Pinus halepensis* Mill.) and Shortleaf pine (*Pinus echinata* Mill.).
- Rathgeber *et al.* (2003) used tree-ring width and density chronologies (in both earlywood and latewood) from 21 stands of Aleppo pines in the Provence region of southeast France to calibrate the BIOME3 biogeochemistry model of forest productivity in terms of growth responses to known historical changes in atmospheric temperature, precipitation, and CO₂ concentration. They then used the calibrated model to calculate changes in the mean productivity of the same forest stands that could be expected to result from changes in these parameters driven by a doubling of the air's CO₂ content, as calculated by Meteo-France's ARPEGE atmospheric general circulation model when downscaled to that specific part of the country.
- In response to the predicted changes in climate, forest productivity increased moderately for all stands (17% to 24%), and in response to the aerial fertilization effect of the doubling of the air's CO₂ content, it rose considerably more (72% to 86%). Even more impressively, when the climatic changes and atmospheric CO₂ increase were considered together, forest productivity increased still more (107% to 141%).
- This latter response range is even greater than what is implied by the sum of the individual responses, due to the amplifying synergy of the atmospheric compositional and climatic factors on

basic plant physiological processes. Therefore, the researchers conclude, “although the detected effects of global change during the 20th century were slight, acceleration of these changes is likely to lead to great changes in the future productivity of *P. halepensis* forests.” Their study suggests a doubling of the air’s CO₂ content could more than double the growth of Aleppo pine forests in southeast France.

Working with Shortleaf pine in the Ozark Mountains of Missouri, USA, Voelker *et al.* (2006) cross-dated a large number of increment cores and aligned the ring-width data by pith date for accurate age-constant assessments of growth over the past 150 years, thereby circumventing “changes in growth trend associated with differences in physiological functioning during development, as well as the need for statistical detrending that removes an unknown degree of long-term environmental signal, the so-called segment length curse that applies to standard dendrochronological investigations.” In addition, they similarly analyzed previously acquired data for Shortleaf pine stretching back to nearly AD 1600. Since 1850, the stem growth of the trees rose “coincidentally with increases in atmospheric CO₂,” such that the overall trend in ring-width in recent years is “nearly two times that” experienced prior to 1850. In addition, “long-term increases in radial growth appear unrelated to historical disturbance levels for the region, to long-term changes in relevant climatic variables, or to productivity of sites sampled.” Consequently, the four Department of Forestry researchers from the University of Missouri (USA) conclude the rising atmospheric CO₂ concentration—aided by continued nitrogen deposition—will likely “stimulate further increases in the rates of stand development and carbon storage.”

References

Rathgeber, C., Nicault, A., Kaplan, J.O., and Guiot, J. 2003. Using a biogeochemistry model in simulating forests productivity responses to climatic change and [CO₂] increase: example of *Pinus halepensis* in Provence (southeast France). *Ecological Modelling* **166**: 239–255.

Voelker, S.L., Muzika, R.-M., Guyette, R.P., and Stambaugh, M.C. 2006. Historical CO₂ growth enhancement declines with age in *Quercus* and *Pinus*. *Ecological Monographs* **76**: 549–564.

1.1.3.2.3 Sour Orange

- The long-term equilibrium response of sour orange trees to a 75% increase in the air’s CO₂ concentration after 17 years of study was a CO₂-enriched/ambient-treatment biomass ratio of 1.69 for all above-ground parts of the trees (other than fruit), 1.85 for the cumulative amount of biomass due to fruit production, and 1.07 for the vitamin C content of the fruit (though this latter ratio was based on samples from the fourth through the 12th years of the experiment only).

In July 1987, as described by U.S. Department of Agriculture researchers Idso and Kimball (2001), eight 30-cm-tall sour orange tree (*Citrus aurantium* L.) seedlings were planted directly into the ground at the Agricultural Research Service’s U.S. Water Conservation Laboratory in Phoenix, Arizona, where they were enclosed in pairs within four clear-plastic-wall open-top chambers. In November of that year, the two scientists began to continuously pump ambient air through two of the chambers via perforated plastic tubes that lay upon the ground beneath the trees, and through the other two chambers they pumped air enriched with carbon dioxide to a concentration 300 ppm greater than the surrounding ambient air, which had an average CO₂ concentration of 400 ppm. Thus began one of the longest atmospheric CO₂ experiments ever conducted anywhere in the world.

Throughout the experiment, the Phoenix global-change research team irrigated and fertilized the trees according to standard agronomic practices in the area, to keep them as free as possible from water and nutrient stresses. They measured the circumferences of the trees’ trunks at a height of 45 cm above the surface of the ground at the midpoint of every month. At the end of the second and third years of the study, they also determined the total trunk and branch volume of each tree from trunk and branch length and diameter measurements. From these data they developed a relationship between trunk cross-sectional area and trunk plus branch volume that applied equally well to the CO₂-enriched and ambient-treatment trees. Then they made numerous wood density measurements that allowed them to calculate the total aboveground woody biomass of each tree at the midpoint of every month. In addition, all the oranges produced by the trees were picked, counted, and weighed each year, and a large number of the fruit were dried in ovens to determine the amount of dry matter they contained. The two

researchers thus developed a yearly record of total fruit biomass production to accompany their monthly record of wood biomass production.

As the experiment progressed, the CO₂-enriched/ambient-treatment ratio of cumulative aboveground wood biomass rose rapidly from an initial value of unity to a value slightly greater than 3.0 at the two-year point of the study, as shown in Figure 1.1.3.2.3.1, which depicts the changing ratio of the aboveground wood biomass of the CO₂-enriched trees to the ambient-treatment trees over the first two years of the study.

From the data of Figure 1.1.3.2.3.1, it could reasonably be assumed the CO₂-enriched/ambient-treatment wood biomass ratio might rise a little higher but would have to level off sometime soon. Hence, the researchers decided to continue collecting data to determine the long-term asymptotic growth response of the trees. After seven additional months, they obtained the results depicted in Figure 1.1.3.2.3.2.

To the researchers' surprise, the wood biomass ratio not only did not rise any higher, or even level out, it began a steep decline. Projecting forward in time, it appeared a continuation of the new trend could result in all the biomass advantage acquired by the CO₂-enriched trees possibly disappearing altogether over the next couple of years. To continue the experiment, they obtained the additional data depicted in Figure 1.1.3.2.3.3.

The results portrayed in Figure 1.1.3.2.3.3 were enlightening. They suggest, after an initial "overshoot" of the long-term response of the trees to atmospheric CO₂ enrichment, things finally settled down and a final answer was obtained: The ultimate equilibrium response of the trees was a 150% increase in wood biomass production in response to the 75% increase in the air's CO₂ concentration. The research team continued collecting data, only to be surprised once again as depicted in Figure 1.1.3.2.3.4.

The results portrayed in Figure 1.1.3.2.3.3 were enlightening. They suggest, after an initial "overshoot" of the long-term response of the trees to atmospheric CO₂ enrichment, things finally settled down and a final answer was obtained: The ultimate equilibrium response of the trees was a 150% increase in wood biomass production in response to the 75% increase in the air's CO₂ concentration. The research team continued collecting data, only to be surprised once again as depicted in Figure 1.1.3.2.3.4.

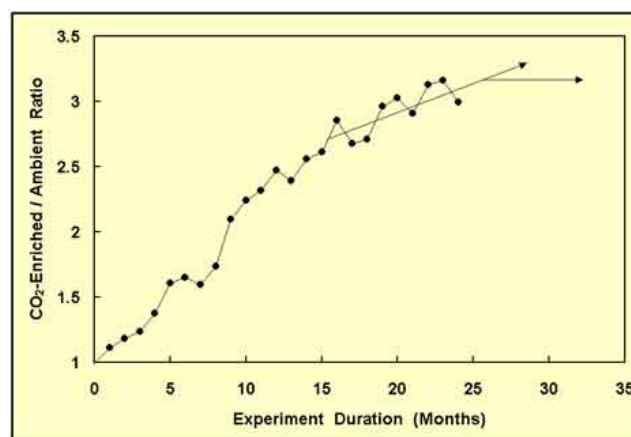


Figure 1.1.3.2.3.1. The CO₂-enriched/ambient-treatment ratio of total aboveground sour orange tree wood biomass plotted as a function of time since the start of the experiment, along with arrows that depict two logical projections of what might happen to this ratio if the experiment were continued beyond the last point shown. Adapted from Idso and Kimball (2001).

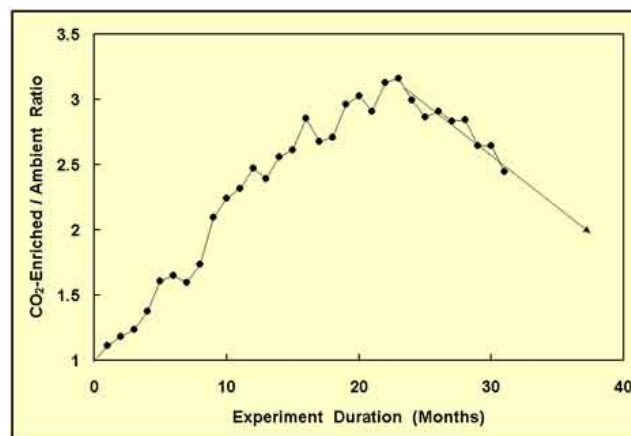


Figure 1.1.3.2.3.2. Same as Figure 1.1.3.2.3.1, but with seven additional months of data and a new forward projection of the CO₂-enriched/ambient-treatment wood biomass ratio. Adapted from Idso and Kimball (2001).

After having maintained a near-constant value for more than a year and a half, the wood biomass ratio began to decline again, as shown in Figure 1.1.3.2.3.4 not as rapidly as it had the first time, but at a still substantial rate. As it dropped ever-lower, the researchers decided to continue collecting data, which yielded the results depicted in Figure 1.1.3.2.3.5.

Climate Change Reconsidered II: Biological Impacts

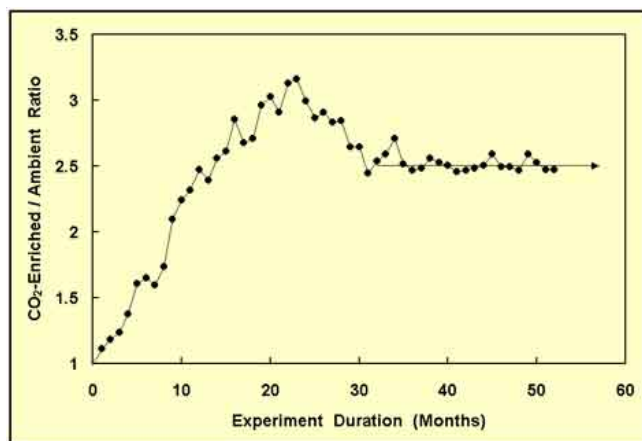


Figure 1.1.3.2.3.3. Same as Figure 1.1.3.2.3.2, but with 21 additional months of data and a new forward projection of the wood biomass ratio. Adapted from Idso and Kimball (2001).

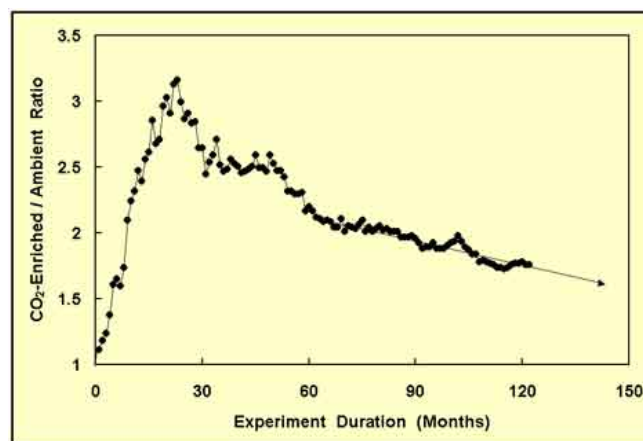


Figure 1.1.3.2.3.5. Same as Figure 1.1.3.2.3.4, but with 58 months of additional data and one more projection of the CO₂-enriched/ambient-treatment wood biomass ratio. Adapted from Idso and Kimball (2001).

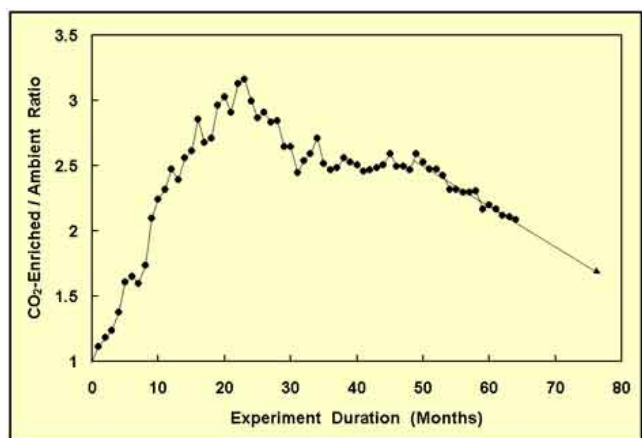


Figure 1.1.3.2.3.4. Same as Figure 1.1.3.2.3.3, but with 12 more months of data and yet another forward projection of the CO₂-enriched/ambient-treatment wood biomass ratio. Adapted from Idso and Kimball (2001).

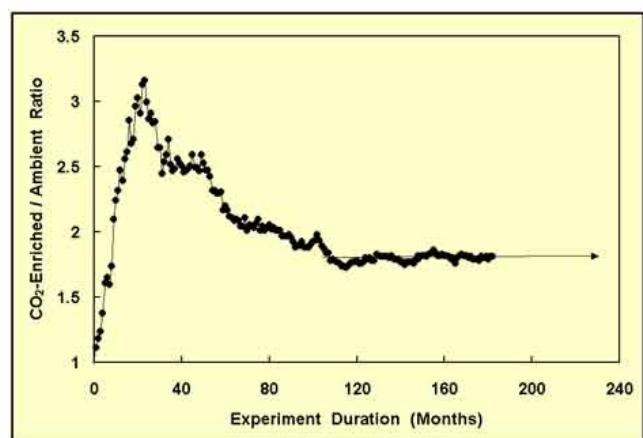


Figure 1.1.3.2.3.6. Same as Figure 1.1.3.2.3.5, but with 60-plus months of additional data and one last forward projection of the wood biomass ratio. Adapted from Idso and Kimball (2001).

This time, the change was to a reduced rate of decline in the wood biomass ratio, and it persisted for nearly five years. At this point, the experiment had passed the decade point, and it appeared the wood biomass ratio was going to continue to decline slowly and probably approach some asymptotic limit that might not be much greater than unity. As that possibility would be of extreme significance, Idso and Kimball continued collecting data, obtaining the results portrayed in Figure 1.1.3.2.3.6.

Finally, at the nine-year point of the study, the CO₂-enriched/ambient-treatment wood biomass ratio leveled out at 1.80, which the researchers concluded was the true long-term growth response of the trees to

the 75% increase in atmospheric CO₂ concentration.

Providing additional support for this conclusion, fruit production began in the third year of the study, when the CO₂-enriched trees produced an average of 25 fruit per tree and the ambient-treatment trees produced an average of only one fruit per tree. Thereafter, the cumulative CO₂-enriched/ambient-treatment fruit biomass ratio also dropped substantially, ultimately leveling out just a little above the 1.80 CO₂-enriched/ ambient-treatment wood biomass ratio. These findings, Idso and Kimball (2001) write, “are indicative of the likelihood that the CO₂-enriched trees may have reached an equilibrium condition with respect to the CO₂-induced

enhancement of wood biomass and fruit production, and that they will not substantially depart from these steady-state responses over the remainder of their lifespan.”

Giving added confidence to these conclusions was the ancillary study of Leavitt *et al.* (2003). They evaluated the intrinsic water use efficiencies of the trees via analyses of the stable carbon isotopes of leaves collected from each of them every two months throughout 1992, as well as on three occasions in 1994–95, plus wood samples extracted five years later from two cores that passed through the center of each tree’s trunk at a height of 45 cm above the ground. The ultimate finding of this endeavor was an 80% increase in intrinsic water use efficiency in response to the 75% increase in atmospheric CO₂ concentration employed in the study. Since the earlier work of Idso *et al.* (1993) had demonstrated there was very little difference in leaf stomatal conductance between the two CO₂ treatments, nearly all this water use efficiency increase had to have resulted from the CO₂-induced increase in net primary productivity that led to the 80% increases in wood and fruit production.

This result may be typical of trees in general. In a massive review of the pertinent scientific literature, Saxe *et al.* (1998) observed “increasing numbers of experiments show a lack of stomatal sensitivity to CO₂,” especially when the data come “from long-term experiments on larger trees rooted directly in the ground,” as also may be deduced from Eamus (1996). And Feng (1999) reports, for 23 sets of trees in locations across western North America, the average stable-carbon-isotope-derived increase in intrinsic water use efficiency (iWUE) that occurred in response to the historical increase in the air’s CO₂ concentration experienced over the period 1800–1985 yielded essentially the same value of iWUE/CO₂ as derived from the sour orange tree study of Leavitt *et al.* In addition, even greater natural CO₂-induced increases in iWUE have been documented in various trees in Europe: by Bert *et al.* (1997) in the case of white fir, and by Hemming (1998) in the cases of beech, oak, and pine.

Perhaps the most convincing evidence for the validity of the long-term equilibrium response of the sour orange trees in the CO₂-enriched chambers came from the harvesting of the trees after 17 years of study at the conclusion of the experiment, in January 2005, as described by Kimball *et al.* (2007). The scientists found the final CO₂-enriched/ambient-treatment biomass ratio of all of the above-ground parts of the trees (other than fruit) was 1.69, and “the cumulative amount of biomass due to fruit production over the

duration of the experiment was increased 85% due to elevated CO₂.” In addition, they report, “the vitamin C content of the fruit was increased 7% based on samples taken from the fourth through the 12th years of the experiment,” citing Idso *et al.* (2002). Many more oranges were produced by the trees in the CO₂-enriched chambers, and those oranges were of a higher quality as well.

In addition, Idso *et al.* (2001) discovered three soluble proteins in the leaves of the sour orange trees whose synthesis and transference from second- to first-year leaves in the early springtime of each year were influenced by the atmosphere’s CO₂ concentration in ways likely to facilitate the trees’ large positive photosynthetic and biomass responses to atmospheric CO₂ enrichment. The proteins appeared to function as vacuolar storage proteins, which may supply each year’s first flush of new foliage with the large amounts of nitrogen needed to sustain the ultra-enhanced spring branch growth of the CO₂-enriched trees, which was four to six times more rapid than the trees growing in ambient air in their experiment (Idso *et al.*, 2000), and which likely provided the yearly initial impetus for the 70 to 80% long-term growth enhancement of the trees maintained throughout the remainder of each year of the last half of their long-term study.

References

- Bert, D., Leavitt, S.W., and Dupouey, J.-L. 1997. Variations in wood $\delta^{13}\text{C}$ and water use efficiency of *Abies alba* during the last century. *Ecology* **78**: 1588–1595.
- Eamus, D. 1996. Responses of field grown trees to CO₂ enrichment. *Commonwealth Forestry Review* **75**: 39–47.
- Feng, X. 1999. Trends in intrinsic water use efficiency of natural trees for the past 100–200 years: A response to atmospheric CO₂ concentration. *Geochimica et Cosmochimica Acta* **63**: 1891–1903.
- Hemming, D.L. 1998. *Stable Isotopes in Tree Rings: Biosensors of Climate and Atmospheric Carbon-Dioxide Variations*. Ph.D. Dissertation. University of Cambridge, Cambridge, UK.
- Idso, C.D., Idso, S.B., Kimball, B.A., Park, H.-S., Hooper, J.K., and Balling Jr., R.C. 2000. Ultra-enhanced spring branch growth in CO₂-enriched trees: Can it alter the phase of the atmosphere’s seasonal CO₂ cycle? *Environmental and Experimental Botany* **43**: 91–100.
- Idso, K.E., Hooper, J.K., Idso, S.B., Wall, G.W., and Kimball, B.A. 2001. Atmospheric CO₂ enrichment influences the synthesis and mobilization of putative

Climate Change Reconsidered II: Biological Impacts

vacuolar storage proteins in sour orange tree leaves. *Environmental and Experimental Botany* **48**: 199–211.

Idso, S.B. and Kimball, B.A. 2001. CO₂ enrichment of sour orange trees: 13 years and counting. *Environmental and Experimental Botany* **46**: 147–153.

Idso, S.B., Kimball, B.A., Akin, D.E., and Kridler, J. 1993. A general relationship between CO₂-induced reductions in stomatal conductance and concomitant increases in foliage temperature. *Environmental and Experimental Botany* **33**: 443–446.

Idso, S.B., Kimball, B.A., Shaw, P.E., Widmer, W., Vanderslice, J.T., Higgs, D.J., Montanari, A., and Clark, W.D. 2002. The effect of elevated atmospheric CO₂ on the vitamin C concentration of (sour) orange juice. *Agriculture, Ecosystems and Environment* **90**: 1–7.

Kimball, B.A., Idso, S.B., Johnson, S., and Rillig, M.C. 2007. Seventeen years of carbon dioxide enrichment of sour orange trees: final results. *Global Change Biology* **13**: 2171–2183.

Leavitt, S.W., Idso, S.B., Kimball, B.A., Burns, J.M., Sinha, A., and Stott, L. 2003. The effect of long-term atmospheric CO₂ enrichment on the intrinsic water use efficiency of sour orange trees. *Chemosphere* **50**: 217–222.

Saxe, H., Ellsworth, D.S., and Heath, J. 1998. Tree and forest functioning in an enriched CO₂ atmosphere. *New Phytologist* **139**: 395–436.

1.1.3.2.4 Spruce

- Spruce trees have a good chance of indefinitely maintaining the long-term positive growth responses to the ongoing rise in the air's CO₂ content, even when growing on nutrient-deficient soils.

Spunda *et al.* (1998) grew 15-year-old Norway spruce (*Picea abies*) trees in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm for four years. At the end of this period they found current-year shoots of the trees growing in the CO₂-enriched chambers displayed rates of net photosynthesis 78% greater than those exhibited by the current-year shoots of the trees growing in ambient air.

Spinnler *et al.* (2003) grew Norway spruce seedlings originating from eight different provenances for four full years on a nutrient-poor acidic soil and a nutrient-rich calcareous soil placed in lysimeters located within open-top chambers maintained at CO₂ concentrations of either 370 or 570 ppm. When growing in the nutrient-poor soil, total spruce biomass

increased by 9 to 38% across the eight different provenances, and in the nutrient-rich soil it increased by 10 to 74%.

In an experiment that ran for five years and focused on Sitka spruce (*Picea sitchensis*), Liu *et al.* (2002) grew seedlings in open-top chambers maintained for five years at CO₂ concentrations of either 350 or 700 ppm. For the first three years, the seedlings were grown in well-watered and -fertilized pots placed within the chambers. They were then planted directly in native nutrient-deficient forest soil and maintained for two more years in larger open-top chambers, either with or without an extra supply of nitrogen (N).

After the first three years of growth in pots, the CO₂-enriched trees were found to possess 11.6% more total biomass than the ambient-treatment trees. At the end of the next two years of the study, the trees supplied with extra N possessed 15.6% more total biomass than their similarly treated ambient-air counterparts, and those receiving no extra N had 20.5% more total biomass than their ambient-air counterparts.

Liu *et al.* make a point of noting these CO₂-induced increases in growth occurred in spite of a down-regulation of photosynthesis and a reduction of foliar rubisco activity. In addition, they report “visual foliar N-deficiency symptoms (needle yellowing and chlorosis) were obvious on some of the saplings with no added N supply during the final year of the experiment.” However, they further note “such N deficiency is common in many boreal forest sites, and therefore a growth response to rising atmospheric CO₂ can be expected to occur in such forests,” in support of which they state, “growth responses to elevated CO₂ despite nutrient stress have been reported previously in Scots pine (Kellomaki and Wang, 1997), grass (Cannell and Thornley, 1998) and Sitka spruce (Centritto *et al.*, 1999; Murray *et al.*, 2000).”

These findings, plus those cited by Liu *et al.*, indicate spruce trees (and other species) have a good chance of indefinitely maintaining long-term positive growth responses to the ongoing rise in the air's CO₂ content, even on nutrient-deficient soils.

References

Cannell, M.G.R. and Thornley, H.M. 1998. N-poor ecosystems may respond more to elevated [CO₂] than N-rich ones in the long term, a model analysis of grassland. *Global Change Biology* **4**: 101–112.

Centritto, M., Lee, H.S.J., and Jarvis, P.G. 1999. Long-term effects of elevated carbon dioxide concentration and provenance on four clones of Sitka spruce (*Picea sitchensis*). I. Plant growth, allocation and ontogeny. *Tree Physiology* **19**: 799–806.

Kellomaki, S. and Wang, K.Y. 1997. Photosynthetic response of Scots pine to elevated CO₂ and nitrogen supply: results of a branch-in-bag experiment. *Tree Physiology* **17**: 231–240.

Liu, S.R., Barton, C., Lee, H., Jarvis, P.G., and Durrant, D. 2002. Long-term response of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) to CO₂ enrichment and nitrogen supply. I. Growth, biomass allocation and physiology. *Plant Biosystems* **136**: 189–198.

Murray, M.B., Smith, R.I., Friend, A., and Jarvis, P.G. 2000. Effect of elevated [CO₂] and varying nutrient application rates on physiology and biomass accumulation of Sitka spruce (*Picea sitchensis*). *Tree Physiology* **20**: 421–434.

Spinnler, D., Egli, P., and Körner, C. 2003. Provenance effects and allometry in beech and spruce under elevated CO₂ and nitrogen on two different forest soils. *Basic and Applied Ecology* **4**: 467–478.

Spunda, V., Kalina, J., Cajanek, M., Pavlickova, H., and Marek, M.V. 1998. Long-term exposure of Norway spruce to elevated CO₂ concentration induces changes in photosystem II mimicking an adaptation to increased irradiance. *Journal of Plant Physiology* **152**: 413–419.

1.1.3.2.5 Sweetgum

- Long-term FACE studies of mature sweetgum trees demonstrate significant increases in net primary production and give no evidence of decline.

In spring 1988, a single-species sweetgum (*Liquidambar styraciflua* L.) plantation was established in nutrient-rich soil at the Oak Ridge National Environmental Research Park in Roane County, Tennessee, USA, where a group of scientists constructed five circular FACE plots of 25 meters' diameter several years later. They began initial atmospheric CO₂ enrichment to a daytime average concentration of 533 ppm (as opposed to the ambient concentration of 394 ppm) in two of the plots in April 1998, well after the 1996 date at which the young forest's canopy had achieved closure and the trees had entered the stable linear growth phase in which annual growth increments are approximately the same each year (as opposed to the exponential growth that precedes this more mature state).

In April 1997 (a full year before the start of differential CO₂ treatments), the scientists began monthly bole circumference measurements at a height of 1.3 meters above the ground on every tree within 10 meters of the centers of the ambient and CO₂-enriched plots. Several of these trees were subsequently sacrificed to determine their aboveground biomass, and a relationship was developed between this parameter and the tree basal area derived from the bole circumference measurements. Based on these data, Norby *et al.* (2001) state, “there was no pretreatment bias to confound subsequent effects of CO₂ on growth.”

Over the next two years of differential CO₂ exposure, they determined the increase in atmospheric CO₂ concentration employed in their study increased the biomass production of the trees by an average of 24% over the first two years of the experiment. That result indicated, they write, “large trees have the capacity to respond to elevated CO₂ just as much as younger trees that are in exponential growth,” which had been highly conjectural until that time.

After three years of exposure to different CO₂ concentrations (reported at this subsequent time to be 360 and 550 ppm in the ambient and CO₂-enriched plots, respectively), Gunderson *et al.* (2002) found the 53% increase in the air's CO₂ concentration imposed on the trees was boosting rates of net photosynthesis by 46% in both upper- and mid-canopy foliage. In addition, they report there was no decline in photosynthetic enhancement over the preceding three years of their study.

Norby *et al.* (2002) state the elevated CO₂ increased ecosystem net primary productivity of the trees by 21% in all of the three preceding years, stating once again, “this experiment has provided the first evidence that CO₂ enrichment can increase productivity in a closed-canopy deciduous forest.” After an additional year of measurements, Norby *et al.* (2003) determined net primary productivity was enhanced by an average of 22% over years 2–5 of the study, reaffirming their conclusions of the year before.

A second long-term FACE study of sweetgum trees was conducted at the Duke Forest in the Piedmont region of North Carolina, USA, where the soils are low in available nitrogen and phosphorus. In August 1996, three 30m-diameter CO₂ delivery rings began to enrich the air around the then-13-year-old trees they encircled—including loblolly pine (1733 stems per ha), sweetgum (620 stems per ha), and yellow poplar (68 stems per ha)—to 190 ppm above the ambient CO₂ concentration, and three other FACE

rings were used as ambient-air control plots.

In the initial stages of this study, Herrick and Thomas (1999) found elevated CO₂ significantly increased photosynthetic rates in both Sun and shade leaves, with the greatest CO₂-induced photosynthetic stimulation occurring in August, when the mean maximum air temperature was 4°C higher and monthly rainfall was 66% lower than in June. In June, the extra CO₂ increased photosynthetic rates of Sun and shade leaves by 92 and 54%, respectively, whereas in August corresponding increases were 166 and 68%.

Two years later, Herrick and Thomas (2001) observed mean photosynthetic enhancements of 63 and 48% in Sun and shade leaves during the middle portion of the study's third full growing season, indicating little to no down-regulation of photosynthesis over the first three years of the experiment. After two more years, Herrick and Thomas (2003) found there were still large increases in the net photosynthetic rates of the leaves of the CO₂-enriched trees: 51 to 96% in Sun leaves and 23 to 51% in shade leaves.

These two long-term FACE studies of mature sweetgum trees demonstrate significant increases in net primary production and give no evidence of decline.

References

Gunderson, C.A., Sholtis, J.D., Wullschleger, S.D., Tissue, D.T., Hanson, P.J., and Norby, R.J. 2002. Environmental and stomatal control of photosynthetic enhancement in the canopy of a sweetgum (*Liquidambar styraciflua* L.) plantation during 3 years of CO₂ enrichment. *Plant, Cell and Environment* **25**: 379–393.

Herrick, J.D. and Thomas, R.B. 1999. Effects of CO₂ enrichment on the photosynthetic light response of Sun and shade leaves of canopy sweetgum trees (*Liquidambar styraciflua*) in a forest ecosystem. *Tree Physiology* **19**: 779–786.

Herrick, J.D. and Thomas, R.B. 2001. No photosynthetic down regulation in sweetgum trees (*Liquidambar styraciflua* L.) after three years of CO₂ enrichment at the Duke Forest FACE experiment. *Plant, Cell and Environment* **24**: 53–64.

Herrick, J.D. and Thomas, R.B. 2003. Leaf senescence and late-season net photosynthesis of Sun and shade leaves of overstory sweetgum (*Liquidambar styraciflua*) grown in elevated and ambient carbon dioxide concentrations. *Tree Physiology* **23**: 109–118.

Norby, R.J., Hanson, P.J., O'Neill, E.G., Tschaplinski, T.J.,

Weltzin, J.F., Hansen, R.A., Cheng, W., Wullschleger, S.D., Gunderson, C.A., Edwards, N.T., and Johnson, D.W. 2002. Net primary productivity of a CO₂-enriched deciduous forest and the implications for carbon storage. *Ecological Applications* **12**: 1261–1266.

Norby, R.J., Sholtis, J.D., Gunderson, C.A., and Jawdy, S.S. 2003. Leaf dynamics of a deciduous forest canopy: no response to elevated CO₂. *Oecologia* **10.1007/s00442-003-1296-2**.

Norby, R.J., Todd, D.E., Fuels, J., and Johnson, D.W. 2001. Allometric determination of tree growth in a CO₂-enriched sweetgum stand. *New Phytologist* **150**: 477–487.

1.1.4 Lifetime Exposure to Elevated CO₂

- Trees and shrubs growing for multiple generations in CO₂-enriched air near CO₂-emitting springs and vents provide a unique opportunity for evaluating the effects of permanently elevated atmospheric CO₂ concentrations on their physiology and growth. Such effects indicate a doubling, tripling, or even greater enhancement of the atmosphere's CO₂ concentration will only further improve the productivity and water use efficiency of woody plants.

A number of woody plants, including shrubs and trees, have been growing for multiple generations in CO₂-enriched air near CO₂-emitting springs and vents at various locations around the world. These circumstances provide unique settings for evaluating the effects of permanently elevated atmospheric CO₂ concentrations on their physiology and productivity.

Taking advantage of one of these natural situations—CO₂-emitting springs near Pisa, Italy—Tognetti *et al.* (2000a) studied the water relations of three woody shrubs (*Erica arborea*, *Myrtus communis*, and *Juniperus communis*) growing at small distances from the springs, where atmospheric CO₂ concentrations of approximately 700 ppm prevailed, as well as at greater distances from the springs, where normal concentrations of 360 ppm prevailed at the time of their study. Two common responses were evident in all the shrubs: The CO₂-enriched air reduced leaf stomatal conductances and increased leaf water potentials (making them less negative and, therefore, less stressful). The group of five scientists conclude the CO₂-induced adjustments in the shrubs' internal water relations would likely allow them "to endure severe periodic drought."

In an analysis of other aspects of the same study, Tognetti *et al.* (2000b) report the plants growing in

the CO₂-enriched air closer to the springs experienced increased leaf turgor pressure, particularly during the warmer summer months, which is also indicative of better plant water relations. And in another study at that location, Tognetti *et al.* (2002) found elevated CO₂ altered the elastic cell-wall properties of all three shrubs in such a way as to endow the shrubs with greater capacities for water uptake from the soil than by control plants growing in ambient air. In addition, the CO₂-enriched shrubs displayed greater relative water content than did ambiently grown plants as leaf water potentials declined with available soil moisture.

Bartak *et al.* (1999) studied various physiological processes of mature *Arbutus unedo* trees growing in the general vicinity of CO₂-emitting vents located in central Italy. At different distances from the vents, physiological measurements were made on trees exposed to average atmospheric CO₂ concentrations of approximately 355 ppm (ambient) and 465 ppm (CO₂-enriched) over 30 years. Bartak *et al.* determined this modest 30% increase in atmospheric CO₂ concentration boosted net photosynthetic rates in the perennial evergreen species by 110 to 140%, depending on light intensity. They also found the CO₂-enriched trees experienced no photosynthetic acclimation to the extra vent-derived CO₂ to which they were continuously exposed.

At the high end of the CO₂ concentration spectrum, Fernandez *et al.* (1998) studied a number of the effects of very high CO₂ levels produced by natural CO₂ springs on an indigenous tree during the rainy and dry seasons in Venezuela. They found the ultra-high CO₂ concentrations—some as much as 100 times the current global mean—were in no way detrimental to the trees. Instead, photosynthesis was stimulated by the high CO₂ in all seasons and in spite of the likely presence of toxic hydrocarbons and sulfur gases typically released to the air along with CO₂ in such situations. During the dry season, in fact, trees growing away from the springs at ambient CO₂ levels displayed net losses of carbon from their leaves, whereas trees growing near the springs at elevated CO₂ concentrations exhibited net carbon gains. In addition, the high CO₂ concentrations reduced leaf stomatal densities by about 70%, causing the water use efficiency of the trees to rise twofold and 19-fold, respectively, during the rainy and dry seasons, when measured at a CO₂ concentration of 1,000 ppm compared to an ambient concentration of 350 ppm, which represents less than a tripling of the air's CO₂ content.

Consequently, and because of the trees' long-term exposure to these high CO₂ concentrations under

totally natural conditions, Fernandez *et al.* conclude their work provides “a positive answer to the question of whether increases in carbon assimilation will be sustained throughout the growing season and over multiple seasons” in a high-CO₂ world of the future.

Schwanz *et al.* (1998) measured various parameters in leaves of mature holm and white oak trees growing near natural CO₂ springs in central Italy for 30 to 50 years in order to determine the effects of elevated CO₂ on their antioxidative systems. They report elevated CO₂ decreased the activities of superoxide dismutase, which detoxifies highly reactive oxygen species, by approximately 30 and 47% in leaves of holm and white oak trees, respectively, when compared with activities measured in leaves of trees growing some distance away from the CO₂-emitting springs. Trees of both species growing near the springs also exhibited lower activities of catalase and other enzymes involved in the degradation of hydrogen peroxide (H₂O₂), which is produced during photorespiration. Thus, atmospheric CO₂ enrichment generally decreased the activities of protective enzymes that reduce oxidative stress brought about by unfavorable environmental factors such as drought, high light intensity, high air temperature, and aerial pollutants.

To determine whether the CO₂-induced decreases in the antioxidative machinery of the CO₂-enriched trees increased their susceptibility to oxidative damage, the authors evaluated the degree of lipid peroxidation within the leaves. They report trees growing near the CO₂-emitting springs did not display increased levels of lipid peroxidation in their leaves, and in some cases they exhibited significant reductions in their amounts of lipid peroxidation. Thus, as the CO₂ content of the air increases, most plants will likely experience an amelioration of unfavorable environmental growing conditions that often lead to oxidative stresses within leaves.

This study was the first to identify changes in leaf physiology that have persisted for decades in response to elevated CO₂. Specifically, it shows reductions in antioxidative enzymes, which have been observed in seedlings, can persist indefinitely as trees mature. Furthermore, because these enzymes remove reactive compounds that can cause cellular damage, their reduced activities at high CO₂ implies plants experience less intrinsic oxidative stress and produce fewer harmful oxidants as the amount of CO₂ in the air increases. Thus this beneficial consequence of atmospheric CO₂ enrichment should allow plants to increase their productivity, growth, and yield as the air's CO₂ content climbs.

Rapparini *et al.* (2004) measured isoprenoid emissions over two consecutive years from two species of mature oak trees—the deciduous downy oak (*Quercus pubescens* Willd.) and the evergreen holm oak (*Quercus ilex* L.)—growing close to a natural CO₂ spring in central Italy, where atmospheric CO₂ concentrations averaged about 1,000 ppm, and at a nearby control site where the air’s CO₂ content was unaffected by the spring. Rapparini *et al.* report long-term exposure to high levels of atmospheric CO₂ did not significantly affect actual isoprenoid emissions from the trees—emissions experienced under prevailing environmental conditions at the time of measurement. However, they report, “when leaves of plants grown in the control site were exposed for a short period to an elevated CO₂ level by rapidly switching the CO₂ concentration in the gas-exchange cuvette, both isoprene and monoterpene basal emissions were clearly inhibited,” where basal emissions are defined as those that occur at standard measuring conditions of 30°C air temperature and 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ light intensity.

In commenting on these findings, the authors say “these results generally confirm the inhibitory effect of elevated CO₂ on isoprenoid emission.” In addition, they note the absence of a CO₂ effect on actual emissions might indicate “an interaction with multiple stresses,” such as the “recurrent droughts” that are typical of the Mediterranean climate in which the experiment was conducted, and these stresses are known to enhance isoprenoid emissions. Thus, evidence continues to mount for the beneficial phenomenon of CO₂-induced decreases in isoprene emissions.

Paoletti *et al.* (2007) measured rates of net photosynthesis during a two-week period in June 2002 “at the end of the spring rains,” when midday air temperatures rose above 40°C, in upper, sunlit leaves of mature holm oak (*Quercus ilex* L.) trees growing close to (5 m) and further away from (130 m) a natural CO₂-emitting spring near Laiatico (Pisa, Italy), where the trees had experienced lifetime exposure to atmospheric CO₂ concentrations of approximately 1,500 and 400 ppm, respectively.

At the midpoint of the 14-day measurement period, the net photosynthetic rates of the leaves on the trees growing closest to the CO₂ spring were approximately 250% greater than those of the leaves on the trees growing 125 meters further away, where the air’s CO₂ concentration was 1,100 ppm less. The four Italian researchers say “the considerable photosynthetic stimulation at the very high CO₂ site suggests no photosynthetic down-regulation over

long-term CO₂ enrichment.”

Polle *et al.* (2001) collected acorns from mature holm oak (*Quercus ilex* L.) trees growing naturally for their entire lifetimes at ambient and twice-ambient atmospheric CO₂ concentrations due to their different distances from a CO₂-emitting spring in central Italy. After germinating the acorns, the resulting seedlings were grown for eight months at both atmospheric CO₂ concentrations to determine whether atmospheric CO₂ enrichment of parent trees had any effect on seedling response to atmospheric CO₂ enrichment.

The results reveal elevated CO₂ increased whole-plant biomass by 158% and 246% in seedlings derived from acorns produced in ambient and twice-ambient atmospheric CO₂ concentrations, respectively, so the final biomass of the CO₂-enriched seedlings derived from acorns produced in the CO₂-enriched air was 25% greater than the CO₂-enriched seedlings derived from acorns produced in ambient air. In addition, gas exchange measurements indicate CO₂-enriched seedlings derived from acorns produced on CO₂-enriched trees exhibited less-pronounced photosynthetic acclimation to elevated CO₂ concentrations than CO₂-enriched seedlings derived from acorns produced on trees exposed to ambient air.

Onoda *et al.* (2009) state the ongoing rise in the air’s CO₂ content “is likely to act as a selective agent” among Earth’s plants, citing Woodward *et al.* (1991), Thomas and Jasienski (1996), Ward *et al.* (2000), Kohut (2003), Ward and Kelly (2004), and Lau *et al.* (2007). They report, “evolutionary responses have been found in selection experiments with short-lived organisms, such as *Arabidopsis thaliana* (e.g. development rate and biomass production; Ward *et al.*, 2000) and *Chlamydomonas reinhardtii* (e.g. photosynthesis and cell size; Collins and Bell, 2004).” They hasten to add, however, “the evolutionary response of wild plants (especially long-lived plants) is, in general, difficult to evaluate using growth experiments,” because of the long time spans needed to evaluate the phenomenon properly.

They avoid this problem in their study by utilizing plants growing around natural CO₂ springs where they “have been exposed to a CO₂-enriched atmosphere over many generations,” which provides what they call “a unique opportunity to explore the micro-evolutionary response of wild plants to elevated CO₂.”

The three researchers write, “the adaptation of leaf photosynthesis to elevated CO₂ was tested by a common garden experiment with herbaceous species originating from three different natural CO₂ springs in Japan: Nibu, Ryuzin-numa and Yuno-kawa,” where

“several genotypes were collected from each high-CO₂ area (spring population) and nearby control areas (control population), and each genotype was propagated or divided into two ramets, and grown in pots at 370 and 700 ppm CO₂.” The researchers assessed the plants’ photosynthetic nitrogen use efficiency (PNUE), water use efficiency (WUE), and degree of carbohydrate accumulation in the plants’ leaves, which if too large can lead to the down-regulation of photosynthesis.

Onoda *et al.* report “high CO₂ concentration directly and greatly increased PNUE and WUE, suggesting that plants will show higher growth rates at a given resource availability.” They also found “a significant reduction in stomatal conductance, which contributed to higher WUE, and a trend of reduced down-regulation of photosynthesis with a lower starch accumulation,” and they note these results suggest “there is substantial room for plant evolution in high-CO₂ environments.” Further to this point, they say a still-to-be-published molecular study “also found relatively large genetic differentiation across the CO₂ gradient in these plants.” Consequently, as a result of their own work and “the increasing number of studies on CO₂ springs (e.g. Fordham *et al.*, 1997; Polle *et al.*, 2001; Schulte *et al.* 2002) and selection experiments (Ward *et al.*, 2000; Collins and Bell, 2004),” Onoda *et al.* conclude, “high CO₂ will act as a selection agent” as the air’s CO₂ content rises. This phenomenon should enable plants to fare even better in the CO₂-enriched air of the future than they do currently.

The several observations above suggest a doubling, tripling, or even greater enhancement of the atmosphere’s CO₂ concentration will only further improve the productivity and water use efficiencies of woody plants.

References

- Bartak, M., Raschi, A., and Tognetti, R. 1999. Photosynthetic characteristics of Sun and shade leaves in the canopy of *Arbutus unedo* L. trees exposed to *in situ* long-term elevated CO₂. *Photosynthetica* **37**: 1–16.
- Collins, S. and Bell, G. 2004. Phenotypic consequences of 1000 generations of selection at elevated CO₂ in a green alga. *Nature* **431**: 566–569.
- Fernandez, M.D., Pieters, A., Donoso, C., Tezara, W., Azuke, M., Herrera, C., Rengifo, E., and Herrera, A. 1998. Effects of a natural source of very high CO₂ concentration on the leaf gas exchange, xylem water potential and stomatal characteristics of plants of *Spatiphyllum cannifolium* and *Bauhinia multinervia*. *New Phytologist* **138**: 689–697.
- Fordham, M., Barnes, J.D., Bettarini, I., Polle, A., Slee, N., Raines, C., Miglietta, F., and Raschi, A. 1997. The impact of elevated CO₂ on growth and photosynthesis in *Agrostis canina* L ssp. *monteluccii* adapted to contrasting atmospheric CO₂ concentrations. *Oecologia* **110**: 169–178.
- Kohut, R. 2003. The long-term effects of carbon dioxide on natural systems: issues and research needs. *Environment International* **29**: 171–180.
- Lau, J.A., Shaw, R.G., Reich, P.B., Shaw, F.H., and Tiffin, P. 2007. Strong ecological but weak evolutionary effects of elevated CO₂ on a recombinant inbred population of *Arabidopsis thaliana*. *New Phytologist* **175**: 351–362.
- Onoda, Y., Hirose, T., and Hikosaka, K. 2009. Does leaf photosynthesis adapt to CO₂-enriched environments? An experiment on plants originating from three natural CO₂ springs. *New Phytologist* **182**: 698–709.
- Paoletti, E., Seufert, G., Della Rocca, G., and Thomsen, H. 2007. Photosynthetic responses to elevated CO₂ and O₃ in *Quercus ilex* leaves at a natural CO₂ spring. *Environmental Pollution* **147**: 516–524.
- Polle, A., McKee, I., and Blaschke, L. 2001. Altered physiological and growth responses to elevated [CO₂] in offspring from holm oak (*Quercus ilex* L.) mother trees with lifetime exposure to naturally elevated [CO₂]. *Plant, Cell & Environment* **24**: 1075–1083.
- Rapparini, F., Baraldi, R., Miglietta, F., and Loreto, F. 2004. Isoprenoid emission in trees of *Quercus pubescens* and *Quercus ilex* with lifetime exposure to naturally high CO₂ environment. *Plant, Cell and Environment* **27**: 381–391.
- Schulte, M., Von Ballmoos, P., Rennenberg, H., and Herschbach, C. 2002. Life-long growth of *Quercus ilex* L. at natural CO₂ springs acclimates sulphur, nitrogen and carbohydrate metabolism of the progeny to elevated pCO₂. *Plant, Cell & Environment* **25**: 1715–1727.
- Schwanz, P. and Polle, A. 1998. Antioxidative systems, pigment and protein contents in leaves of adult mediterranean oak species (*Quercus pubescens* and *Q. ilex*) with lifetime exposure to elevated CO₂. *New Phytologist* **140**: 411–423.
- Thomas, S.C. and Jasienski, M. 1996. Genetic variability and the nature of microevolutionary response to elevated CO₂. In: Körner, C. and Bazzaz, F.A. (Eds.) *Carbon Dioxide, Populations and Communities*. Academic Press, Inc., San Diego, California, USA, pp. 51–81.
- Tognetti, R., Minnocci, A., Penuelas, J., Rashi, A., and Jones, M.B. 2000a. Comparative field water relations of three Mediterranean shrub species co-occurring at a natural CO₂ vent. *Journal of Experimental Botany* **51**: 1135–1146.

Tognetti, R., Rashi, A., and Jones, M.B. 2000b. Seasonal patterns of tissue water relations in three Mediterranean shrubs co-occurring at a natural CO₂ spring. *Plant, Cell and Environment* **23**: 1341–1351.

Tognetti, R., Raschi, A., and Jones M.B. 2002. Seasonal changes in tissue elasticity and water transport efficiency in three co-occurring Mediterranean shrubs under natural long-term CO₂ enrichment. *Functional Plant Biology* **29**: 1097–1106.

Ward, J.K., Antonovics, J., Thomas, R.B., and Strain, B.R. 2000. Is atmospheric CO₂ a selective agent on model C₃ annuals? *Oecologia* **123**: 330–341.

Ward, J.K. and Kelly, J.K. 2004. Scaling up evolutionary responses to elevated CO₂: lessons from *Arabidopsis*. *Ecology Letters* **7**: 427–440.

Woodward, F.I., Thompson, G.B., and McKee, I.F. 1991. The effects of elevated concentrations of carbon dioxide on individual plants, populations, communities and ecosystems. *Annals of Botany* **67**: 23–38.

1.1.5 Growth Response to Very High CO₂ Concentrations

- Several studies indicate plants are not harmed by super-elevated atmospheric CO₂ concentrations an order of magnitude or more greater than the globe's current mean. Positive growth responses are reported in all instances. Thus it is likely most plants will display enhanced rates of photosynthesis and biomass production as the atmosphere's CO₂ concentration rises.

Terrestrial plants grown in elevated atmospheric CO₂ typically exhibit increased rates of photosynthesis and biomass production. Most of the studies establishing this fact have historically utilized CO₂ concentration increases on the order of 300 to 400 ppm, which represents an approximate doubling of the atmosphere's current CO₂ concentration. This section examines the growth response of plants when the air's CO₂ content is *super*-enriched, to a concentration an order of magnitude or more larger.

Louche-Tessandier *et al.* (1999) grew potato plantlets inoculated with an arbuscular mycorrhizal fungus at ambient and super-elevated (10,000 ppm) CO₂ for one month at a number of different light intensities. They report the high CO₂ treatment stimulated root colonization by the fungus, but biomass production in the CO₂-enriched inoculated plantlets increased significantly only when they were grown at high light intensity.

Also studying potatoes, Teixeira da Silva *et al.* (2005) grew single-node explants of sweet potato (*Ipomoea batatas* cv. Naruto Kintok) for five weeks *in vitro* within special culture vessels supplied with a 3% sugar-containing agar, during which time the vessels were maintained at atmospheric CO₂ concentrations of either 400 ppm (ambient) or 1,000, 2,000, or 3,000 ppm. The plants were then transplanted into soil and grown *ex vitro* for three additional weeks. Relative to the plants exposed to ambient air, those exposed to air of 1,000, 2,000, and 3,000 ppm CO₂ produced 20%, 20%, and 65% more total biomass, respectively, after having been grown for five weeks *in vitro*, and they produced 20%, 32%, and 82% more biomass, respectively, after having been grown for three additional weeks *ex vitro*. Thus, for sweet potato plants, a several-fold increase in the atmosphere's CO₂ concentration appears to pose no problem to the plants' growth and development.

Dempster *et al.* (2009) grew a mixture of cowpeas, pinto beans, and wheat for three months, measuring the net fixation rate of carbon by the entire three-crop system during the greater portion of this "growing season." Relative to a CO₂ concentration of 385 ppm, net photosynthesis at 1,000 ppm, 2,000 ppm, and 2,800 ppm were 150%, 275%, and 355% greater, respectively. The authors note the "high productivity from these crops and the increase of fixation rates with elevated CO₂ concentration supports the concept that enhanced CO₂ can be a useful strategy for remote life support systems," presumably on long manned space flights or outposts on other planets or moons.

Schubert and Jahren (2011) grew radishes (*Raphanus sativus*) from seed to maturity (four months) in standard potting soil within eight growth chambers maintained at optimum temperature, humidity, and soil water and fertility conditions in air of eight different CO₂ concentrations (348, 388, 413, 426, 760, 1,090, 1,425, and 1,791 ppm). They then harvested the plants and determined their above- and below-ground biomass, both of which they found to be well described by a two-parameter rectangular hyperbola, "employing the method used by Hunt *et al.* (1991, 1993) for assessing the trajectory of the biomass response for 36 herbaceous species grown under CO₂ levels ranging from 365 to 812 ppm."

Going from the lowest to the highest CO₂ concentration employed in their study, the two U.S. researchers state above-ground biomass rose by a modest 58%, but below-ground biomass rose by a phenomenal 279%, the trajectory of which "greatly exceeded a trajectory based on extrapolation of

previous experiments for plants grown at CO₂ < 800 ppm.” Commenting on these findings, Schubert and Jahren state, “if the below-ground biomass enhancement that we have quantified for *R. sativus* represents a generalized root-crop response that can be extrapolated to agricultural systems, below-ground fertilization under very high CO₂ levels could dramatically augment crop production in some of the poorest nations of the world.” They continue, “needless to say, a doubling or tripling of below-ground crop tissue due to CO₂ fertilization would be welcome on both a nutritional and economic basis.”

Gouk *et al.* (1999) grew orchid plantlets at ambient and super-elevated (10,000 ppm) CO₂ for three months. In their study, the extra CO₂ more than doubled plant dry weight, stimulated the induction of new roots, increased the total chlorophyll contents of both roots and leaves, and boosted tissue starch contents nearly 20-fold, all without any disruption of or damage to chloroplasts.

Also working with orchids were Norikane *et al.* (2010), who grew *Cymbidium* (Music Hour ‘Maria’) shoots in air augmented with either 0, 3,000, or 10,000 ppm CO₂ under photosynthetic photon flux densities of either 45 or 75 $\mu\text{mol m}^{-2} \text{s}^{-1}$ provided by cold cathode fluorescent lamps for 90 days. The plants then were transferred to *ex vitro* culture for an additional 30 days. Relative to plants grown *in vitro* in ambient air, the percentage increases in shoot and root dry weight due to enriching the air in which the plants grew by 3,000 ppm CO₂ were, respectively, 216% and 1,956% under the low light regime and 249% and 1,591% under the high light regime. Corresponding increases for the plants grown in air enriched with an extra 10,000 ppm CO₂ were 244% and 2,578% under the low light regime and 310% and 1,879% under the high light regime.

In the *ex vitro* experiment, percentage increases in shoot and root dry weight due to enriching the air in which the plants grew by 3,000 ppm CO₂ were, respectively, 223% and 436% under the low light regime and 279% and 469% under the high light regime. Corresponding increases for the plants grown in air enriched with an extra 10,000 ppm CO₂ were 271% and 537% under the low light regime and 332% and 631% under the high light regime. The four Japanese researchers conclude “super-elevated CO₂ enrichment of *in vitro*-cultured *Cymbidium* could positively affect the efficiency and quality of commercial production of clonal orchid plantlets.”

Hew *et al.* (1995) grew orchids at ambient and 10,000 ppm CO₂ and found the elevated CO₂ boosted dry weights by 28 to 37%. Likewise, Tisserat *et al.*

(2002) fumigated mint and thyme with air containing 10,000 ppm CO₂ and determined the super-CO₂-enrichment increased the fresh weights of the two species by 3.1- and 5.8-fold, respectively.

In a study of an epiphytic fern, Ong *et al.* (1998) grew the seedless vascular species *Pyrrosia piloselloides* (which is less adapted to terrestrial habitats than its seed-producing relatives) from spores in small containers maintained at atmospheric CO₂ concentrations of 350, 515, and 3,360 ppm to study the effects of elevated CO₂ on the fern’s photosynthesis and growth. Forty days after germination, light-saturated rates of net photosynthesis were 22% and 114% greater at 515 and 3,360 ppm, respectively, than they were at 350 ppm. Over time, the elevated CO₂ induced photosynthetic acclimation in the plants, but in a concentration-dependent manner. After 100 days of exposure to elevated CO₂, for example, the photosynthetic stimulation of plants grown at 515 ppm CO₂ had dropped to 10%, representing a 50% decline from their original stimulation, but the photosynthetic adjustment was much less at the super-enriched CO₂ concentration of 3,360 ppm—plants in this treatment reduced their original photosynthetic enhancement by only 10%.

As part of their acclimation response to elevated CO₂, gametophytes exposed to 515 and 3,360 ppm CO₂ reallocated limiting resources away from their photosynthetic apparatus, as indicated by respective 11 and 28% reductions in their tissue chlorophyll contents. Despite these reductions, resulting from an optimization of resources at elevated CO₂ concentrations, total gametophytic dry mass at 515 and 3,360 ppm was still 43 and 214% greater, respectively, than at ambient CO₂, at physiological maturity (100 and 80 days for plants grown at 515 and 3,360 ppm CO₂, respectively).

These findings suggest Earth’s rising atmospheric CO₂ content likely will promote the photosynthesis and growth of ferns, which are considered more primitive forms of terrestrial plant life than the planet’s more-numerous seed-bearing plants. Thus, ferns should continue to maintain their presence in many ecosystems across the globe. Ong *et al.* conclude, the “sum responses of *Pyrrosia piloselloides* gametophytes to elevated CO₂ concentration suggest greater success against competitors in the future environment, enabling this fern to continue to establish itself in a future world with high atmospheric CO₂.”

Teixeira Da Silva *et al.* (2006) grew ornamental *Spathiphyllum* cv. Merry plantlets for five weeks in

novel culture vessels on a sugar-free liquid medium at low light intensity in controlled-environment chambers maintained at atmospheric CO₂ concentrations of 375, 1,000, 2,000, or 3,000 ppm. Relative to the growth experienced by the plantlets exposed to ambient air of 375 ppm CO₂, the plantlets exposed to 1,000, 2,000, and 3,000 ppm CO₂ produced 39%, 81%, and 129% more shoot dry weight, respectively, plus 316%, 639%, and 813% more root dry weight, respectively, for corresponding total CO₂-induced biomass enhancements of 61%, 127%, and 185%.

Ali *et al.* (2005) worked with the ginseng plant (*Panax ginseng*), which is widely cultivated in China, South Korea, and Japan, the roots of which have been used for medicinal purposes since Greek and Roman times and are well known for their anti-inflammatory, diuretic, and sedative properties and are also acknowledged to be effective healing agents (Gillis, 1997; Ali *et al.*, 2005). Ginseng roots normally require four to six years to accumulate the amounts of the various phenolic compounds needed to produce their health-promoting effects. In an important step toward developing an efficient culture system for the commercial production of ginseng roots, Ali *et al.* investigated the effects of growing them in suspension culture in bioreactors maintained in equilibrium with air enriched to CO₂ concentrations of 10,000 ppm, 25,000 ppm, and 50,000 ppm for periods of up to 45 days.

Of most immediate concern in such an experiment would be the effects of the ultra-high CO₂ concentrations on root growth. Would they be toxic and lead to biomass reductions or even root death? The answer was a resounding no. After 45 days of growth at 10,000 ppm CO₂, for example, root dry weight was increased by 37% relative to the dry weight of roots produced in bioreactors in equilibrium with normal ambient air. Root dry mass was increased by 27% after 45 days at 25,000 ppm CO₂, and by 9% after 45 days at 50,000 ppm CO₂. Thus, although the optimum CO₂ concentration for ginseng root growth likely resided at some value lower than 10,000 ppm in this study, the concentration at which root growth rate was reduced below that characteristic of ambient air was somewhere significantly above 50,000 ppm, for even at that extremely high CO₂ concentration, ginseng root growth was greater than in ambient air.

Almost everything else measured by Ali *et al.* was even more dramatically enhanced by the ultra-high CO₂ concentrations employed in their experiment. After 45 days of treatment, total root phenolic concentrations were 58% higher at

10,000 ppm CO₂ than at ambient CO₂, 153% higher at 25,000 ppm CO₂, and 105% higher at 50,000 ppm CO₂, as best as can be determined from the bar graphs of their results. Likewise, total root flavonoid concentrations were enhanced by 228%, 383%, and 232%, respectively, at the same ultra-high CO₂ concentrations. Total protein contents rose by 14%, 22%, and 30%; non-protein thiol contents by 12%, 43%, and 62%; and cysteine contents by 27%, 65%, and 100% under the identical respective set of conditions. There were equally large CO₂-induced increases in the activities of a large number of phenol biosynthetic enzymes.

Discussing the implications of their results, Ali *et al.* write, “the consumption of foodstuffs containing antioxidant phytonutrients such as flavonoids, polyphenolics, ascorbate, cysteine and non-protein thiol is advantageous for human health,” citing Cervato *et al.* (2000) and Noctor and Foyer (1998). They thus conclude their technique for the culture of ginseng roots in CO₂-enriched bioreactors could be used for the large-scale production of an important health-promoting product that could be provided to the public in much greater quantities than is currently possible.

Levine *et al.* (2008) grew well-watered and well-fertilized wheat plants (*Triticum aestivum*, cv Yocoro roho) from seed in custom-designed root modules—“consisting of a porous tube embedded in Turface (1–2 mm particle size) substrate containing 5 g Osmocote time release fertilizer per liter”—housed in Plexiglas chambers maintained at atmospheric CO₂ concentrations of 400, 1,500, or 10,000 ppm for periods of 14, 21, and 28 days. They measured a number of plant metabolic properties, among which were the leaf concentrations of several flavonoids capable of scavenging reactive oxygen species (ROS).

They found “elevated CO₂ promoted the accumulation of secondary metabolites (flavonoids) progressively to a greater extent as plants became mature.” As best as can be determined from the bar graphs of their results, for example, the percentage increase in total wheat leaf flavonoid concentration in going from an atmospheric CO₂ concentration of 400 to 1,500 ppm was 22%, 38%, and 27% (the one exception to this general rule) at 14, 21, and 28 days after planting, respectively. In going from a CO₂ concentration of 400 to 10,000 ppm, the percentage increase in total flavonoid concentration was 38%, 56%, and 86%, respectively, at 14, 21, and 28 days after planting. In addition, they report “both elevated CO₂ levels resulted in an overall 25% increase in biomass over the control plants.”

With respect to the cultivation of trees, Tisserat (2005) notes “vitrified shoots are characterized as being small, succulent (i.e., ‘glassy’ or ‘wet’ in appearance) and immature, but [are] capable of readily proliferating additional axillary shoots.” However, he also notes vitrified shoots of the type that are cultured *in vitro* “do not transfer readily into soil well.” Consequently, because there is a need for literally millions of sweetgum seedlings to be planted annually (Lin *et al.*, 1995), it would be advantageous if a technique could be developed to increase the success of transferring tissue-culture-produced vitrified shoots to *ex vitro* growth in soil.

In searching for a technique to accomplish this feat, Tisserat first produced sweetgum shoots in an automated plant culture system in which ten times more shoots developed than in prior plant culture systems, and where vitrification was observed in fully 80% of the shoots. He then studied the effects of ultra-high atmospheric CO₂ concentrations on the vitrified shoots when they were transferred to soil and grown in air enriched with CO₂ to concentrations as high as 30,000 ppm. After four weeks of growth at atmospheric CO₂ concentrations of 350, 1,500, 3,000, 10,000, and 30,000 ppm, survival percentages of 1cm-long explants were found to be 48.6, 56.5, 65.7, 93.1, and 67.1%, respectively, and corresponding survival percentages of 2cm-long explants were 61.2, 64.1, 69.2, 93.9, and 64.3%. For these same CO₂ concentrations, the numbers of leaves produced per shoot were 4.17, 5.38, 5.85, 6.14, and 4.83, and the numbers of roots produced per shoot were 5.35, 8.58, 9.19, 9.66, and 9.82. Also, leaf and shoot lengths were similarly enhanced by the suite of increased CO₂ concentrations.

Tisserat concludes the procedures he developed should “minimize the time and labor involved in sweetgum micropropagation” and “can be readily adapted to the micropropagation of other woody and non-woody plants.” Tisserat’s results suggest anthropogenic emissions will never raise the air’s CO₂ concentration so high as to retard the growth and development of sweetgum trees and, by implication, many (if not most) other plants. Even in those cases where plant growth responses did decline between 10,000 and 30,000 ppm in Tisserat’s study, for example, the responses at 30,000 ppm CO₂ were still greater than those observed at 350 ppm.

Tisserat and Vaughn (2003) grew four-week-old loblolly pine seedlings for 30 days at the same suite of atmospheric CO₂ concentrations within 17.6-liter transparent containers, where the seedlings were watered three times per week but not fertilized. Three

repetitions of this procedure revealed seedling fresh weight, needle number, root number, and shoot length increased 341%, 200%, 74%, and 75%, respectively, after 30 days of growth at 10,000 ppm CO₂. There were no further increases—or decreases—when going to an atmospheric CO₂ concentration of 30,000 ppm. Also, associated with increased growth and morphogenesis, the researchers found a corresponding increase in secondary metabolites (more than 99% of which were α - and β -pinene) in the ultra-high CO₂ environments, and they note “high α - and β -pinene levels may confer an additional positive survival advantage” on the seedlings, because these substances “have fungicidal and insecticidal activity (Harbone, 1982; Klepzig *et al.*, 1995).”

In a field study, Fernandez *et al.* (1998) investigated the effects of even higher CO₂ concentrations (some as great as 35,000 ppm) on an herb and a tree growing in the vicinity of natural CO₂ springs in Venezuela. These high CO₂ concentrations stimulated the photosynthetic rates of both plants in all seasons of the year. In the dry season, this effect was particularly important: Plants exposed to elevated CO₂ continued to maintain positive net photosynthetic rates, whereas those exposed to ambient air a few tens of meters away exhibited negative rates, which if prolonged, would be expected to lead to their eventual demise. The researchers thus note their work provides “a positive answer to the question of whether increases in carbon assimilation will be sustained throughout the growing season and over multiple seasons.” It also demonstrates very high atmospheric CO₂ concentrations—some as much as two orders of magnitude greater than the current global mean—are not detrimental to but in fact helped the plants they investigated.

Garcia *et al.* (1994) grew two Eldarica pine (*Pinus eldarica* L.) seedlings out-of-doors in a field of Avondale loam at Phoenix, Arizona (USA) within transparent open-top enclosures. They maintained one for 15 months at a mean atmospheric CO₂ concentration of 402 ppm and one at 788 ppm. They then measured short-term whole-tree net photosynthetic rates (one-hour averages) at a number of different CO₂ concentrations (changed at 1.5-hour intervals) ranging from ambient (360 ppm) to 3,000 ppm.

Garcia *et al.* report “the two trees responded identically to short-term atmospheric CO₂ enrichment to about a tripling of the ambient CO₂ concentration.” As the CO₂ content of the air was increased further, they write, “the net CO₂ assimilation responses of the two trees diverged: the photosynthetic response curve

of the low-CO₂-grown tree exhibited the classical form of a rate-limiting rectangular hyperbola, while that of the high-CO₂-grown tree maintained its linearity to the highest CO₂ concentration investigated.” At this latter CO₂ concentration (3,000 ppm), the photosynthetic rate of the low-CO₂-grown tree had long since plateaued at a value approximately five times its value at 360 ppm, whereas the photosynthetic rate of the high-CO₂-grown tree was still rising linearly at a value approximately ten times greater than what it had exhibited at 360 ppm. The three researchers conclude, “atmospheric CO₂ enrichment produces a type of up-regulation of carbon assimilation in Eldarica pine trees, as long-term exposure to elevated CO₂ enabled the high-CO₂-grown tree to continue to respond to further increases in the CO₂ content of the air while the photosynthetic rate of the tree grown in ambient air reached an asymptotic limit.” This observation suggests plants may continuously adapt to—and thereby continuously profit from—the ongoing increase of the air’s CO₂ content.

Tisserat *et al.* (2008) grew three types of well-watered two-week-old *Cuphea viscosissima* x *C. lanceolata* L. (McCoy GT #1, Morton GT #1, and Morris heavy) seedlings within 162-L transparent containers maintained for 30 days at atmospheric CO₂ concentrations of either 350, 1,500, 3,000, 10,000, or 30,000 ppm CO₂, after which they were harvested and assessed for a number of measures of growth. The authors report the “fresh weight of seedlings, leaves per seedling, roots per seedling, and seedling length in cuphea Morris heavy seedlings increased 607%, 184%, 784%, and 175%, respectively, after 30-day exposure to 10,000 ppm CO₂ over those obtained from seedlings grown on ambient [350 ppm] CO₂ levels,” with a leveling off of growth stimulation between 10,000 and 30,000 ppm CO₂. They further note the other two cuphea varieties “showed similar response trends.”

The three USDA Agricultural Research Service scientists say their data suggest “ultrahigh CO₂ treatments may be effective for enhancing cuphea growth and benefit breeding treatments.” In addition, their data indicate large increases in the air’s CO₂ concentration can lead to huge increases in plant growth and development.

The results of the several studies reviewed above indicate plants are not harmed by super-elevated atmospheric CO₂ concentrations an order of magnitude or more greater than the globe’s current mean. The studies all report positive growth responses, with some being particularly large, even

huge. Most plants should display enhanced rates of photosynthesis and biomass production as the atmosphere’s CO₂ concentration rises.

References

- Ali, M.B., Hahn, E.J., and Paek, K.-Y. 2005. CO₂-induced total phenolics in suspension cultures of *Panax ginseng* C.A. Mayer roots: role of antioxidants and enzymes. *Plant Physiology and Biochemistry* **43**: 449–457.
- Cervato, G., Carabelli, M., Gervasio, S., Cittera, A., Cazzola, R., and Cestaro, B. 2000. Antioxidant properties of oregano (*Origanum vulgare*) leaf extracts. *Journal of Food Biochemistry* **24**: 453–465.
- Dempster, W.F., Nelson, M., Silverstone, S., and Allen, J.P. 2009. Carbon dioxide dynamics of combined crops of wheat, cowpea, pinto beans in the Laboratory Biosphere closed ecological system. *Advances in Space Research* **43**: 1229–1235.
- Fernandez, M.D., Pieters, A., Donoso, C., Tezara, W., Azuke, M., Herrera, C., Rengifo, E., and Herrera, A. 1998. Effects of a natural source of very high CO₂ concentration on the leaf gas exchange, xylem water potential and stomatal characteristics of plants of *Spatiphyllum cannifolium* and *Bauhinia multinervia*. *New Phytologist* **138**: 689–697.
- Garcia, R.L., Idso, S.B., and Kimball, B.A. 1994. Net photosynthesis as a function of carbon dioxide concentration in pine trees grown at ambient and elevated CO₂. *Environmental and Experimental Botany* **34**: 337–341.
- Gillis, C.N. 1997. *Panax ginseng* pharmacology: a nitric oxide link? *Biochemical Pharmacology* **54**: 1–8.
- Gouk, S.S., He, J., and Hew, C.S. 1999. Changes in photosynthetic capability and carbohydrate production in an epiphytic CAM orchid plantlet exposed to super-elevated CO₂. *Environmental and Experimental Botany* **41**: 219–230.
- Harbone, J.B. 1982. *Introduction to Ecological Biochemistry*. Academic Press, New York, NY, USA.
- Hew, C.S., Hin, S.E., Yong, J.W.H., Gouk, S.S., and Tanaka, M. 1995. *In vitro* CO₂ enrichment of CAM orchid plantlets. *Journal of Horticultural Science* **70**: 721–736.
- Hunt, R., Hand, D.W., Hannah, M.A., and Neal, A.M. 1991. Response to CO₂ enrichment in 27 herbaceous species. *Functional Ecology* **5**: 410–421.
- Hunt, R., Hand, D.W., Hannah, M.A., and Neal, A.M. 1993. Further responses to CO₂ enrichment in British herbaceous species. *Functional Ecology* **7**: 661–668.

Klepzig, K.D., Kruger, E.L., Smalley, E.B., and Raffa, K.F. 1995. Effects of biotic and abiotic stress on induced accumulation of terpenes and phenolics in red pines inoculated with bark beetle-vectored fungus. *Journal of Chemical Ecology* **21**: 601–625.

Kubler, J.E., Johnston, A.M., and Raven, J.A. 1999. The effects of reduced and elevated CO₂ and O₂ on the seaweed *Lomentaria articulata*. *Plant, Cell and Environment* **22**: 1303–1310.

Levine, L.H., Kasahara, H., Kopka, J., Erban, A., Fehrl, I., Kaplan, F., Zhao, W., Littell, R.C., Guy, C., Wheeler, R., Sager, J., Mills, A., and Levine, H.G. 2008. Physiologic and metabolic responses of wheat seedlings to elevated and super-elevated carbon dioxide. *Advances in Space Research* **42**: 1917–1928.

Lin, X., Bergmann, B.A., and Stomp, A.-M. 1995. Effect of medium physical support, shoot length and genotype on *in vitro* rooting and plantlet morphology of sweetgum. *Journal of Environmental Horticulture* **13**: 117–121.

Louche-Tessandier, D., Samson, G., Hernandez-Sebastia, C., Chagvardieff, P., and Desjardins, Y. 1999. Importance of light and CO₂ on the effects of endomycorrhizal colonization on growth and photosynthesis of potato plantlets (*Solanum tuberosum*) in an *in vitro* tripartite system. *New Phytologist* **142**: 539–550.

Noctor, G. and Foyer, C.H. 1998. Ascorbate and glutathione: keeping active oxygen under control. *Annual Review of Plant Physiology and Plant Molecular Biology* **49**: 249–279.

Norikane, A., Takamura, T., Morokuma, M., and Tanaka, M. 2010. *In vitro* growth and single-leaf photosynthetic response of *Cymbidium* plantlets to super-elevated CO₂ under cold cathode fluorescent lamps. *Plant Cell Reports* **29**: 273–282.

Ong, B.-L., Koh, C.K.-K., and Wee, Y.-C. 1998. Effects of CO₂ on growth and photosynthesis of *Pyrrosia piloselloides* (L.) Price gametophytes. *Photosynthetica* **35**: 21–27.

Schubert, B.A. and Jahren, A.H. 2011. Fertilization trajectory of the root crop *Raphanus sativus* across atmospheric pCO₂ estimates of the next 300 years. *Agriculture, Ecosystems and Environment* **140**: 174–181.

Teixeira da Silva, J.A., Giang, D.T.T., and Tanaka, M. 2005. Micropropagation of sweet potato (*Ipomoea batatas*) in a novel CO₂-enriched vessel. *Journal of Plant Biotechnology* **7**: 67–74.

Teixeira Da Silva, J.A., Giang, D.T.T., and Tanaka, M. 2006. Photoautotrophic micropropagation of *Spathiphyllum*. *Photosynthetica* **44**: 53–61.

Tisserat, B. 2005. Establishing tissue-cultured sweetgum plants in soil. *HortTechnology* **15**: 308–312.

Tisserat, B. and Vaughn, S.F. 2003. Ultra-high CO₂ levels enhance loblolly pine seedling growth, morphogenesis, and secondary metabolism. *HortScience* **38**: 1083–1085.

Tisserat, B., Vaughn, S.F., and Berhow, M.A. 2008. Ultrahigh CO₂ levels enhance cuphea growth and morphogenesis. *Industrial Crops and Products* **27**: 133–135.

Tisserat, B., Vaughn, S.F., and Silman, R. 2002. Influence of modified oxygen and carbon dioxide atmospheres on mint and thyme plant growth, morphogenesis and secondary metabolism *in vitro*. *Plant Cell Reports* **20**: 912–916.

1.2 Ecosystem Responses to CO₂ Enrichment

1.2.1 Forests

Forests contain perennial trees that remove CO₂ from the atmosphere during the process of photosynthesis and store its carbon within their woody tissues for decades to periods of sometimes more than a thousand years. It is important to understand how increases in the air's CO₂ content affect forest productivity and carbon sequestration, which has a great impact on the rate of rise of the air's CO₂ concentration. The subsections below review scientific publications pertaining to these subjects.

1.2.1.1 Tropical

- Where tropical forests have not been decimated by the targeted and direct destructive actions of human society, such as the felling and burning of trees, forest productivity has been growing ever-greater with the passing of time, rising with the increasing CO₂ content of the air. This has occurred despite all concomitant changes in atmospheric, soil, and water chemistry, including twentieth century global warming, which IPCC claims to have been unprecedented over the past one to two millennia.

Perhaps the most striking evidence for the significant growth enhancement of Earth's forests being driven by the historical increase in the air's CO₂ concentration was provided by Phillips and Gentry (1994). Noting turnover rates of mature tropical forests correlate well with measures of net productivity (Weaver and Murphy, 1990), the two scientists assessed the turnover rates of 40 tropical

forests around the world in order to test the hypothesis that global forest productivity was increasing, *in situ*. They found the turnover rates of these highly productive forests had indeed been rising since at least 1960, with an apparent pan-tropical acceleration since 1980. In discussing what might have been causing this phenomenon, they state, “the accelerating increase in turnover coincides with an accelerating buildup of CO₂.” As Pimm and Sugden (1994) state in a companion article, it was “the consistency and simultaneity of the changes on several continents that [led] Phillips and Gentry to their conclusion that enhanced productivity induced by increased CO₂ is the most plausible candidate for the cause of the increased turnover.”

Four years later, Phillips *et al.* (1998) reported another impressive finding. Working with data on tree basal area (a surrogate for tropical forest biomass) for the period 1958–1996, which they obtained from several hundred plots of mature tropical trees around the world, they found the average forest biomass for the tropics as a whole had increased substantially. They calculate the increase amounted to approximately 40% of the missing terrestrial carbon sink of the entire globe. Hence, they suggest, “intact forests may be helping to buffer the rate of increase in atmospheric CO₂, thereby reducing the impacts of global climate change,” as Idso (1991a,b) had earlier suggested. Phillips *et al.* also identified the aerial fertilization effect of the increasing CO₂ concentration of the atmosphere as one of the primary factors responsible for this phenomenon. Other contemporary studies (Grace *et al.*, 1995; Malhi *et al.*, 1998) support their findings, verifying the fact neotropical forests were indeed accumulating ever-more carbon at ever-increasing rates. Phillips *et al.* (2002) subsequently suggested this phenomenon was occurring “possibly in response to the increasing atmospheric concentrations of carbon dioxide (Prentice *et al.*, 2001; Malhi and Grace, 2000).”

Lin *et al.* (1998) measured the ecosystem carbon exchange rate of a 1,700-m³ synthetic rainforest mesocosm alternately maintained at atmospheric CO₂ concentrations of either 430 or 740 ppm. This enormous study site, managed by Columbia University, was located in the 1.25 ha naturally lit Biosphere 2 research “dome,” which contained several large synthetic ecosystems enclosed by stainless steel sheets and glass. After the dome’s air was stabilized at a treatment CO₂ level for about a week, the rainforest mesocosm was isolated from the rest of the dome for one to three days so its carbon exchange rate could be measured. This work revealed

the 72% increase in atmospheric CO₂ concentration increased the daytime net ecosystem carbon exchange rate of the synthetic rainforest by 79%, without affecting the amount of carbon respired from the soil, indicating the increased carbon uptake in the CO₂-enhanced ecosystem was primarily caused by increased canopy net photosynthesis, as the elevated CO₂ had no significant effect on soil respiration.

Wurth *et al.* (1998) enclosed upper-canopy leaves of four species of trees located in a semi-deciduous tropical forest near Panama City, Republic of Panama, in small transparent cups enriched with CO₂ to about twice the current ambient concentration, to determine the effects of elevated CO₂ on sugar and starch production in the trees’ leaves. “Against expectation,” they write, they determined the elevated CO₂ caused 30 and 100% increases in leaf sugar and starch concentrations, respectively, for all four of the tropical tree species, regardless of whether they were sampled in the morning or evening or under high or low light intensities. This finding demonstrates atmospheric CO₂ enrichment can significantly stimulate individual-leaf total nonstructural carbohydrate contents in tropical tree species, even when there is a very large “sink” (the rest of the tree) to which the carbohydrates readily could be exported.

Working concurrently in Panama, Lovelock *et al.* (1998) grew ten tropical tree species in open-top chambers on the edge of a tropical forest for six months at both ambient and twice-ambient atmospheric CO₂ concentrations, to determine the effects of elevated CO₂ on them. They found the leaf starch concentrations of the trees approximately doubled in the doubled-CO₂ environment.

Lovelock *et al.* (1999b) enclosed branchlets of 30m-tall *Luehea seemannii* trees in small open-top chambers suspended within their upper canopies, and exposed them to atmospheric CO₂ concentrations of 360 or 750 ppm for nearly 40 weeks, to study the effects of elevated CO₂ on photosynthesis, growth, and reproduction in this deciduous tropical tree. They found the leaves of branchlets grown in elevated CO₂ had net photosynthetic rates approximately 30% greater than those in leaves of ambiently grown branchlets. However, the extra carbohydrates produced by this phenomenon were not used by CO₂-enriched branchlets to increase leaf growth or reproductive efforts. Instead, they were stored away in terminal woody tissues, which led the four researchers to speculate the enhanced carbohydrate storage in terminal branchlets may facilitate greater first-flush leaf growth the following year.

Breaking from experimental work to conduct a

mini-review of the scientific literature dealing with subtropical and tropical fruit tree responses to atmospheric CO₂ enrichment to that point in time, Schaffer *et al.* (1999) found exposure to elevated CO₂ concentrations significantly enhanced photosynthesis in leaves of avocado, banana, citrus, mango, and mangosteen trees. After being exposed to an atmospheric CO₂ concentration of 800 ppm for one year, for example, the leaves of mangosteen trees displayed photosynthetic rates 40 to 60% greater than rates observed in ambiently grown leaves.

In addition, atmospheric CO₂ enrichment increased biomass accumulation in each of these species, and in macadamia trees as well. In most cases, elevated CO₂ also increased total yield and fruit weight. However, when it did not immediately increase yield in avocado, mango, and macadamia, plants showed a preferential allocation of carbon belowground to their roots, suggesting “increasing water and nutrient uptake resulting from increased root mass would eventually increase assimilate partitioning to the aboveground organs,” ultimately enhancing yield.

Sheu and Lin (1999) grew 50-day-old seedlings of the subtropical tree *Schima superba* for six additional months in pots placed within glass chambers maintained at atmospheric CO₂ concentrations of 360 and 720 ppm. In addition, at each CO₂ concentration half of the seedlings were grown at an optimal day/night temperature regime of 25/20°C, and the other half were subjected to a higher temperature treatment of 30/25°C. The CO₂-enriched seedlings exhibited photosynthetic rates 20% greater than those displayed by ambiently grown trees at the original “optimal” day/night temperatures, and their photosynthetic rates were fully 40% greater than those displayed by the ambiently grown trees in the elevated temperature regime, demonstrating the optimal growth temperature for this species had to have increased with the increasing CO₂ concentration. As a result, the CO₂-enriched seedlings displayed total dry weights 14 and 49% greater than control seedlings at the lower and higher set of growth temperatures, respectively.

Lovelock *et al.* (1999a) grew seedlings of the tropical tree *Copaifera aromatica* for 50 days in pots placed in open-top chambers maintained at atmospheric CO₂ concentrations of 390 and 860 ppm. After 14 days of differential CO₂ exposure, half the seedlings in each treatment were subjected to mechanical defoliation, which removed about 40% of their leaf area and enabled the three researchers to study the influence of simulated herbivory on the CO₂

growth response of this species.

During the experiment, the seedlings grown in the elevated CO₂ treatment displayed rates of net photosynthesis between 50 and 100% greater than those of plants grown in ambient CO₂, regardless of defoliation, which had little to no impact on photosynthesis in either CO₂ treatment. Mechanical defoliation did, however, temporarily reduce seedling leaf area and leaf relative growth rates in both CO₂ environments. But by the end of the experiment, leaf relative growth rates had recovered, and there were no differences between defoliated and undefoliated seedlings in either CO₂ treatment. In contrast, the leaf area of defoliated seedlings never recovered to match undefoliated controls in either CO₂ treatment. But defoliated seedlings grown at ambient CO₂ ultimately attained leaf areas 77% of their un-defoliated controls, and those exposed to elevated CO₂ attained leaf areas 67% of their respective controls.

Despite that difference, the defoliated seedlings grown in elevated CO₂ still possessed about 20% more leaf area than the defoliated plants grown in ambient CO₂. In addition, final plant dry weight, which better represents the total impact of any stress upon a plant and indicates how well a plant is able to deal with a stress, was 15% greater in defoliated seedlings exposed to elevated CO₂ than in defoliated seedlings growing in ambient CO₂. Therefore, even with leaf destruction resulting from herbivory, *Copaifera aromatica* seedlings likely will exhibit increased photosynthetic rates and greater biomass accumulation as the air’s CO₂ content rises.

Hoffmann *et al.* (2000) germinated and grew specimens of a tree common to the Brazilian savannah (*Keilmeyera coriacea*) in controlled-environment chambers maintained at combinations of ambient (350 ppm) and elevated (700 ppm) atmospheric CO₂ concentration and low- and high-strength soil nutrient solutions. At 10 weeks post-germination, they clipped to the ground half of the seedlings in each treatment, to simulate burning and allow the five researchers to study the interactive effects of elevated CO₂ and soil nutrients on seedling growth and regrowth with and without the presence of a simulated burning event.

Among the uncut seedlings, the doubled atmospheric CO₂ treatment increased total dry weight by about 50%, and the high nutrient solution increased it by 22%, with no significant interactions between the two factors. In seedlings subjected to the simulated burning, elevated CO₂ had a significant impact on regrowth, but only in the presence of high soil nutrient availability, when it stimulated regrowth

by nearly 300%. This observation, coupled with the knowledge that large pulses of nutrients typically become available in soils following burning events, led Hoffmann *et al.* to conclude, “under elevated CO₂, enhanced growth following fire will reduce the time required for individuals to regain the pre-burn size, minimizing the negative effect of fire on population growth.” As a result, they write, “greater growth rates and higher capacities of regeneration under elevated CO₂ are expected to increase the ability of woody plants to withstand the high fire frequencies currently prevalent in moist savannahs throughout the tropics.”

Aidar *et al.* (2002) note the leguminous *Hymenaea courbaril* L. tree—which is commonly known as jatoba and grows to a height of 20 to 30 meters with a trunk diameter of 200 cm—is “a late secondary/climax species that is one of the most important trees in mature tropical forests of the Americas.” It occurs “in more than 30% of 43 inventories made in the extra-Amazonian riparian forests (Rodrigues and Nave, 2000),” they write, and it shows “wide distribution in [the] neotropics, from the Caribbean isles, Mexico and Peru to Southeastern Brazil (Allen and Allen, 1981).”

The six scientists sprouted and grew jatoba seedlings in pots placed in small open-top chambers maintained at atmospheric CO₂ concentrations of 360 and 720 ppm in a shaded glasshouse (to simulate the low light regime at the forest floor where the seeds typically germinate) for 70 days. During that time they measured rates of net photosynthesis in seedlings with and without cotyledons, which they removed from half of the plants.

These efforts revealed a persistent doubling of photosynthesis both with and without cotyledons, when the seedlings were exposed to elevated CO₂. In addition, the scientists observed a 35% increase in the water use efficiency of the seedlings. As a result, Aidar *et al.* state, “under the climatic conditions forecasted on the basis of the present carbon dioxide emissions, *Hymenaea courbaril* should establish faster in its natural environment and might also serve as an efficient mechanism of carbon sequestration within the forest.” They also opine the CO₂-induced increase in water use efficiency may enable jatoba “to tolerate dryer and more open environments, which should allow them to better cope with drought stress or a more seasonal climate.” Finally, they state the jatoba tree likely would exhibit similar positive responses to even greater emissions of CO₂ because light-saturated photosynthesis in jatoba seedlings continued to rise in response to increasing atmospheric CO₂ concentrations well above 1,000 ppm. In

addition, they report they “have measured the saturation level of some other tropical trees from the rain forest (*Caesalpinia echinata*, *Piptadenia gonoacantha*, *Tibouchina granulose*, *T. pulchra*) and all of them [also] saturate at relatively high CO₂ concentrations.” It is thus quite likely neotropical forests in general are suited to much higher-than-present atmospheric CO₂ concentrations and would fare far better than they do today in a CO₂-enriched world of the future.

Laurance *et al.* (2004a) reported accelerated growth in the 1990s relative to the 1980s for the large majority (87%) of tree genera in 18 one-hectare plots spanning an area of about 300 km² in central Amazonia, and Laurance *et al.* (2004b) observed similarly accelerated tree community dynamics in the 1990s relative to the 1980s. And in Laurance *et al.* (2005), the scientists once again suggest these “pervasive changes in central Amazonian tree communities were most likely caused by global- or regional-scale drivers, such as increasing atmospheric CO₂ concentrations (Laurance *et al.*, 2004a,b).”

Expanding upon this theme, Laurance *et al.* (2005) interpret the observed changes as “being consistent with an ecological ‘signature’ expected from increasing forest productivity (cf., Phillips and Gentry, 1994; Lewis *et al.* 2004a,b; Phillips *et al.*, 2004).” However, they note Nelson (2005) had challenged this conclusion, so Laurance *et al.* went on to consider his arguments in some detail, methodically dismantling them one by one.

Others questioned the findings of Phillips *et al.* (Sheil, 1995; Sheil and May, 1996; Condit, 1997; Clark, 2002; Clark *et al.*, 2003), and in response to these challenges, Phillips and 17 other researchers (Lewis *et al.*, 2005), including one scientist who had earlier criticized the group’s conclusions, published a new analysis vindicating their earlier results.

One of the primary criticisms of Phillips *et al.*’s findings was their meta-analyses included sites with a wide range of tree census intervals (2–38 years), which critics contended could be confounding. In their detailed study of this potential problem, however, Lewis *et al.* (2005) found a re-analysis of Phillips *et al.*’s published results shows the pan-tropical increase in turnover rates over the late twentieth century “cannot be attributed to combining data with differing census intervals.” Or as they state in another place, “the conclusion that turnover rates have increased in tropical forests over the late 20th century is robust to the charge that this is an artifact due to the combination of data that vary in census interval (cf. Sheil, 1995).”

Lewis *et al.* additionally note “Sheil’s (1995) original critique of the evidence for increasing turnover over the late 20th century also suggests that the apparent increase could be explained by a single event, the 1982–83 El Niño Southern Oscillation (ENSO), as many of the recent data spanned this event.” However, Lewis *et al.* report “recent analyses from Amazonia have shown that growth, recruitment and mortality rates have simultaneously increased within the same plots over the 1980s and 1990s, as has net above-ground biomass, both in areas largely unaffected, and in those strongly affected, by ENSO events (Baker *et al.*, 2004a; Lewis *et al.*, 2004a; Phillips *et al.*, 2004).” These developments further support the view there has been an increase in forest growth rates throughout the world that has gradually accelerated over the years in concert with the historical increase in the air’s CO₂ concentration.

In another analysis of the subject, Lewis (2006) reports, over the prior two decades, intact tropical forests had exhibited “concerted changes in their ecology, becoming, on average, faster growing—more productive—and more dynamic, and showing a net increase in above-ground biomass,” and the rates of increase of all these factors were greater than the previously documented increases. In addition, Lewis notes “preliminary analyses also suggest the African and Australian forests are showing structural changes similar to South American forests.”

As for what had been causing this suite of concerted changes, Lewis writes, “the results appear to show a coherent fingerprint of increasing net primary productivity across tropical South America, caused by a long-term increase in resource availability (Lewis *et al.*, 2004a,b).”

As to what “resources” might have been involved, Lewis postulates four possibilities: increases in solar radiation, air temperature, nutrient deposition, and atmospheric CO₂ concentration. After analyzing each of them in detail, he concludes, “the most parsimonious explanation is the increase in atmospheric CO₂, because of the undisputed long-term historical increase in CO₂ concentrations, the key role of CO₂ in photosynthesis, and the demonstrated positive effects of CO₂ fertilization on plant growth rates including experiments on whole temperate-forest stands (Ainsworth and Long, 2005).” As he states in another place in his review, the explanation resides in “the anthropogenic increase in atmospheric carbon dioxide concentrations, increasing forest net primary productivity leading to accelerated forest growth and dynamics.”

In light of the voluminous and undeniable real-

world observations Lewis reported, it is clear that where tropical forests have not been damaged by the felling and burning of trees, forest productivity has been growing ever-greater with the passing of time, rising with the increasing CO₂ content of the air. Research published since 2004 suggests this view is widely shared in the scientific community.

Working in a primary rain forest in Ariuana, Brazil, Hietz *et al.* (2005) collected samples of wood from 37 tropical cedar (*Cedrela odorata* L.) trees between 11 and 151 years old in 2001 and from 16 big-leaf mahogany (*Swietenia macrophylla* King) trees between 48 and 126 years old at that time. They then measured wood cellulose $\delta^{13}\text{C}$ in 10-year growth increments. They found cellulose $\delta^{13}\text{C}$ decreased by 1.3 per mil in *Cedrela* and by 1.1 per mill in *Swietenia* over the past century, with the largest changes occurring during the past 50 years. Based on these data and known trends in atmospheric CO₂ and $\delta^{13}\text{CO}_2$, they calculated the intrinsic water use efficiency of the trees increased by 34% in *Cedrela* and by 52% in *Swietenia* over this period, which they say is about the same as what was deduced from similar measurements of the wood of temperate trees (Freyer, 1979; Bert *et al.*, 1997; Feng, 1999). And because “water is probably not a strong limiting factor in tropical rain forest trees,” they conclude “the gain in water use efficiency translates mostly to increased carbon assimilation, which may explain the observed increase in tree growth and turnover (Phillips, 1996; Laurance *et al.*, 2004).”

Three years later, Phillips *et al.* (2008) synthesized recent observational results from the network of Amazon-forest researchers known as RAINFOR (*Red Amazonica de Inventarios Forestales*), which represents the combined long-term ecological monitoring efforts of 35 institutions from around the world, with plots spanning Amazonia “from the driest southeast to the wettest northwest and the least fertile east to the most fertile west.” The team of five researchers report finding evidence for “concerted changes in the structure, dynamics and composition of old-growth Amazonian forests in the late twentieth century,” noting “in the 1980s and 1990s, mature forests gained biomass and underwent accelerated growth and dynamics, all consistent with a widespread, long-acting stimulation of growth” that was “normally distributed” and “occurred across regions and environmental gradients and through time,” indicating “continued biomass sink strength through to the end of the century.”

In numerical terms, they state, “in the late twentieth century, biomass of trees of more than

10cm diameter increased by $0.62 \text{ t C ha}^{-1} \text{ yr}^{-1}$ averaged across the basin,” which implies “a carbon sink in Neotropical old-growth forest of at least $0.49 \text{ Pg C yr}^{-1}$.” They add, “if other biomass and necromass components are increased proportionally, then the old-growth forest sink here has been $0.79 \text{ Pg C yr}^{-1}$, even before allowing for any gains in soil carbon stocks.” This finding, they write, is “consistent with the evidence from recent global inversions of atmospheric CO_2 measurements and local aircraft measurements of atmospheric CO_2 profiles, showing that the tropics are either carbon-neutral or sink regions, despite widespread deforestation.”

As to what has been driving these changes, the five researchers state “the simplest explanation for the ensemble result—more biomass, more stems, faster recruitment, faster mortality, faster growth and more lianas—is that improved resource availability has increased net primary productivity, in turn increasing growth rates.” They conclude “the only change for which there is unambiguous evidence that the driver has widely changed and that such a change should accelerate forest growth is the increase in atmospheric CO_2 ,” because of “the undisputed long-term increase in concentrations, the key role of CO_2 in photosynthesis, and the demonstrated effects of CO_2 fertilization on plant growth rates.”

Lloyd and Farquhar (2008)—as part of an international workshop held at Oriel College, Oxford, UK, in March 2007—reviewed the effects of rising temperatures and atmospheric CO_2 concentrations on the productivity of tropical forest trees. Based on their examination of the pertinent scientific literature, and using a mixture of observations and climate model outputs together with a simple parameterization of leaf-level photosynthesis incorporating known temperature sensitivities, they could find “no evidence for tropical forests currently existing ‘dangerously close’ to their optimum temperature range.” Quite to the contrary, they state increases in photosynthetic rates associated with increases in ambient CO_2 over forthcoming decades should “more than offset” any decline in photosynthetic productivity due to higher leaf temperatures, leaf-to-air vapor pressure deficits, or autotrophic respiration rates. And they affirm “the magnitude and pattern of increases in forest dynamics across Amazonia observed over the last few decades are consistent with a CO_2 -induced stimulation of tree growth.” Thus not only have past increases in the atmosphere’s CO_2 content and temperature apparently been a boon to the productivity of Amazonia’s tropical forests—as well as the world’s other tropical forests—the materials

reviewed by these two highly regarded scientists, as well as their own original research, indicate the productivity of Earth’s tropical forests will likely rise even higher in response to predicted future increases in the atmosphere’s temperature and CO_2 concentration.

A subsequent report by Oliver L. Phillips of the UK’s University of Leeds and 65 coauthors (Phillips *et al.*, 2009) suggests a similar conclusion. The scientists note, over the prior quarter-century of intensive region-wide measurements, the productivity of the Amazon rainforest—even in its extreme old age—has been “increasing with time,” in support of which they cite the comprehensive observational studies of Phillips *et al.* (1998), Nemani *et al.* (2003), Baker *et al.* (2004a), Lewis *et al.* (2004), and Ichii *et al.* (2005). In their own new study, they find, although extremely severe drought conditions can indeed bring a halt to biomass accumulation in old growth tropical forests—and sometimes even lead to minor reductions in biomass due to selective tree mortality—the vast majority of the aged trees are able to regain their photosynthetic capability and add to their prior store of biomass once the moisture stress subsides, thanks in large measure to the enhanced growth and water use efficiency experienced by nearly all woody plants as the air’s CO_2 content rises.

Lewis *et al.* (2009) documented changes in aboveground carbon storage in 79 permanent sample plots spanning 40 years (1968–2007), located in closed-canopy moist forest, spanning West, Central, and Eastern Africa, based on data regarding more than 70,000 individual trees spread across ten countries. They found “aboveground carbon storage in live trees increased by $0.63 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ between 1968 and 2007,” and “extrapolation to unmeasured forest components (live roots, small trees, necromass) and scaling to the continent implies a total increase in carbon storage in African tropical forest trees of $0.34 \text{ Pg C year}^{-1}$.”

The 33 researchers say the observed changes in carbon storage “are similar to those reported for Amazonian forests per unit area, providing evidence that increasing carbon storage in old-growth forests is a pan-tropical phenomenon,” and “combining all standardized inventory data from this study and from tropical America and Asia together yields a comparable figure of $0.49 \text{ Mg C ha}^{-1} \text{ year}^{-1}$,” which equates to “a carbon sink of $1.3 \text{ Pg C year}^{-1}$ across all tropical forests during recent decades” and could account for roughly half of the so-called missing carbon sink.

As for the identity of the driving force that

seemed to have breathed new life into old trees, Lewis *et al.* write, in the concluding sentence of the abstract of their paper, “taxon-specific analyses of African inventory and other data suggest that widespread changes in resource availability, such as increasing atmospheric carbon dioxide concentrations, may be the cause of the increase in carbon stocks, as some theory (Lloyd and Farquhar, 1996) and models (Friedlingstein *et al.*, 2006; Stephens *et al.*, 2007; Ciais *et al.*, 2008) predict.”

Laurance *et al.* (2009) report what they learned while working within 20 one-hectare plots in approximately 300 km² of intact rainforests in the Amazon, where they evaluated forest dynamics over the period 1981–2003, based on data for 21,667 individual trees. Their “large-scale, long-term study appears to illustrate two contrasting patterns: (1) long-term trends in which tree mortality, recruitment, turnover, and basal area are progressively increasing over time in most (80–100%) of our study plots; and (2) shorter-term fluctuations in which strong pulses of tree mortality and poor growth have more transitory impacts on forest dynamics.”

With respect to the first of these findings, Laurance *et al.* note “the increasing forest dynamics, growth and basal area observed are broadly consistent with the CO₂ fertilization hypothesis.” With respect to the second finding, they state “tree mortality peaked, and tree recruitment and growth declined during atypically wet periods,” and “tree growth was fastest during dry periods, when reduced cloudiness might have increased available solar radiation.” These findings indicate the historical increase in the atmosphere’s CO₂ concentration, driven by the burning of fossil fuels, has been good for the Amazon’s trees and very likely for the rest of the region’s plants and animals, even in the face of a local warming of 0.26°C per decade reported for the region since the mid-1970s.

In assessing this latter suggestion, Lapola *et al.* (2009) used a potential vegetation model (CPTEC-PVM2) “to analyze biome distribution in tropical South America under a range of climate projections,” while taking into consideration the aerial fertilization and transpiration-reducing effects of atmospheric CO₂ enrichment. The Brazilian and German researchers say their modeling work revealed, “if the CO₂ ‘fertilization effect’ indeed takes place and is maintained in the long term in tropical forests, then it will avoid biome shifts in Amazonia in most of the climate scenarios, even if the effect of CO₂ fertilization is halved.” They state the CO₂ fertilization effect, “when fully or half considered,

overwhelms the impacts arising from temperature (in agreement with Lloyd and Farquhar, 2008) and even some of the precipitation changes projected by most of the global climate models, resulting in higher net primary production by the end of the century.”

Gloor *et al.* (2009) write, “analysis of earlier tropical plot data has suggested that large-scale changes in forest dynamics are currently occurring in Amazonia (Phillips and Gentry, 1994; Phillips *et al.*, 2004), and that an increase in aboveground biomass has occurred, with increases in mortality tending to lag increases in growth (Phillips *et al.*, 1998; Baker *et al.*, 2004a,b; Lewis *et al.*, 2004).” However, they state this conclusion has been challenged recently by what they call an overzealous application of the “Slow in, Rapid out” dictum. This concept is based on the fact forest growth is a slow process, whereas mortality can be dramatic and singular in time, such that sampling over relatively short observation periods may miss these more severe events, leading to positively biased estimates of aboveground biomass trends, when either no trend or negative trends actually exist.

In evaluating this claim, Gloor *et al.* statistically characterize “the disturbance process in Amazon old-growth forests as recorded in 135 forest plots of the RAINFOR network up to 2006,” as well as other independent research programs; and they “explored the consequences of sampling artifacts using a data-based stochastic simulator.” The researchers say this work revealed, “over the observed range of annual aboveground biomass losses, standard statistical tests show that the distribution of biomass losses through mortality follow an exponential or near-identical Weibull probability distribution and not a power law as assumed by others.” In addition, they write, “the simulator was parameterized using both an exponential disturbance probability distribution as well as a mixed exponential-power law distribution to account for potential large-scale blow-down events,” and “in both cases, sampling biases turn out to be too small to explain the gains detected by the extended RAINFOR plot network.” In light of these findings, Gloor *et al.* conclude their results lend “further support to the notion that currently observed biomass gains for intact forests across the Amazon are actually occurring over large scales at the current time, presumably as a response to climate change,” which many of their earlier papers explicitly state as including the aerial fertilization effect of the historical increase in the air’s CO₂ content.

Lewis *et al.* (2009) set out to evaluate tropical forest inventory data, plant physiology experiments, ecosystem flux observations, Earth observations,

atmospheric measurements, and dynamic global vegetation models, which, “taken together,” they write, “provide new opportunities to cross-validate results.” The five researchers confirm both theory and experiments suggest, over the past several decades, “plant photosynthesis should have increased in response to increasing CO₂ concentrations, causing increased plant growth and forest biomass.” Also in this regard, they report, “long-term plot data collectively indicate an increase in carbon storage, as well as significant increases in tree growth, mortality, recruitment, and forest dynamism.” In addition, they confirm satellite measurements “indicate increases in productivity and forest dynamism,” and “five Dynamic Global Vegetation Models, incorporating plant physiology, competition, and dynamics, all predict increasing gross primary productivity, net primary productivity, and carbon storage when forced using late-twentieth century climate and atmospheric CO₂ concentration data.” In addition, they state “the predicted increases in carbon storage via the differing methods are all of similar magnitude (0.2% to 0.5% per year).”

“Collectively,” therefore, Lewis *et al.* conclude, “these results point toward a widespread shift in the ecology of tropical forests, characterized by increased tree growth and accelerating forest dynamism, with forests, on average, getting bigger (increasing biomass and carbon storage)—results just the opposite of what IPCC predicted.

Friend (2010) worked with the Hybrid6.5 model of terrestrial primary production, which simulates the carbon, nitrogen, phosphorus, water and energy fluxes, and structural changes in terrestrial ecosystems at hourly to decadal timescales and at spatial scales ranging from individual plants to the whole Earth, while employing the climate change anomalies predicted by the GISS-AOM GCM under the A1B emissions scenario for the 2090s relative to observed modern climate. With atmospheric CO₂ increased from 375.7 ppm to 720 ppm—a 92% increase—Friend calculated the percentage changes in terrestrial plant production that would occur throughout the world in response to (1) the projected climate changes alone and (2) the projected concurrent changes in climate and atmospheric CO₂ concentration.

In response to the projected climate changes alone between 2001–2010 and 2091–2100, the net primary production (NPP) of the entire planet was reduced by 2.5%, with the largest negative impacts occurring over southern Africa, central Australia, northern Mexico, and the Mediterranean region,

where reductions of more than 20% were common. At the other extreme, climatic impacts were modestly positive throughout most of the world’s boreal forests, as might have been expected when these colder regions received an influx of welcome heat.

But when both climate and atmospheric CO₂ concentrations were changed concurrently, the story was vastly different, with a mean increase in global NPP of 37.3%, driven by mean increases of 43.9–52.9% among C₃ plants and 5.9% among C₄ species. In this case of concurrent increases in the globe’s air temperature and CO₂ concentration, the largest increases occurred in tropical rainforests and C₃ grass and croplands.

Jaramillo *et al.* (2010) looked back in time—way back in time—to the days of the Paleocene-Eocene Thermal Maximum (PETM) of some 56 million years ago, which they note “was one of the most abrupt global warming events of the past 65 million years (Kennett and Stott, 1991; Zachos *et al.*, 2003; Westerhold *et al.*, 2009).” It was driven, as they describe it, by “a massive release of ¹³C-depleted carbon (Pagani *et al.*, 2006; Zeebe *et al.*, 2009)” that led to “an approximate 5°C increase in mean global temperature in about 10,000 to 20,000 years (Zachos *et al.*, 2003).” During this period of warming, according to many scientists, Earth’s tropical ecosystems “suffered extensively because mean temperatures are surmised to have exceeded the ecosystems’ heat tolerance (Huber, 2008).”

In an attempt to discover whether that warming did major damage to rainforests, the 29 researchers from eight countries analyzed pollen and spore contents and the stable carbon isotopic composition of organic materials obtained from three tropical terrestrial PETM sites in eastern Colombia and western Venezuela. Their work reveals—contrary to the prevailing wisdom of the recent past—the onset of the PETM was “concomitant with an increase in diversity produced by the addition of many taxa (with some representing new families) to the stock of preexisting Paleocene taxa.” And they report this increase in biodiversity “was permanent and not transient.”

In discussing their findings, Jaramillo *et al.* write, “today, most tropical rainforests are found at mean annual temperatures below 27.5°C,” and they note several scientists have argued “higher temperatures could be deleterious to the health of tropical ecosystems,” citing Huber (2008, 2009) and Tewksbury *et al.* (2008) in this regard. They report tropical warming during the PETM was postulated to have produced intolerable conditions for tropical

ecosystems. Nevertheless, they reiterate, at the sites they studied, “tropical forests were maintained during the warmth of the PETM (~31° to 34°C),” concluding “it is possible that higher Paleocene CO₂ levels (Royer, 2010) contributed to their success.”

Rasineni *et al.* (2011a) introduce their study by explaining “excess light limits photosynthesis by photoinhibition, resulting in reduced carbon gain and also causing photo-damage (Oquist and Huner, 1993; Pastenes *et al.*, 2003; Allakhverdiev and Murata, 2004; Nishiyama *et al.*, 2006),” and “plants grown in tropical climates usually experience significantly high irradiance leading to the strong midday depression of photosynthesis (Hymus *et al.*, 2001).”

To investigate how this problem might be overcome, the authors conducted an experiment utilizing two open-top chambers in the Botanical Gardens of the University of Hyderabad, India. Each chamber contained four six-month-old specimens of the fast-growing tropical *Gmelina arborea* tree, which they maintained at optimum moisture and nutrient levels. During the course of their experiment the three scientists measured several plant physiological properties and processes related to leaf photosynthesis and photosystem II (PSII) photochemistry and photoinhibition at both ambient and elevated CO₂ concentrations (360 and 460 ppm, respectively), working with “well-expanded and light-exposed leaves randomly chosen from the upper half of the plant canopy.”

Their work revealed no significant differences in CO₂ assimilation rates between the ambient- and elevated CO₂-grown plants during early morning hours; but thereafter, they report, “photosynthesis typically maximized between 0900 hours and 1000 hours in both ambient and elevated CO₂-grown plants,” which experienced net photosynthetic rates of 20 and 32.5 $\mu\text{mol}/\text{m}^2/\text{s}$, respectively, for a CO₂-induced enhancement of 62%. For the more standard CO₂ enrichment of 300 ppm, that would be roughly equivalent to an enhancement of 180%. Subsequently, during the following midday period of 1100–1300 hours, the rate of net photosynthesis was still significantly enhanced by about 37% (roughly equivalent to a 300-ppm-induced increase of more than 100%) in the elevated CO₂ treatment, after which the difference between the net photosynthetic rates of the two CO₂ treatments once again became insignificant. Noting the “elevated CO₂ treatment mitigated PSII-photoinhibition through enhanced electron transport rates and through efficient biochemical reactions in leaves of *G. arborea*,” Rasineni *et al.* conclude their data “demonstrate that

future increases in atmospheric CO₂ may have positive effects on photochemical efficiency in fast growing tropical tree species,” allowing them to take great advantage of the high-light midday period of potential maximum growth in Earth’s tropical regions.

Bonal *et al.* (2011) introduce their work by writing, “an increase in tree radial growth increment over recent decades in Amazonian tropical rainforests has been observed, leading to increased above-ground biomass at most study sites,” citing Phillips *et al.* (1998, 2009) and Malhi *et al.* (2004), noting “the stimulating impact on photosynthesis of increased CO₂ concentrations in the air (C_a) could explain these growth patterns (Lloyd and Farquhar, 2008).” Further investigating this phenomenon, the 11 researchers assessed the impacts of historical environmental changes on several leaf morphological and physiological traits of two tropical rainforest species (*Dicorynia guianensis*; *Humiria balsamifera*) abundant in the Guiana shield (Northern Amazonia), working with leaf samples from different international herbariums that covered a 200-year time period (AD 1790–2004).

Bonal *et al.* state their results revealed “a clear response of leaf physiological characteristics to increasing C_a for both species,” consistent with previous studies “from different ecosystems (Penuelas and Azcon-Bieto, 1992; Beerling *et al.*, 1993; Van de Water *et al.*, 1994; Pedicino *et al.*, 2002; Penuelas *et al.*, 2008), and with data from tree rings in Europe (Bert *et al.*, 1997; Duquesnay *et al.*, 1998; Saurer *et al.*, 2004), Africa (Gebrekirstos *et al.*, 2009) and in tropical rainforests (Hietz *et al.*, 2005; Silva *et al.*, 2009; Nock *et al.*, 2011).” More specifically, they say their results point to “an increase in water use efficiency over recent decades of about 23.1 and 26.6% for *Humiria* and *Dicorynia*, respectively,” driven mostly by increases in leaf photosynthesis. And they state “the range of change in water use efficiency for these two species was consistent with many results observed not only in tropical forests (Hietz *et al.*, 2005; Nock *et al.*, 2011), but in boreal (Saurer *et al.*, 2004) and temperate forests (Francey and Farquhar, 1982; Penuelas and Azcon-Bieto, 1992; Bert *et al.*, 1997; Duquesnay *et al.*, 1998).” Bonal *et al.* conclude the responses of the two tree species they studied to increasing C_a appear to be “simply related to the availability of CO₂ in the air (fertilization effect),” and “this trend seems to be consistent with recent tree growth patterns in the Amazonian region.”

Rasineni *et al.* (2011b) describe growing well-watered and -fertilized five-week-old fast-growing

Gmelina arborea trees out-of-doors at the University of Hyderabad, India, in open-top chambers maintained at ambient and ambient+100 ppm atmospheric CO₂ concentrations throughout the 120 days of that region's spring and summer seasons, while they periodically made numerous measurements of the trees' physical properties and physiological prowess. The trees in the modestly elevated CO₂ chambers exhibited net photosynthetic rates 38% greater than the trees growing in ambient air. Also, aided by a significant CO₂-induced reduction in leaf transpiration rates, the mean instantaneous water use efficiency of the leaves of the CO₂-enriched trees was 87% greater than the ambient-treatment trees. As a result of these CO₂-induced plant physiological benefits, the above-ground biomass of the CO₂-enriched trees at the end of the growing season was 45% greater than the trees growing in ambient air, and their total biomass (above and below ground) was 53% higher.

In discussing their findings, Rasineni *et al.* note elevated atmospheric CO₂ "persistently enhanced all the growth characteristics in *Gmelina*, including plant height, number of branches, internodes, internodal distance, aerial biomass and total plant biomass." They suggest "high sink demand and better growth dynamics" are what led to the huge sustained increase in carbon sequestration in the tropical deciduous tree. They conclude their findings indicate "there are management options for creating short-rotation deciduous tree plantations to achieve increased sequestration of carbon in a future elevated CO₂ environment."

Dick *et al.* (2012) introduce the final study we review here by noting, "tropical rain forest has been a persistent feature in South America for at least 55 million years" and "at times in the past, Amazon surface air temperatures have been higher than those today," citing Feely and Silman (2010), Hoorn *et al.* (2010), Jaramillo *et al.* (2010), and Haywood *et al.* (2011). They also report "experiments show that tropical plants can photosynthesize and maintain a positive carbon balance under higher temperatures than those occurring today (Krause *et al.*, 2010; Way and Oren, 2010)." So the question naturally arises: How high can Amazon temperatures rise and its trees still survive?

Dick *et al.* hypothesize "the older the age of a species prior to the Pleistocene, the warmer the climate it has previously survived," noting Pliocene and late-Miocene air temperatures of 2.6 to 5 million years ago (Ma) and late-Miocene air temperatures of 8 to 10 Ma across Amazonia were "similar to AD

2100 temperature projections under low and high carbon emission scenarios, respectively." They note "some 56.3 Ma during the Paleocene-Eocene Thermal Maximum (PETM), global mean temperature increased by 5–6°C over a period of ≤ 20 ka," citing Haywood *et al.* (2011). And they affirm "fossil pollen from the PETM showed an increase in tree diversity in three South American rainforest sites with abundant rainfall (Jaramillo *et al.*, 2010)." Thus they used comparative phylogeographic analyses to determine the age of the tropical tree *species* currently found in Amazonia. The four researchers report, "9 of 12 widespread Amazon tree species have Pliocene or earlier lineages (>2.6 Ma), with seven dating from the Miocene (>5.6 Ma) and three >8 Ma."

Based on these findings, Dick *et al.* conclude "the remarkably old age of these species suggests that Amazon forests passed through warmth similar to AD 2100 levels [predicted by climate models] and that in the absence of other major environmental changes, near-term high temperature-induced mass species extinction is unlikely."

These and the many other positive findings of the studies reviewed above indicate rising atmospheric CO₂ concentrations probably will enhance the rates of photosynthesis and biomass production of tropical and sub-tropical trees, even under conditions of herbivory, water stress, and elevated air temperature. That, in turn, likely will allow greater sequestration of carbon in Earth's tropical and sub-tropical forests.

References

- Aidar, M.P.M., Martinez, C.A., Costa, A.C., Costa, P.M.F., Dietrich, S.M.C., and Buckeridge, M.S. 2002. Effect of atmospheric CO₂ enrichment on the establishment of seedlings of jatoba, *Hymenaea courbaril* L. (Leguminosae, Caesalpinioideae). *Biota Neotropica* 2: BN01602012002.
- Allakhverdiev, S.I. and Murata, N. 2004. Environmental stress inhibits the synthesis de novo of proteins involved in the photodamage-repair cycle of photosystem II in *Synechocystis* sp. PCC 6803. *Biochimica et Biophysica Acta* 1657: 23–32.
- Allen, O.N. and Allen, E.K. 1981. *The Leguminosae*. The University of Wisconsin Press, Madison, Wisconsin, USA, pp. 337–338.
- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Núñez Vargas, P., Pitman, N.C.A., Silva, J.N.M., and Vásquez Martínez, R. 2004a. Increasing

- biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* **359**: 353–365.
- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neil, D.A., Patiño, S., Pitman, N.C.A., Silva, J.M.N., and Vásquez Martínez, R. 2004b. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology* **10**: 545–562.
- Beerling, D.J., Matthey, D.P., and Chaloner, W.G. 1993. Shifts in the $\delta^{13}\text{C}$ composition of *Salix herbacea* L. leaves in response to spatial and temporal gradients of atmospheric CO₂ concentration. *Proceedings of the Royal Society of London* **253**: 53–60.
- Bert, D., Leavitt, S.W., and Dupouey, J.L. 1997. Variations of wood $\delta^{13}\text{C}$ and water use efficiency of *Abies alba* during the last century. *Ecology* **78**: 1588–1596.
- Bonal, D., Ponton, S., Le Thiec, D., Richard, B., Ningre, N., Herault, B., Ogee, J., Gonzalez, S., Pignat, M., Sabatier, D., and Guehl, J.-M. 2011. Leaf functional response to increasing atmospheric CO₂ concentrations over the last century in two northern Amazonian tree species: a historical $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ approach using herbarium samples. *Plant, Cell and Environment* **34**: 1332–1344.
- Ciais, P., Piao, S.-L., Cadule, P., Friedlingstein, P., and Chedin, A. 2008. Variability and recent trends in the African carbon balance. *Biogeosciences* **5**: 3497–3532.
- Clark, D.A. 2002. Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. *Ecological Applications* **12**: 3–7.
- Clark, D.A., Piper, S.C., Keeling, C.D., and Clark, D.B. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences, USA* **100**: 10.1073/pnas.0935903100.
- Condit, R. 1997. Forest turnover, density, and CO₂. *Trends in Ecology and Evolution* **12**: 249–250.
- Dick, C.W., Lewis, S.L., Maslin, M., and Bermingham, E. 2012. Neogene origins and implied warmth tolerance of Amazon tree species. *Ecology and Evolution* **3**: 162–169.
- Duquesnay, A., Breda, N., Stievenard, M., and Dupouey, J.L. 1998. Changes of tree-ring $\delta^{13}\text{C}$ and water use efficiency of beech (*Fagus sylvatica* L.) in north-eastern France during the past century. *Plant, Cell and Environment* **21**: 565–572.
- Feeley, K.J. and Silman, M.R. 2010. Biotic attrition from tropical forests correcting for truncated temperature niches. *Global Change Biology* **16**: 1830–1836.
- Feng, X. 1999. Trends in intrinsic water use efficiency of natural trees for the past 100–200 years: a response to atmospheric CO₂ concentration. *Geochimica et Cosmochimica Acta* **63**: 1891–1903.
- Francey, R.J. and Farquhar, G.D. 1982. An explanation of $^{13}\text{C}/^{12}\text{C}$ variations in tree rings. *Nature* **297**: 28–31.
- Freyer, H.D. 1979. On the ^{13}C record in tree rings. Part I. ^{13}C variations in northern hemispheric trees during the last 150 years. *Tellus* **31**: 124–137.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H.D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K.-G., Schnur, R., Strassmann, K., Weaver, A.J., Yoshikawa, C., and Zeng, N. 2006. Climate-carbon cycle feedback analysis: Results from the (CMIP)-M-4 model intercomparison. *Journal of Climate* **19**: 3337–3353.
- Friend, A.D. 2010. Terrestrial plant production and climate change. *Journal of Experimental Botany* **61**: 1293–1309.
- Gebrekirstos, A., Worbes, M., Teketay, D., Fetene, M., and Mitlohner, R. 2009. Stable carbon isotope ratios in tree rings of co-occurring species from semi-arid tropics in Africa: patterns and climatic signals. *Global and Planetary Change* **66**: 253–260.
- Gloor, M., Phillips, O.L., Lloyd, J.J., Lewis, S.L., Malhi, Y., Baker, T.R., Lopez-Gonzalez, G., Peacock, J., Almeida, S., Alves de Oliveira, A.C., Alvarez, E., Amaral, I., Arroyo, L., Aymard, G., Banki, O., Blanc, L., Bonal, D., Brando, P., Chao, K.-J., Chave, J., Davila, N., Erwin, T., Silva, J., DiFiore, A., Feldpausch, T.R., Freitzs, A., Herrera, R., Higuchi, N., Honorio, E., Jimenez, E., Killeen, T., Laurance, W., Mendoza, C., Monteagudo, A., Andrade, A. Neill, D., Nepstad, D., Nunez Vargas, P., Penuela, M.C., Pena Cruz, A., Prieto, A., Pitman, N., Quesada, C., Salomao, R., Silveira, M., Schwarz, M., Stropp, J., Ramirez, F., Ramirez, H., Rudas, A., ter Steege, H., Silva, N., Torres, A., Terborgh, J., Vasquez, R., and van der Heijden, G. 2009. Does the disturbance hypothesis explain the biomass increase in basin-wide Amazon forest plot data? *Global Change Biology* **15**: 2418–2430.
- Grace, J., Lloyd, J., McIntyre, J., Miranda, A.C., Meir, P., Miranda, H.S., Nobre, C., Moncrieff, J., Massheder, J., Malhi, Y., Wright, I., and Gash, J. 1995. Carbon dioxide uptake by an undisturbed tropical rain-forest in Southwest Amazonia, 1992–1993. *Science* **270**: 778–780.
- Haywood, A.M., Ridgwell, A., Lunt, D.J., Hill, D.J., Pound, M.J., Dowsett, H.J., Dolan, A.M., Francis, J.E., and Williams, M. 2011. Are there pre-Quaternary geological analogues for a future greenhouse warming? *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **369**: 933–956.
- Hietz, P., Wanek, W., and Dunisch, O. 2005. Long-term

Climate Change Reconsidered II: Biological Impacts

trends in cellulose $\delta^{13}\text{C}$ and water use efficiency of tropical *Cedrela* and *Swietenia* from Brazil. *Tree Physiology* **25**: 745–752.

Hoffmann, W.A., Bazzaz, F.A., Chatterton, N.J., Harrison, P.A., and Jackson, R.B. 2000. Elevated CO_2 enhances resprouting of a tropical savanna tree. *Oecologia* **123**: 312–317.

Hoorn, C., Wesselingh, F.P., ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartin, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Sarkinen, T., and Antonelli, A. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* **330**: 927–931.

Huber, M. 2008. A hotter greenhouse? *Science* **321**: 353–354.

Huber, M. 2009. Snakes tell a torrid tale. *Nature* **457**: 669–670.

Hymus, G.J., Baker, N.R., and Long, S.P. 2001. Growth in elevated CO_2 can both increase and decrease photochemistry and photoinhibition of photosynthesis in a predictable manner. *Dactylis glomerata* growth in two levels of nitrogen nutrition. *Plant Physiology* **127**: 1204–1211.

Ichii, K., Hashimoto, H., Nemani, R., and White, M. 2005. Modeling the interannual variability and trends in gross and net primary productivity of tropical forests from 1982 to 1999. *Global and Planetary Change* **48**: 274–286.

Idso, S.B. 1991a. The aerial fertilization effect of CO_2 and its implications for global carbon cycling and maximum greenhouse warming. *Bulletin of the American Meteorological Society* **72**: 962–965.

Idso, S.B. 1991b. Reply to comments of L.D. Danny Harvey, Bert Bolin, and P. Lehmann. *Bulletin of the American Meteorological Society* **72**: 1910–1914.

Jaramillo, C., Ochoa, D., Conteras, L., Pagani, M., Carvajal-Ortiz, H., Pratt, L.M., Krishnan, S., Cardona, A., Romero, M., Quiroz, L., Rodriguez, G., Rueda, M.J., de la Parra, F., Moron, S., Green, W., Bayona, G., Montes, C., Quintero, O., Ramirez, R., Mora, G., Schouten, S., Bermudez, H., Navarrete, R., Parra, F., Alvaran, M., Osorno, J., Crowley, J.L., Valencia, V., and Vervoort, J. 2010. Effects of rapid global warming at the Paleocene-Eocene boundary on neotropical vegetation. *Science* **330**: 957–961.

Kennett, J.P. and Stott, L.D. 1991. Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene. *Nature* **353**: 225–229.

Krause, G.H., Winter, K., Krause, B., Jahns, P., Garcia, M., Aranda, J., and Virgo, A. 2010. High-temperature tolerance

of a tropical tree, *Ficus insipida*: methodological reassessment and climate change considerations. *Functional Plant Biology* **37**: 890–900.

Lapola, D.M., Oyama, M.D., and Nobre, C.A. 2009. Exploring the range of climate biome projections for tropical South America: The role of CO_2 fertilization and seasonality. *Global Biogeochemical Cycles* **23**: 10.1029/2008GB003357.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Condit, R., D'Angelo, S., and Andrade, A. 2004b. Inferred longevity of Amazonian rainforest trees based on a long-term demographic study. *Forest Ecology and Management* **190**: 131–143.

Laurance, W.F., Oliveira, A.A., Laurance, S.G., Condit, R., Dick, C.W., Andrade, A., Nascimento, H.E.M., Lovejoy, T.E., and Ribeiro, J.E.L.S. 2005. Altered tree communities in undisturbed Amazonian forests: A consequence of global change? *Biotropica* **37**: 160–162.

Laurance, W.F., Oliveira, A.A., Laurance, S.G., Condit, R., Nascimento, H.E.M., Sanchez-Thorin, A.C., Lovejoy, T.E., Andrade, A., D'Angelo, S., and Dick, C. 2004a. Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* **428**: 171–175.

Lewis, S.L. 2006. Tropical forests and the changing Earth system. *Philosophical Transactions of the Royal Society B* **361**: 195–210.

Lewis, S.L., Lloyd, J., Sitch, S., Mitchard, E.T.A., and Laurance, W.F. 2009. Changing ecology of tropical forests: Evidence and drivers. *Annual Review of Ecology, Evolution, and Systematics* **40**: 529–549.

Lewis, S.L., Lopez-Gonzalez, G., Sonke, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo K., M.-N., Ewango, C.E.N., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J.C., Makana, J.-R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K. S.-H., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R., and Woll, H. 2009. Increasing carbon storage in intact African tropical forests. *Nature* **457**: 1003–1006.

Lewis, S.L., Malhi, Y., and Phillips, O.L. 2004b. Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* **359**: 437–462.

Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W.F., Neill, D.A., Silva, J.N.M., Terborgh, J., Lezama, A.T., Vásquez Martinez, R., Brown, S., Chave, J., Kuebler, C., Núñez Vargas, P., and Vinceti, B. 2004a. Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical*

Transactions of the Royal Society of London Series B—Biological Sciences **359**: 421–436.

Lewis, S.L., Phillips, O.L., Sheil, D., Vinceti, B., Baker, T.R., Brown, S., Graham, A.W., Higuchi, N., Hilbert, D.W., Laurance, W.F., Lejoly, J., Malhi, Y., Monteagudo, A., Vargas, P.N., Sonke, B., Nur Supardi, M.N., Terborgh, J.W., and Vasquez, M.R. 2005. Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary. *Journal of Ecology* **92**: 929–944.

Lin, G., Marino, B.D.V., Wei, Y., Adams, J., Tubiello, F., and Berry, J.A. 1998. An experimental and modeling study of responses in ecosystems carbon exchanges to increasing CO₂ concentrations using a tropical rainforest mesocosm. *Australian Journal of Plant Physiology* **25**: 547–556.

Lloyd, J. and Farquhar, G.D. 2008. Effects of rising temperatures and [CO₂] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B* **363**: 1811–1817.

Lovelock, C.E., Posada, J., and Winter, K. 1999a. Effects of elevated CO₂ and defoliation on compensatory growth and photosynthesis of seedlings in a tropical tree, *Copaifera aromatica*. *Biotropica* **31**: 279–287.

Lovelock, C.E., Virgo, A., Popp, M., and Winter, K. 1999b. Effects of elevated CO₂ concentrations on photosynthesis, growth and reproduction of branches of the tropical canopy trees species, *Luehea seemannii* Tr. & Planch. *Plant, Cell and Environment* **22**: 49–59.

Lovelock, C.E., Winter, K., Mersits, R., and Popp, M. 1998. Responses of communities of tropical tree species to elevated CO₂ in a forest clearing. *Oecologia* **116**: 207–218.

Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C.I., Di Fiore, A., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Montoya, L.M.M., Agudo, A., Neill, D.A., Vargas, P.N., Patino, S., Pitman, N.C.A., Quesadah, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Martinez, R.V., Terborgh, J., Vinceti, B., and Lloyd, J. 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology* **10**: 563–591.

Malhi, Y. and Grace, J. 2000. Tropical forests and atmospheric carbon dioxide. *Trends in Ecology and Evolution* **15**: 332–337.

Malhi, Y., Nobre, A.D., Grace, J., Kruijt, B., Pereira, M.G.P., Culf, A., and Scott, S. 1998. Carbon dioxide transfer over a Central Amazonian rain forest. *Journal of Geophysical Research* **103**: 31,593–31,612.

Nelson, B.W. 2005. Pervasive alteration of tree communities in undisturbed Amazonian forests. *Biotropica* **37**: 158–159.

Nemani, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneni, R.B., and Running, S.W. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* **300**: 1560–1563.

Nishiyama, Y., Allakhverdiev, S.I., and Murata, N. 2006. A new paradigm for the action of reactive oxygen species in the photoinhibition of photosystem II. *Biochimica et Biophysica Acta* **1757**: 742–749.

Nock, C.A., Baker, P.J., Wanek, W., Albrecht, L., Grabner, M., Bunyavejchewin, S., and Hietz, P. 2011. Long-term increases in intrinsic water use efficiency do not lead to increased stem growth in a tropical monsoon forest in western Thailand. *Global Change Biology* **17**: 1049–1063.

Oquist, G. and Huner, N.P.A. 1993. Cold-hardening-induced resistance to photoinhibition of photosynthesis in winter rye is dependent upon an increased capacity for photosynthesis. *Planta* **189**: 150–156.

Pagani, M., Caldeira, K., Archer, D., and Zachos, J.C. 2006. An ancient carbon mystery. *Science* **314**: 1556–1557.

Pastenes, C., Santa-Maria, E., Infante, R., and Franck, N. 2003. Domestication of the Chilean guava (*Ugni molinae* Turcz.), a forest understory shrub, must consider light intensity. *Scientia Horticulturae* **98**: 71–84.

Pedicino, L., Leavitt, S.W., Betancourt, J.L., and Van De Water, P.K. 2002. Historical variations in $\delta^{13}\text{C}$ leaf of herbarium specimens on the Southwestern U.S. *Western North American Naturalist* **62**: 348–359.

Penulas, J. and Azcon-Bieto, J. 1992. Changes in leaf $\delta^{13}\text{C}$ of herbarium plant species during the last 3 centuries of CO₂ increase. *Plant, Cell and Environment* **15**: 485–489.

Penuelas, J., Hunt, J.M., Ogaya, R., and Jump, A.S. 2008. Twentieth century changes of tree-ring $\delta^{13}\text{C}$ at the southern range-edge of *Fagus sylvatica*: increasing water use efficiency does not avoid the growth decline induced by warming at low altitudes. *Global Change Biology* **14**: 1076–1088.

Phillips, O.L. 1996. Long-term environmental change in tropical forests: increasing tree turnover. *Environmental Conservation* **23**: 235–248.

Phillips, O.L., Aragao, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., Lopez-Gonzalez, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Banki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., de Oliveira, A.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jimenez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patino, S., Penuela, M.C., Prieto, A., Ramirez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., ter Steege, H., Stropp, J., Vasquez, R., Zelazowski, P., Davila,

Climate Change Reconsidered II: Biological Impacts

- E.A., Andelman, S., Andrade, A., Chao, K.-J., Erwin, T., Di Fiore, A., Honorio C., E., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C.A., Vargas, P.N., Ramirez-Angulo, H., Rudas, A., Salamao, R., Silva, N., Terborgh, J., and Torres-Lezama, A. 2009. Drought sensitivity of the Amazon rainforest. *Science* **323**: 1344–1347.
- Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D.A., Núñez Vargas, P., Silva, J.N.M., Terborgh, J., Vásquez Martínez, R., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patiño, S., Pitman, N.C.A., Quesada, C.A., Saldias, M., Torres Lezama, A., and Vinceti, B. 2004. Pattern and process in Amazon tree turnover: 1976–2001. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* **359**: 381–407.
- Phillips, O.L. and Gentry, A.H. 1994. Increasing turnover through time in tropical forests. *Science* **263**: 954–958.
- Phillips, O.L., Lewis, S.L., Baker, T.R., Chao, K.-J., and Higuchi, N. 2008. The changing Amazon forest. *Philosophical Transactions of the Royal Society B* **363**: 1819–1827.
- Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Nunez, P.V., Vasquez, R.M., Laurance, S.G., Ferreira, L.V., Stern, M., Brown, S., and Grace, J. 1998. Changes in the carbon balance of tropical forests: Evidence from long-term plots. *Science* **282**: 439–442.
- Phillips, O.L., Malhi, Y., Vinceti, B., Baker, T., Lewis, S.L., Higuchi, N., Laurance, W.F., Vargas, P.N., Martinez, R.V., Laurance, S., Ferreira, L.V., Stern, M., Brown, S., and Grace, J. 2002. Changes in growth of tropical forests: Evaluating potential biases. *Ecological Applications* **12**: 576–587.
- Pimm, S.L. and Sugden, A.M. 1994. Tropical diversity and global change. *Science* **263**: 933–934.
- Prentice, I.C., Farquhar, G.D., Fasham, M.J.R., Goulden, M.L., Heimann, M., Jaramillo, V.J., Kheshgi, H.S., Le Quere, C., Scholes, R.J., Wallace, D.W.R., Archer, D., Ashmore, M.R., Aumont, O., Baker, D., Battle, M., Bender, M., Bopp, L.P., Bousquet, P., Caldeira, K., Ciais, P., Cox, P.M., Cramer, W., Dentener, F., Enting, I.G., Field, C.B., Friedlingstein, P., Holland, E.A., Houghton, R.A., House, J.I., Ishida, A., Jain, A.K., Janssens, I.A., Joos, F., Kaminski, T., Keeling, C.D., Keeling, R.F., Kicklighter, D.W., Hohfeld, K.E., Knorr, W., Law, R., Lenton, T., Lindsay, K., Maier-Reimer, E., Manning, A.C., Mearns, R.J., McGuire, A.D., Melillo, J.M., Meyer, R., Mund, M., Orr, J.C., Piper, S., Plattner, K., Rayner, P.J., Sitch, S., Slater, R., Taguchi, S., Tans, P.P., Tian, H.Q., Weirig, M.F., Whorf, T., and Yool, A. 2001. The carbon cycle and atmospheric carbon dioxide. Chapter 3 of the Third Assessment Report of the Intergovernmental Panel on Climate Change. *Climate Change 2001: The Scientific Basis*. Cambridge University Press, Cambridge, UK, pp. 183–238.
- Rasineni, G.K., Guha, A., and Reddy, A.R. 2011a. Elevated atmospheric CO₂ mitigated photoinhibition in a tropical tree species, *Gmelina arborea*. *Journal of Photochemistry and Photobiology B: Biology* **103**: 159–165.
- Rasineni, G.K., Guha, A., and Reddy, A.R. 2011b. Responses of *Gmelina arborea*, a tropical deciduous tree species, to elevated atmospheric CO₂: Growth, biomass productivity and carbon sequestration efficacy. *Plant Science* **181**: 428–438.
- Royer, D.L. 2010. Fossil soils constrain ancient climate sensitivity. *Proceedings of the National Academy of Sciences, USA* **107**: 517–518.
- Saurer, M., Siegwolf, R.T.W., and Schweingruber, F.H. 2004. Carbon isotope discrimination indicates improving water use efficiency of trees in northern Eurasia over the last 100 years. *Global Change Biology* **10**: 2109–2120.
- Schaffer, B., Whaley, A.W., and Searle, C. 1999. Atmospheric CO₂ enrichment, root restriction, photosynthesis, and dry-matter partitioning in subtropical and tropical fruit crops. *HortScience* **34**: 1033–1037.
- Sheil, D. 1995. Evaluating turnover in tropical forests. *Science* **268**: 894.
- Sheil, D. and May, R.M. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* **84**: 91–100.
- Sheu, B.-H. and Lin, C.-K. 1999. Photosynthetic response of seedlings of the sub-tropical tree *Schima superba* with exposure to elevated carbon dioxide and temperature. *Environmental and Experimental Botany* **41**: 57–65.
- Silva, L.C.R., Anand, M., Oliveira, J.M., and Pillar, V.D. 2009. Past century changes in *Araucaria angustifolia* (Bertol.) Kuntze water use efficiency and growth in forest and grassland ecosystems of southern Brazil: implications for forest expansion. *Global Change Biology* **15**: 2109–2120.
- Stephens, B.B., Gurney, K.R., Tans, P.P., Sweeney, C., Peters, W., Bruhwiler, L., Ciais, P., Ramonet, M., Bousquet, P., Nakazawa, T., Aoki, S., Machida, T., Inoue, G., Vinnichenko, N., Lloyd, J., Jordan, A., Heimann, M., Shibistova, O., Langenfelds, R.L., Steele, L.P., Francey, R.J., and Denning, A.S. 2007. Weak northern and strong tropical land carbon uptake from vertical profiles of atmospheric CO₂. *Science* **316**: 1732–1735.
- Tewksbury, J.J., Huey, R.B., and Deutsch, C.A. 2008.

Putting the heat on tropical animals. *Science* **320**: 1296–1297.

Van de Water, P.K., Leavitt, S.W., and Betancourt, J.L. 1994. Trends in stomatal density and ¹³C/¹²C ratios of *Pinus flexilis* needles during last glacial-interglacial cycle. *Science* **264**: 239–243.

Way, D.A. and Oren, R. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology* **30**: 669–688.

Weaver, P.L. and Murphy, P.G. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica* **22**: 69–82.

Westerhold, T., Rohl, U., McCarren, H.K., and Zachos, J.C. 2009. Latest on the absolute age of the Paleocene-Eocene Thermal Maximum (PETM): New insights from exact stratigraphic position of key ash layers + 19 and - 17. *Earth and Planetary Science Letters* **287**: 412–419.

Wurth, M.K.R., Winter, K., and Körner, C. 1998. Leaf carbohydrate responses to CO₂ enrichment at the top of a tropical forest. *Oecologia* **116**: 18–25.

Zachos, J.C., Wara, M.W., Bohaty, S., Delaney, M.L., Petrizzo, M.R., Brill, A., Bralower, T.J., and Premoli-Silva, I. 2003. A transient rise in tropical sea surface temperature during the Paleocene-Eocene Thermal Maximum. *Science* **302**: 1551–1554.

Zeebe, R.E., Zachos, J.C., and Dickens, G.R. 2009. Carbon dioxide forcing alone insufficient to explain Palaeocene-Eocene Thermal Maximum warming. *Nature Geoscience* **2**: 576–580.

1.2.1.2 Other Forest Observations

- Forest growth rates throughout the world have gradually accelerated over the years in concert with, and in response to, the historical increase in the air's CO₂ concentration. As the atmosphere's CO₂ concentration rises, forests likely will respond by exhibiting significant increases in biomass production, and thus likely will grow much more robustly and significantly expand their ranges, as is already being documented in many parts of the world.

In a small booklet published by the University of Minnesota (USA) nearly two decades ago, Idso (1995) laid out the evidence for a worldwide increase in the growth rates of Earth's forests coeval with the progression of the Industrial Revolution and the rising CO₂ content of the atmosphere. The development of

this concept began with LaMarche *et al.* (1984), who analyzed annual growth rings of two species of pine tree growing near the timberline in California, Colorado, Nevada, and New Mexico, and in doing so discovered large increases in growth rate between 1859 and 1983, which exceeded what might have been expected from climatic trends but were consistent with the global trend of atmospheric CO₂.

The next stage of the research was inspired by a study of ring-width measurements of Douglas fir trees in British Columbia, Canada, which also revealed a marked increase in the growth rates of the trees in later decades (Parker *et al.*, 1987). This finding led the principal investigator of the project to state “environmental influences other than increased CO₂ have not been found that would explain this [phenomenon].” West (1988) reports much the same thing with respect to long-leaf pines in Georgia—their annual growth increments had begun to rise at an unusual rate about 1920, increasing by approximately 30% by the mid-1980s. He states, “the increased growth cannot be explained by trends in precipitation, temperature, or Palmer Drought Severity Index,” leaving the rising CO₂ content of the atmosphere as the likely cause of the observed increase in productivity.

Contemporaneously, stands of Scots pines in northern Finland were found to have experienced growth increases ranging from 15 to 43% between 1950 and 1983 (Hari *et al.*, 1984; Hari and Arovaara, 1988). As for the cause of this phenomenon, the researchers involved in the work state “CO₂ seems to be the only environmental factor that has been changing systematically during this century in the remote area under study,” and it was thus to this factor that they looked for an explanation of their observations.

A few years later, Graybill and Idso (1993) reported very long ring-width chronologies (some stretching back nearly 1,800 years) of high-altitude, long-lived bristlecone, foxtail, and limber pine trees in Arizona, California, Colorado, and Nevada all showed an unprecedented upward growth trend beginning in the 1850s that continued as far toward the present as the records extended. Comparisons of the chronologies with temperature and precipitation records ruled out the possibility either of these variables played a significant role in enhancing the trees' growth rates, strongly implicating the historical rise in the air's CO₂ concentration as the factor responsible for their ever-increasing productivity over the prior century and a half.

Duquesnay *et al.* (1998) analyzed the relative

amounts of ^{12}C and ^{13}C present in yearly growth rings of beech trees raised in silviculture regimes in northeastern France. They discovered the trees' intrinsic water-use efficiencies rose by approximately 33% during the prior century, as the atmosphere's CO_2 concentration rose from approximately 280 to 360 ppm. Rathgeber *et al.* (2000) used tree-ring density data to create a historical productivity baseline for forest stands of *Pinus halepensis* in southeastern France, from which they determined the net productivity of such forests likely would increase by 8 to 55% with a doubling of the air's CO_2 content.

Running a forest growth model based on empirical observations reported in the literature, Lloyd (1999) determined the rise in the atmospheric CO_2 concentration since the onset of the Industrial Revolution likely increased the net primary productivity of mature temperate deciduous forests by about 7%. In addition, he determined a proportional increase in anthropogenic nitrogen deposition likely increased forest net primary productivity by 25%. When he combined the two effects, the net primary productivity stimulation rose to 40%, which, as a result of synergetic interactions, was actually more than the sum of the growth enhancements resulting from the individual increases in CO_2 and nitrogen acting by themselves.

Medlyn *et al.* (1999) conducted a meta-analysis of data from 15 atmospheric CO_2 enrichment studies of European forest species growing in field environments to determine their overall photosynthetic response to elevated (approximately doubled) atmospheric CO_2 concentrations. The resulting meta-analysis by the 21 researchers revealed the twice-ambient CO_2 concentrations stimulated the trees' net photosynthetic rates by an average of 51%.

In 1996, circular Free-Air CO_2 Enrichment (FACE) plots (30m diameter) maintained at atmospheric CO_2 concentrations of 360 and 560 ppm were established in a 15-year-old loblolly pine (*Pinus taeda*) plantation in North Carolina, USA, to study the effects of elevated CO_2 on the growth and productivity of this particular forest community, which also had several hardwood species present in its understory. Based on some of the first sets of data to come out of this endeavor, Hymus *et al.* (1999) report net photosynthetic rates of the CO_2 -enriched loblolly pines trees were 65% greater than rates observed in control trees exposed to ambient air. These greater rates of carbon fixation contributed to the 24% greater growth rates observed in the CO_2 -enriched pine trees in the first year of this long-term study, according to Naidu and DeLucia (1999). In

addition, DeLucia and Thomas (2000) report the elevated CO_2 increased rates of net photosynthesis by 50 to 160% in four subdominant hardwood species present in the forest understory. Moreover, for one species—sweetgum (*Liquidambar styraciflua*)—the extra CO_2 enhanced the rates of net photosynthesis in Sun and shade leaves by 166 and 68%, respectively, even when the trees were naturally subjected to summer seasonal stresses imposed by high temperature and low soil water availability, as Herrick and Thomas (1999) report. After two years of atmospheric CO_2 enrichment, total ecosystem net primary productivity in the CO_2 -enriched plots was found to be 25% greater than what was measured in control plots fumigated with ambient air.

In a similar large-scale study, circular (25m diameter) FACE plots maintained at atmospheric CO_2 concentrations of 400 and 530 ppm were constructed within a ten-year-old sweetgum plantation in Tennessee, USA, to study the effects of elevated CO_2 on the growth and productivity of this forest community. After two years of treatment, Norby *et al.* (2001) report the modest 35% increase in the air's CO_2 content boosted tree biomass production by an average of 24%. In addition, Wullschlegel and Norby (2001) note the CO_2 -enriched trees displayed rates of transpirational water loss approximately 10% lower than those exhibited by control trees growing in ambient air. As a result, elevated CO_2 enhanced seasonal water-use efficiencies of the mature sweetgum trees by 28 to 35%.

On a smaller scale, Pritchard *et al.* (2001) constructed idealized ecosystems containing five different species representative of regenerating longleaf pine (*Pinus palustris* Mill.) communities of the southeastern United States, fumigating them for 18 months with air containing 365 and 720 ppm CO_2 , to study the effects of elevated CO_2 on this forest community. They report elevated CO_2 increased the above- and below-ground biomass of the dominant longleaf pine individuals by 20 and 62%, respectively. At the ecosystem level, elevated CO_2 stimulated total aboveground biomass production by an average of 35%. Berntson and Bazzaz (1998) report similar results for regenerating temperate forest communities, documenting a 31% increase in Transition Hardwood-White Pine-Hemlock forest mesocosm biomass in response to two years of fumigation with twice-ambient concentrations of atmospheric CO_2 .

Near the turn of the century, therefore, it was becoming quite clear that as the atmosphere's CO_2 concentration continued to rise, forests likely would

respond by exhibiting significant increases in biomass production, with the result that they likely would grow much more robustly and significantly expand their ranges, as was already being documented in many parts of the world, including Kansas, USA (Knight *et al.*, 1994) and the Budal and Sjødal valleys of Norway (Olsson *et al.*, 2000).

In the first of these cases, aerial photographs taken over a 46-year period were used to analyze the dynamics and spatial extent of gallery forest on the Konza Prairie Research Natural Area (KPRNA) in Kansas, USA, between 1939 and 1985. Over the 46-year period of study, total gallery forest area increased from 157 hectares to 241 hectares. Looking further back in time and studying additional historical information obtained from the Original Land Office Surveys of KPRNA, the scientists found total forest area in the region increased fully 97% between 1859 and 1939, leading Knight *et al.* to conclude there was “no question that the absolute amount of forested areas has increased.”

Taking an even longer view of the subject, the explorer Coronado in 1541 stated, in reference to the Great Plains of America, “there is not any kind of wood in all these plains, away from the gullies and rivers, which are very few.” Clearly, therefore, a dramatic increase in forest growth has occurred in this region since that time, and especially over the last century and a half. One of the reasons for this increase is certainly the historical increase in Earth’s atmospheric CO₂ concentration. Rising from a value of 265 ppm at the time of Coronado, to a value of 370 ppm in 1994, the increased CO₂ likely had a pronounced positive impact on the photosynthesis and growth of woody species on every continent of the globe where trees are found, as has been further elucidated by Idso (1995).

In Norway, domestic livestock have been raised on mountains for the past 4,000 years, but especially since the sixteenth century, which saw the development of the summer farming system there. Olsson *et al.* (2000) thus speculated this activity originally reduced forested areas, and changes in farming practices more recently allowed the forests to return. Investigating this hypothesis, they studied two valleys—Budal and Sjødal—in mid-Norway, which they say were representative of core areas of the Norwegian summer farming ecosystems “shaped by human activities rooted in pre-history.” Specifically, they analyzed changes in land use and landscape patterns in the two areas over the period 1960–1993. This work revealed grasslands and heathlands that had long dominated the mountain slopes of the two

study areas were, in their words, “today decreasing due to forest invasion,” which they say is characterized by “the spread of subalpine woodlands, and a raised treeline.”

Olsson *et al.* conclude the expansion of the subalpine Norwegian woodlands was “primarily related to changes in the human use of those areas,” which in their estimation were “much more influential than possible effects of climate change.” However, it is also possible the concurrent rise in the atmosphere’s CO₂ concentration may have played a role in the forests’ comeback. In any event, the ongoing increase in the presence of forests in the mountain valleys of Norway is but one more manifestation of the spreading of woody species over the face of the planet, which is helping to slow the rate of rise of the atmosphere’s CO₂ concentration.

Walker *et al.* (2000) grew ponderosa pine (*Pinus ponderosa* Dougl.) seedlings for five years in open-top chambers having atmospheric CO₂ concentrations of 350, 525, and 700 ppm on soils of low, medium, and high nitrogen content, to determine the interactive effects of these two variables on the long-term growth response of this particular tree species. They found the moderate level of atmospheric CO₂ enrichment (525 ppm) had the greatest effect on tree height and trunk diameter in the first three years of the experiment. By years four and five, trees grown at 700 ppm CO₂ exhibited the greatest growth responses to elevated CO₂. At final harvest, the trees exposed to twice-ambient levels of atmospheric CO₂ had heights 43, 64, and 25% greater than those of trees exposed to ambient air and conditions of high, medium, and low levels of soil nitrogen, respectively. Similarly, trunk diameters of trees fumigated with 700 ppm CO₂ for five years were 24, 73, and 20% greater than trunk diameters of ambiently grown trees exposed to high, medium, and low levels of soil nitrogen.

Naumburg and Ellsworth (2000) measured photosynthetic rates in leaves of four hardwood saplings growing beneath the canopy of a *Pinus taeda* forest, several portions of which were exposed to either ambient or enriched (ambient + 200 ppm) atmospheric CO₂ concentrations in a FACE study spanning two years. The measurements were made under conditions of both low and high light intensity, which commonly exist beneath maturing forest canopies because of shading and intermittent illumination by sunflecks, respectively. Thus the two researchers studied the effects of elevated CO₂ on sapling performance under the variable light conditions prevailing beneath the canopies of real-world forests.

The data indicate elevated CO₂ increased the mean photosynthetic rates of four hardwood understory saplings by 60 and 40% under high and low light conditions, respectively. Also, in going from shaded to lighted conditions, elevated CO₂ had no effect on photosynthetic induction, with ambient and CO₂-enriched species both reaching 90% of their maximal transient photosynthetic rates at approximately the same time. However, in going from lighted to shaded conditions, elevated CO₂ extended the time during which maximal rates of photosynthesis were maintained. Thus, elevated CO₂ slowed the rate of photosynthetic decline caused by the onset of shading, and as a result, the shaded leaves of CO₂-enriched saplings maintained greater rates of photosynthesis for longer periods of time than did shaded leaves of saplings growing in ambient air, which allowed the CO₂-enriched leaves to sequester greater amounts of carbon than was expected from photosynthetic measurements made under steady-state conditions.

As the air's CO₂ content rises, therefore, saplings growing beneath the canopies of larger trees will likely increase their rates of photosynthesis under both high and low light conditions characteristic of intermittent shading and illumination by sunflecks. Moreover, because elevated CO₂ concentrations allow saplings to maintain higher rates of photosynthesis for longer periods of time when going from lighted to shaded conditions, such trees should be able to sequester greater quantities of carbon than they do now. So powerful is this phenomenon, in fact, the two researchers state current estimates of the enhancement of long-term carbon gains by forests under conditions of elevated atmospheric CO₂ "could be underestimated by steady-state photosynthetic measures."

Hamilton *et al.* (2001) investigated the short- and long-term respiratory responses of loblolly pine (*Pinus taeda*) and sweetgum (*Liquidambar styraciflua*) trees to the ambient and elevated atmospheric CO₂ concentrations (360 and 560 ppm) of the 30-meter-diameter FACE plots of the long-running loblolly pine plantation experiment in North Carolina, USA, where the deciduous trees had naturally established themselves beneath the primarily coniferous canopy. They report the modest 200 ppm increase in atmospheric CO₂ concentration resulted in no significant short-term suppression of dark respiration rates in needles of loblolly pine. It did, however, reduce rates of dark respiration in sweetgum leaves by an average of 10%. The long-term exposure to elevated CO₂ also did not appear to alter

maintenance respiration, which is the amount of CO₂ needed to maintain existing tissue, in either of the tested species. But growth respiration, the amount of CO₂ respired when constructing new tissues, was reduced by 21% in loblolly pine and 39% in sweetgum leaves that reached the top of the canopy. Thus, as the air's CO₂ content rises, it is likely these two forest species will exhibit increased rates of photosynthesis that will provide them with more of the raw materials required for constructing new and greater amounts of biomass, and the costs of respiration during the synthesis of new tissues likely will be reduced, thus allowing greater amounts of carbon to be retained in the trees and thereby helping to reduce the rate of rise of the atmosphere's CO₂ concentration.

Working at the same location, Hussain *et al.* (2001) collected seeds from trees exposed to both atmospheric CO₂ concentrations to study the effects of elevated CO₂ on seed characteristics, germination success, and early seedling growth. Seeds collected from CO₂-enriched trees were 91% heavier than seeds collected from trees growing in ambient air. In addition, the CO₂-enriched seeds had a lipid content 265% greater than that observed in seeds produced on the ambient-treatment trees, and the germination success for seeds developed under atmospheric CO₂ enrichment was more than three times greater than control seeds developed at ambient CO₂, regardless of germination CO₂ concentration. Also, the seeds from the CO₂-enriched trees germinated approximately five days earlier than their ambiently produced counterparts, again regardless of germination CO₂ concentration. And seedlings developing from seeds collected from CO₂-enriched trees displayed significantly greater root lengths and needle numbers than those developing from trees exposed to ambient air, also regardless of current growth CO₂ concentration. Thus, as the CO₂ content of the air increases, loblolly pine trees likely will display significant increases in their photosynthetic rates, and the enhanced carbohydrate supplies resulting from this phenomenon likely will be used to increase seed weight and lipid content. These seeds consequently should exhibit significant increases in germination success, and their enhanced lipid content likely will lead to greater root lengths and needle numbers in developing seedlings. Thus, when these seedlings become photosynthetically active, they likely will photosynthesize and produce biomass at greater rates than those currently exhibited by seedlings growing under ambient CO₂ concentrations, in a positive cycle that keeps repeating.

Kellomaki and Wang (2001) grew birch seedlings (*Betula pendula* Roth.) for approximately five months in enclosed environmental chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm. The seedlings were simultaneously exposed to ambient or elevated (ambient plus 3°C) air temperatures to study the interactive effects of elevated CO₂ and temperature on the growth of this common boreal forest species. During the most rapid phase of growth observed in the study, elevated CO₂ increased rates of net photosynthesis by 21 and 28% at the ambient and elevated air temperatures, respectively. These increases in carbon uptake led to corresponding biomass increases of 17 and 18%, which suggest boreal forests likely will increase their carbon-sequestering abilities, locking up increasing amounts of carbon within their woody tissues as the air's CO₂ content increases.

Hamilton *et al.* (2002) report what they learned from the Duke Forest FACE Experiment over four years. This ecosystem—a predominantly loblolly pine (*Pinus taeda* L.) forest with sweetgum (*Liquidambar styraciflua* L.) and yellow poplar (*Liriodendron tulipifera* L.) trees as sub-dominants, together with numerous other trees, shrubs, and vines—was established in 1983 following the clear-cutting of a regenerating forest in 1979. The experiment was begun in August 1996, when three 30-meter-diameter FACE plots were enriched with CO₂ to atmospheric concentrations 200 ppm above ambient, and three similar plots were maintained at ambient conditions as controls. Based on the standing pool of ecosystem biomass in 1998 and more recent measurements of various carbon fluxes, Hamilton *et al.* calculated a complete carbon budget for the forest for that particular year. They found the extra CO₂ supplied to the FACE plots stimulated net ecosystem productivity (NEP) by 41%, and for a 300 ppm increase in atmospheric CO₂ concentration—the most common increment of CO₂ enrichment employed in CO₂ enrichment experiments over the years—this result translates into a CO₂-induced NEP increase on the order of 60%. That improvement represents a significant stimulation of biological carbon sequestration, especially for trees growing on a soil the researchers described as being of “low nitrogen and phosphorus availability.”

Norby *et al.* (2002) describe a FACE study established in a ten-year-old stand of sweetgum (*Liquidambar styraciflua* L.) trees growing in a forest plantation on nutrient-rich soils in Tennessee, USA, where the trees were exposed to atmospheric CO₂ concentrations of 360 and 550 ppm. In response to

that CO₂ increase, ecosystem net primary productivity rose by 21% in all three years of their study; aboveground woody biomass rose by 33% in the first year, 15% in the second year, and 7% in the third year; and net primary productivity remained unchanged. The biomass drop occurred because an increasing amount of newly fixed carbon in the CO₂-enriched trees was being utilized to increase fine-root and leaf production in each progressive year. Over the three-year period of their study, however, 77% of the additional fixed carbon was nevertheless allocated to aboveground woody biomass, leading the 11 researchers to conclude, “this experiment has provided the first evidence that CO₂ enrichment can increase productivity in a closed-canopy deciduous forest.”

Rathgeber *et al.* (2003) used tree-ring width and density chronologies (both earlywood and latewood) from 21 stands of Aleppo pine (*Pinus halepensis* Mill.) in the Provence region of southeast France to calibrate the BIOME3 biogeochemistry model of forest productivity in terms of growth responses to known historical changes in atmospheric temperature, precipitation, and CO₂ concentration. They then used the BIOME3 model to calculate changes in the mean productivity of the same forest stands expected to result from changes in these parameters driven by a doubling of the air's CO₂ content, as calculated by Meteo-France's ARPEGE atmospheric general circulation model when downscaled to that specific part of the country. In response to the predicted changes in climate, forest productivity increased moderately for all stands (17% to 24%); in response to the aerial fertilization effect of the doubling of the atmosphere's CO₂ concentration, it increased considerably more (72% to 86%). Even more impressively, when the climatic changes and atmospheric CO₂ increase were considered together, forest productivity increased still more (107% to 141%). That response was greater than that provided by the sum of their individual contributions, as a result of the amplifying synergy among these factors with respect to their combined impact on basic plant physiological processes.

Bergh *et al.* (2003) used a boreal version of a process-based simulation model (BIOMASS) to quantify the individual and combined effects of elevated air temperature (2 and 4°C above ambient) and CO₂ concentration (350 ppm above ambient) on the net primary production (NPP) of both coniferous (*Pinus sylvestris*, *Picea abies*) and deciduous broad-leaf (*Fagus sylvatica*, *Populus trichocarpa*) forests growing in Denmark, Finland, Iceland, Norway, and

Sweden. For three of the four species (*P. sylvestris*, *P. abies*, *P. trichocarpa*), air temperature increases of 2 and 4°C led to mean NPP increases of 11 and 20%, respectively. For the other species (*F. sylvatica*), there were corresponding 21 and 48% decreases in NPP. When the atmosphere's CO₂ concentration was simultaneously increased from 350 to 700 ppm, the corresponding mean NPP increases of the three-species group rose to 41 and 55%, and the NPP of *F. sylvatica* jumped from -21 and -48% to +37 and +10%. Finally, when the atmosphere's CO₂ content was doubled at the prevailing ambient air temperature, the mean NPP value of the three-species group rose by 27%, and *F. sylvatica* rose by 58%. Consequently, as the air's CO₂ content climbs higher, the major tree species of Denmark, Finland, Iceland, Norway, and Sweden should become significantly more productive, and if air temperature also rises, most of them will grow even better.

In a study conducted at the Poplar Free Air CO₂ Enrichment (PopFACE) facility described by Miglietta *et al.* (2001), located near Viterbo in Central Italy, Bernacchi *et al.* (2003) worked with three hybrid poplars they describe as “so fast growing that they provide a rare opportunity to grow a plantation forest from planting to canopy closure of tall trees (greater than 9 m) in just 3 years.” This was done in a field previously used for wheat cultivation planted with the hybrid *Populus x euramericana* Dode (Guinier)—(*P. deltoides* Bart. ex Marsh. x *P. nigra* L., I-214)—with the exception of six 30m x 30m square plots that each contained a 22m-diameter FACE ring. Three of the rings were maintained at 370 ppm CO₂, and the other three were maintained at 550 ppm CO₂. Within each of them were grown equal-area sections of *P. alba* L. (genotype 2AS1), *P. nigra* L. (genotype Jean Pourtet), and *P. x euramericana* (genotype I-214), which were maintained free of drought by a drip irrigation system. Periodic measurements of net photosynthesis and stomatal conductance were made over the three-year period of growth from the seedling to closed-canopy forest stage.

Bernacchi *et al.* found no response of leaf stomatal conductance to atmospheric CO₂ enrichment. In the case of net photosynthesis, however, the team of seven scientists observed a 38% increase in light-saturated net photosynthesis at 25°C, which they describe as being “close to the maximum theoretically possible,” in response to the 49% increase in atmospheric CO₂ concentration employed in their study. Daily integrated rates of *in situ* photosynthesis were even higher, rising by 40% to almost 90%

(approximately equivalent to 150% in response to a 300 ppm increase in the air's CO₂ concentration). The cause of this increase, Bernacchi *et al.* write, was “daytime leaf temperatures were typically over 30°C resulting in a larger stimulation of leaf photosynthesis by elevated CO₂ than would be evident at 25°C (Long, 1991).” This stimulation of daily net photosynthesis illustrates the enormous potential for Earth's trees, even in closed-canopy forests, to respond positively to the ongoing rise in the air's CO₂ content.

Su and Sang (2004) used an ecosystem process model, BIOME-BGC, to explore the sensitivity of the net primary productivity (NPP) of an oak (*Quercus liaotungensis* Koidz) forest ecosystem in the Beijing area of China to global climate changes projected to be caused by rising atmospheric CO₂ concentrations. Under a doubling of the air's CO₂ concentration from 355 to 710 ppm, the Beijing oak forest's NPP was calculated to rise by 14.0%, and with a concomitant temperature increase of 2°C, its NPP was calculated to rise by 15.7%. With an additional 20% increase in precipitation, it rose by 25.7%. Finally, with a 20% increase in precipitation and a 4°C increase in temperature, it rose by 25.7%.

In contrast to typical model-based claims of future climate, researchers find many projections of ecosystem responses to potential environmental change are not catastrophically negative, even when the increases in air temperature they employ are unrealistically large, such as the 4°C rise employed by Su and Sang. In fact, as in this particular case, many of the responses are actually positive, and strongly so.

One of the reasons for this discrepancy is the tendency of modelers to downplay or disregard altogether the many mitigating effects of atmospheric CO₂ enrichment, including increased plant growth, significantly reduced plant water loss by transpiration and thereby greatly enhanced plant water use efficiency, and physiological changes to plants to where they prefer warmer temperatures, a phenomenon expressed by an increase in the temperature at which plants photosynthesize most efficiently. Any projections of ecosystem responses to potential climate change, and especially those that assume the rising CO₂ content of the atmosphere is their cause, must include these very real phenomena. And when they are included, the results are often positive, as in the work of Su and Sang.

Hanson *et al.* (2005) used models that performed well in a multiyear simulation of the current carbon and water budgets of an upland-oak forest (Hanson *et al.*, 2004) to evaluate the influence of single and

multifactor environmental change scenarios projected for 2100, with and without modifications to account for physiological and growth responses learned from long-term field experimental studies (Winnett, 1998). The environmental changes they evaluated were a 385 ppm increase in CO₂, a 20 ppb increase in O₃, a 4°C increase in temperature, and a 20% increase in winter precipitation, and the responses to those changes “were derived primarily from field experimental studies on deciduous trees and forest systems.”

Initial simplistic model projections of annual net ecosystem carbon exchange (NEEa) for the single-factor change scenarios yielded NEEa responses of +191% for CO₂, -206% for temperature, 0% for precipitation, and -35% for O₃; the combined influence of the four environmental changes yielded a 29% reduction in mean NEEa. However, as Hanson *et al.* report, “when experimentally observed physiological adjustments were included in the simulations (e.g. acclimation of leaf respiration to warming), the combined influence of the year 2100 scenario resulted in a 20% increase in NEEa, not a decrease.” In addition, “consistent with the annual model’s predictions, simulations with a forest succession model run for gradually changing conditions from 2000 to 2100 indicated an 11% increase in stand wood biomass in the future compared with current conditions.” Thus, even with the unrealistically extreme temperature change investigated in their study, which came from IPCC’s Third Assessment Report (Houghton *et al.*, 2001) and the US National Assessment Synthesis Team’s report on climate-change impacts (NAST, 2000), the knowledge gained from real-world experiments demonstrates desirable plant responses to atmospheric CO₂ enrichment are sufficient to override the negative influence of inflated warming and produce a significant enhancement in NEEa.

In a study published in the *Proceedings of the National Academy of Sciences*, a team of 19 researchers (Norby *et al.*, 2005) note “experiments have unequivocally shown that plants can grow faster and larger in a CO₂-enriched atmosphere, and the mechanisms of response are well understood.” Furthermore, they state computer simulations of climatic responses to atmospheric CO₂ “will be incorrect if the magnitude of the CO₂ fertilization effect is not represented accurately.” To help overcome this deficiency (but one of many inherent in even the most advanced of today’s climate models (Lupo and Kininmonth, 2013)), they provide an analysis of the net primary productivity (NPP)

response of closed-canopy forests to increases in the air’s CO₂ concentration in the only Free-Air CO₂ Enrichment (FACE) studies conducted on assemblages of trees large enough and spatially concentrated enough to meet this important criterion of realism.

The four multiyear experiments Norby *et al.* analyzed were: (1) the Duke-FACE study near Durham, North Carolina, USA, which was initiated in an established monoculture plantation of evergreen loblolly pine (*Pinus taeda*) trees, (2) the ORNL-FACE study near Oak Ridge, Tennessee, USA, which was initiated in an established monoculture of deciduous sweetgum (*Liquidambar styraciflua*) trees, (3) the Aspen-FACE study near Rhinelander, Wisconsin, USA, which was initiated on bare ground but ultimately comprised multi-tree assemblages dominated by *Populus* species, and (4) the POP-EUROFACE study near Tuscania (Viterbo), Italy, which also was initiated on bare ground and ultimately comprised of multi-tree assemblages dominated by *Populus* species.

To be compatible with the first two experiments in terms of the trees’ state of development, no data were used from the latter two experiments until the trees had grown to the point where their canopies were completely closed. Under these conditions, and across all appropriate years of all experiments (six years in the Duke-FACE study, five years in the ORNL-FACE study, one and three years in different portions of the Aspen-FACE study, and two years in the POP-EUROFACE study), the average atmospheric CO₂ concentration in the ambient-air control plots was 376 ppm, and the average concentration in the CO₂-enriched plots was 550 ppm, yielding an average CO₂ concentration differential of 174 ppm between the two CO₂ treatments.

In what the four groups of researchers describe as a “surprising consistency of response across diverse sites,” they found forest NPP was enhanced by 23 ± 2% at the median NPP of their combined data set in response to the 174 ppm increase in the air’s CO₂ concentration. This NPP stimulation is substantial, considering most of the CO₂ stimulation figures seen in the scientific literature are for a 300 ppm increase in atmospheric CO₂ concentration. Linearly extrapolating Norby *et al.*’s median result to correspond to this greater CO₂ concentration differential yields a NPP stimulation of approximately 40% or just slightly less, because as the air’s CO₂ content rises, the NPP stimulation provided by extra CO₂ rises slightly more slowly.

Norby *et al.* note the data in their analyses came

from “fast-growing, early successional stands, and there had been no evidence to date for a negative feedback on NPP through nitrogen availability in these stands,” as some had suggested would occur. Norby *et al.* confidently conclude, “the effect of CO₂ fertilization on forest NPP is now firmly established, at least for young stands in the temperate zone.”

Nevertheless, nitrogen availability does play a role in this phenomenon. In the Duke-FACE study, for example, where Norby *et al.* say “a wide range of response to CO₂ enrichment across replicate plots correlated with differences in soil nitrogen availability,” the scientists observed “under low nitrogen availability, CO₂ enrichment increased NPP by 19%, whereas under intermediate and high nitrogen availability the percent CO₂ stimulation was 27%,” or 42% greater ($27\%/19\% = 1.42$). This observation is very important, for it is “almost certain,” as Shaw *et al.* (2002) write, significant nitrogen deposition originating from anthropogenic activities will continue to accompany the ongoing rise in the atmosphere’s CO₂ concentration throughout the foreseeable future; and this phenomenon should further boost forest NPP.

Lloyd (1999) calculated that from AD 1730 to the early 1980s the increase in temperate deciduous forest NPP due solely to the historical increase in the atmosphere’s CO₂ concentration was approximately 7%, and the increase in NPP due to a modest proportional increase in nitrogen deposition over the same time period would have been about 25%. However, when CO₂ and nitrogen increased together in the model Lloyd employed, the NPP stimulation was 40%, even more than the sum of the individual contributions of the extra CO₂ and nitrogen. Although this exercise does not allow for a precise prediction of the percentage stimulation of forest NPP in response to future concomitant increases in atmospheric CO₂ content and nitrogen deposition, it does suggest the increase will likely be significantly larger than what is suggested by Norby *et al.*, who deal solely with the effects of increasing CO₂.

In spite of the many positive responses discussed above, some researchers have suggested the biological response of forests to rising CO₂ may saturate sometime in the future, and the predicted climatic effects of anthropogenic CO₂ emissions might ultimately overpower this positive effect and cause a significant downturn in forest productivity. Davi *et al.* (2006) studied this possibility.

Noting “predictions for the second half of the 21st century diverge, with some models predicting that the terrestrial carbon sink will tend to level off, while

others predict a decrease,” Davi *et al.* say they were “hoping to shed more light on this important subject.” To do so, they used a meteorological model and a moderate CO₂ emission scenario (B2 of IPCC) to calculate a 1960–2100 average temperature increase of 3.1°C and a mean summer rainfall decrease of 27%, which the nine scientists used as input to a physiologically based multi-layer process-based ecosystem productivity model (which contained a carbon allocation sub-model coupled with a soil model) to evaluate the net productivity changes of six French forest ecosystems representative of oceanic, continental, and Mediterranean climates dominated, respectively, by deciduous species (*Fagus sylvatica*, *Quercus robur*), coniferous species (*Pinus pinaster*, *Pinus sylvestris*), and sclerophyllous evergreen species (*Quercus ilex*). These ecosystems, they write, “are representative of a significant proportion of forests in western Europe.”

“By comparing runs with and without CO₂ effects,” Davi *et al.* write, they found “CO₂ fertilization is responsible from 1960 to 2100 for an NEP [net ecosystem productivity] enhancement of about 427 g(C) on average for all sites (= 3.05 g(C) m⁻² year⁻¹).” They also report the CO₂ fertilization effect turns a warming-and-drying-induced “decrease of NEP into an increase.” In addition, they write, “no saturation of this effect on NEP is found because the differences between the simulations with and without CO₂ fertilization continuously increase with time.” Therefore, even in the face of what was projected to be a truly “unprecedented” global warming and drying scenario, the real-world physiological effects of atmospheric CO₂ enrichment included in the ecosystem productivity model employed by Davi *et al.* more than compensated for the deleterious effects of the dramatic climate-change scenario on the productivity of major European forests.

Sefcik *et al.* (2007) studied the interactive effects of elevated atmospheric CO₂ concentration (658 ppm vs. the ambient concentration of 383 ppm), nitrogen (N) deposition (ambient and ambient + 30 kg N ha⁻¹ year⁻¹), and light availability (limited and saturated) for two full growing seasons on leaf photosynthesis, growth, and survival of understory seedlings of six different hardwood tree species—paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), eastern white pine (*Pinus strobus*), and black cherry (*Prunus serotina*)—which were enclosed by open-top chambers within a 90-year-old N-limited northern hardwood forest in northern Lower Michigan, USA.

Over the course of this two-year study, the 72% increase in the air's CO₂ concentration increased light-limited photosynthesis in the six tree species by an average of 47%, and it increased light-saturated photosynthesis by fully 60%. With respect to survival, at low N-availability seedling survival rates were similar in the ambient and elevated CO₂ treatments at 57% ± 5% and 55% ± 4%, respectively. In addition, as the researchers describe it, "for plants grown with high N availability, those grown in ambient CO₂ demonstrated 78 ± 4% survival, while those grown in elevated CO₂ exhibited the greatest survival rate of all of the treatment combinations with an 85 ± 2% survival rate." Sefcik *et al.* conclude, "N deposition may alleviate some photosynthetic acclimation [i.e., down-regulation] to long-term CO₂ enrichment in N-limited understory seedlings." They therefore further conclude, "increasing CO₂ and nitrogen deposition from fossil fuel combustion can directly impact seedling physiology and survivorship," quite obviously for the better.

Su *et al.* (2007) used a process-based model (BIOME-BGC) to investigate the likely response of *Picea schrenkiana* forest to future climate changes and atmospheric carbon dioxide concentration increases in the Tianshan Mountains of northwestern China, which they validated by comparing simulated net primary productivity (NPP) under current climatic conditions with independent, field-measured data. The specific climate change scenario employed in this endeavor was a double-CO₂-induced temperature increase of 2.6°C and a precipitation increase of 25%. When the precipitation increase predicted by the model was considered by itself, the NPP of the *P. schrenkiana* forest increased by 14.5%. The predicted temperature increase by itself increased forest NPP by 6.4%, and the CO₂ increase by itself boosted NPP by 2.7%. When the predicted increases in precipitation and temperature occurred together, forest NPP increased by a larger 18.6%, just slightly less than the sum of the two individual effects. When the CO₂ concentration increase was added to the mix and all three factors increased together, the Chinese researchers found forest NPP "increased dramatically, with an average increase of about 30.4%." Su *et al.* thus conclude, "the effects of precipitation and temperature change were simply additive," but the synergy between the effects of climate change and doubled CO₂ made the whole response much larger than the sum of its separate responses because "feedback loops associated with the water and nitrogen cycles [which may be influenced significantly by atmospheric CO₂ enrichment]

ultimately influence the carbon assimilation response."

Koutavas (2008), in prefacing his work, notes "tree rings are the primary archive used in annually resolved climate reconstructions spanning recent centuries to millennia, and as such their response to non-climatic factors requires careful evaluation." Stating an important consideration in this regard "is whether radial growth in trees over the 20th century has been influenced by anthropogenic effects, particularly the rising concentration of CO₂ in the global atmosphere," he further notes "LaMarche *et al.* (1984) were the first to attribute late 20th century growth enhancement in high-elevation bristlecone and limber pines from the western US to CO₂ fertilization." He adds, "Graybill and Idso (1993) further argued that a CO₂ growth effect can be detected in tree-ring chronologies from the southwest US in species exhibiting a strip-bark morphology."

In further exploring this subject, Koutavas analyzed ring-width variations obtained from cores of eight Greek fir (*Abies cephalonica*) trees growing at elevations between 1,300 and 1,600 meters on the southern slopes of Mt. Ainos on the island of Cephalonia in the Ionian Sea west of mainland Greece, while employing climate data from the University of East Anglia to determine whether any growth changes noted over the period of the ring-width record (AD 1840–2005) could be ascribed to any regional climate changes to which the trees might have been exposed.

The results of Koutavas's work are depicted in Figure 1.2.1.2.1. As can be seen from these data, and as Koutavas states, there was a "strong acceleration of growth over the second half of the 20th century" and "the sustained increase in growth since 1990 in particular was unprecedented over the full length of the data set." He also states these positive growth trends "bear no relationship to regional temperature or precipitation variations and therefore are unlikely to be climatically induced." And he affirms "disturbance effects from human activities are also unlikely, as the study site lies in a remote forest area with difficult access." Thus, about the only rational explanation for the late twentieth-century growth acceleration seen in the ring-width data is Koutavas's suggestion: "the enhanced growth reflects a fertilization effect due to rising CO₂ in the global atmosphere."

Martinez-Vilalta *et al.* (2008) used tree-ring data from the Catalan Ecological and Forest Inventory "to study the temporal variability of Scots pine stem radial growth (period 1901–1997) across a relatively large region (Catalonia, NE Spain) situated close to

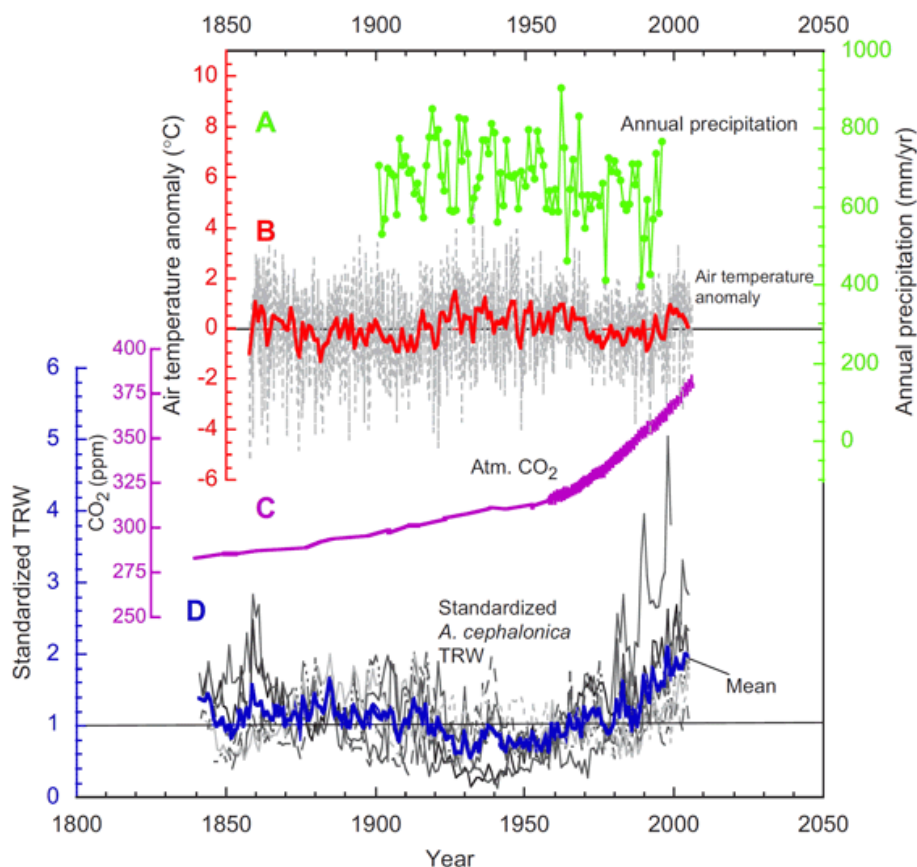


Figure 1.2.1.2.1. Annual precipitation totals, annual air temperature anomalies, atmospheric CO₂ concentrations (from Mauna Loa and Antarctica's Law Dome ice core), and the mean standardized tree-ring series (TRW) of the Greek fir trees. Adapted from Koutavas (2008).

the southern limit of the distribution of the species.” The inventory included 10,664 plots randomly distributed throughout the forested area of Catalonia, where Scots pine was present in 30.2% of the plots and was the dominant tree species in 18.4% of them. The five researchers state their results “showed an overall increase of 84% in Scots pine BAI [basal area increment] during the 20th century, consistent with most previous studies for temperate forests.” They note, “this trend was associated with increased atmospheric CO₂ concentration,” which they interpret to be “a fertilization effect.” There was also, however, “a marked increase in temperature across the study region (0.19°C per decade on average),” but they report “this warming had a negative impact on radial growth, particularly at the drier sites,” although “its magnitude was not enough to counteract the fertilization effect.”

Peng *et al.* (2009) validated the process-based TRIPLEX model of forest growth and carbon and

nitrogen cycling against observed data. They then used the calibrated model to investigate the potential impacts of projected increases in the atmosphere's CO₂ concentration on the climate of northeast China and its interactions with the aerial fertilization effect of the increase in atmospheric CO₂ in computing changes likely to occur in the net primary productivity (NPP) and carbon budget of the region's forests. The model validation results show “the simulated tree total volume, NPP, total biomass and soil carbon are consistent with observed data across the Northeast of China, demonstrating that the improved TRIPLEX model is able to simulate forest growth and carbon dynamics of the boreal and temperate forest ecosystems at regional scale.” Second, the seven scientists note the application of the appropriately calibrated model indicates

climate change would increase forest NPP and biomass carbon but decrease overall soil carbon under all three of the climate change scenarios they studied. However, they report, “the combined effects of climate change and CO₂ fertilization on the increase of NPP were estimated to be 10–12% for [the] 2030s and 28–37% in [the] 2090s,” because “the simulated effects of CO₂ fertilization significantly offset the soil carbon loss due to climate change alone.”

Peng *et al.* thus conclude “overall, future climate change and increasing atmospheric CO₂ will have a significant impact on the forest ecosystems of Northeastern China,” also noting their findings clearly indicate the impact would be beneficial. In addition, they write, “the results of the effects of CO₂ fertilization on NPP simulated by TRIPLEX1.0 are consistent with the recent FACE experiments in temperate forests in North America and Europe (Norby *et al.*, 2005), global analyses of Melillo *et al.* (1993) and Mathews (2007), and site-specific

investigations in Canadian boreal forest ecosystems (Peng and Apps, 1998, 1999).” This consistency leads them to the further conclusion, “the effect of CO₂ fertilization on forest NPP is now firmly established.”

Cole *et al.* (2010) note quaking aspen (*Populus tremuloides* Michx.) is “a dominant forest type in north-temperate, montane, and boreal regions of North America” and is, in fact, “the most widely distributed tree species on the continent.” They also note aspen and related poplars are “quintessential foundation species (Ellison *et al.*, 2005), shaping the structure and function of the communities and ecosystems in which they occur (Whitham *et al.*, 2006; Schweitzer *et al.*, 2008; Madritch *et al.*, 2009).” This being the case, they attempted to determine how this keystone species may have responded to the increase in atmospheric CO₂ concentration that occurred over the past several decades, especially within the context of the climatic changes that occurred concurrently.

To do so, the four researchers collected branches from 919 trees after their leaves had dropped in the fall, obtaining samples that represented 189 genets or clones (five trees per clone) at 11 sites distributed throughout three regions of Wisconsin (USA). The sampled trees ranged from five to 76 years of age and came from second-growth unmanaged forests south of the areas defoliated by forest tent caterpillars in 1980–1982, 1989–1990, and 2001–2002. In addition, they recorded trunk diameter at breast height for each sampled tree, which, in their words, “is very highly correlated with total biomass in aspen,” citing Bond-Lamberty *et al.* (2002).

Results of the analysis, they report, reveal “age-specific ring width increased over time” and “the greatest increase occurred for relatively young trees, so that young trees grew faster in recent years than did young trees several decades ago.” During the past half-century, for example, the growth of trees 11–20 years old rose by 60%. In addition, they observe “rising CO₂ causes ring width to increase at all moisture levels, apparently resulting from improved water use efficiency,” so “the overall increase results from historical increases in both CO₂ and water availability.” And when they separate out the impacts of the two factors, they find “the effect of rising CO₂ had been to increase ring width by about 53%,” as a result of “a 19.2% increase in ambient CO₂ levels during the growing season, from 315.8 ppm in 1958 (when CO₂ records began) to 376.4 ppm in 2003.”

This is a truly remarkable finding; and Cole *et al.* comment, “the magnitude of the growth increase uncovered by this analysis raises the question of how

much other major forest species may have responded to the joint effects of long-term changes in CO₂ and precipitation.” It seems likely other tree species may have experienced similar growth stimulations, particularly in light of Tans (2009), who demonstrated Earth’s land surfaces were a net source of CO₂ to the atmosphere until about 1940—primarily due to the felling of forests and the plowing of grasslands to make way for expanded agricultural activities—but who reports, from 1940 onward, as shown in Figure 1.2.1.2.2, the terrestrial biosphere has become, in the mean, an increasingly greater sink for CO₂, and that it has done so even in the face of massive global deforestation, for which it has apparently more than compensated. The combined findings of the two studies of Tans and Cole *et al.* clearly attest to the ability of the ongoing rise in the air’s CO₂ content to transform the face of Earth.

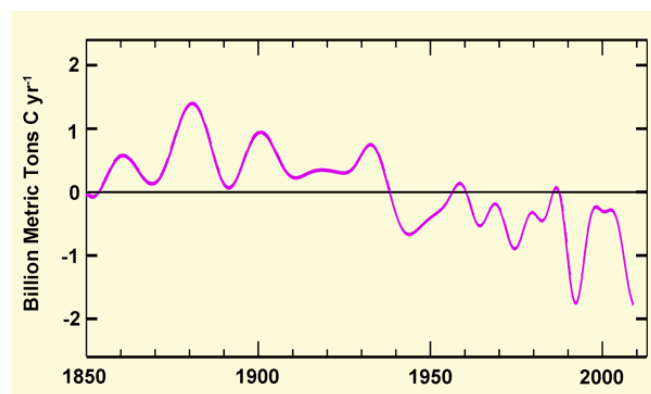


Figure 1.2.1.2.2. Five-year smoothed rates of carbon transfer from land to air (+) or from air to land (-) vs. time. Adapted from Tans (2009).

According to Knapp and Soule (2011), “atmospheric CO₂ concentrations have increased by over 27% since the early 20th century, resulting in enhanced radial tree growth in natural environments for numerous tree species in a variety of climatic regions (e.g., LaMarche *et al.*, 1984; Knapp *et al.*, 2001; Soule and Knapp, 2006; Voelker *et al.*, 2006; Wang *et al.*, 2006; Koutavas, 2008).” In addition, they note, “the principal benefit of elevated CO₂ for radial growth has been linked to increased intrinsic water use efficiency (iWUE), which is the ratio of net CO₂ assimilation through leaf stomata to leaf stomatal conductance.” And they report “increases in iWUE based on carbon isotope chronologies have been identified for trees growing in both controlled (e.g., Leavitt *et al.*, 2003) and natural environments (e.g., Bert *et al.*, 1997; Feng, 1999; Tang *et al.*, 1999;

Arneth *et al.*, 2002; Saurer *et al.*, 2004; Waterhouse *et al.*, 2004; Liu *et al.*, 2007).”

The two researchers “examined radial growth responses of ponderosa pine (*Pinus ponderosa* var. *ponderosa*) between 1905–1954 and 1955–2004 to determine if the effects of increased intrinsic water use efficiencies caused by elevated atmospheric CO₂ concentrations were age-specific,” working with 209 cores collected from mature trees (ranging in age from at least 100 to more than 450 years) from five sites in the USA’s northern Rocky Mountains. They also calculated iWUE using carbon isotope data from 1850 to 2004.

The authors found, “(1) responses to elevated atmospheric CO₂ in old-growth ponderosa forests are age-specific; (2) radial growth increases in older trees coincided with increased iWUE; (3) ponderosa had increased growth rates in their third, fourth, and fifth centuries of life; and (4) age-specific growth responses during 1955–2004 are unique since at least the mid-16th century.” They also report “increases in iWUE during 1955–2004 were 11% greater than during 1905–1954.”

Knapp and Soule say their findings “demonstrate that old-growth ponderosa pine forests of the northern Rockies have likely benefited from the effects of increased atmospheric CO₂ since the mid-20th century and that the benefits increase with tree age.” And since the CO₂-induced radial growth increases in the older trees “were significantly associated with rising iWUE,” they opine the “accelerated growth rates are likely caused by more efficient water use in the semiarid environment where the trees were sampled.”

In concluding, the two scientists state “old-growth trees can be highly responsive to environmental changes,” especially the ongoing rise in the air’s CO₂ content, as their work clearly demonstrates. They note even what many might call ancient trees are still “capable of increased growth rates several hundred years after establishment,” citing McDowell *et al.* (2003) and Martinez-Vilalta *et al.* (2007).

Using data from the website of the International Tree-Ring Data Bank as well as from cores collected previously and stored in their laboratory at The Pennsylvania State University (USA), Johnson and Abrams (2009) explored growth rate (basal area increment, BAI) relationships across age classes (from young to old) for eight tree species commonly found throughout the eastern United States: bigtooth aspen (*Populus grandidentata* Michx.), blackgum (*Nyssa sylvatica* Marsh.), black oak (*Quercus velutina*

Lam.), chestnut oak (*Quercus Montana* L.), hemlock (*Tsuga canadensis* L. Carr.), pitch pine (*Pinus rigida* Mill.), red oak (*Quercus rubra*), and white oak (*Quercus alba* L.). The two researchers report “a remarkable finding of this study was that even the oldest trees of several species had slow but increasing BAI values, which continued throughout the life of most trees.” They characterize this finding as “remarkable,” they explain, because it “contradicts the sigmoidal growth model that predicts growth rate should plateau and then decline, as middle age trees approach old age,” citing Ryan and Yoder (1997) and Weiner and Thomas (2001). They also report, “over the last 50–100 years, younger trees within a species grew faster than did the older trees when they were of the same respective age,” which is what Knapp and Soule (2011) found for ponderosa pine trees in the USA’s northern Rocky Mountains.

Further discussing their findings, the two researchers from Pennsylvania State University’s School of Forest Resources write, “it seems reasonable to assume” the greater growth rates of older trees of the current era compared to older trees of older times “may be due to a stimulatory effect of anthropogenic global change defined in the broadest sense,” including “increased CO₂ levels, warming temperatures, increased precipitation, and changes in precipitation chemistry,” noting “yearly average temperatures, atmospheric CO₂ and nitrogen levels have increased in the eastern US (as well as much of the rest of the world) over the last 50–100 years.”

In another study from Soule and Knapp (2011), the two researchers “examined changes in and relationships between radial growth and intrinsic water use efficiency (iWUE) of ponderosa pine (*Pinus ponderosa*) trees, climate, and atmospheric CO₂ in the western United States since the mid-nineteenth century.” They developed “tree-ring chronologies for eight sites in three climate regions and using carbon isotope data to calculate pentadal values of iWUE,” and then “examined relationships among radial growth, climate, iWUE, and CO₂ via correlation and regression analyses.” They found “trends toward higher rates of iWUE for ponderosa pine are panregional, occurring at eight sites within three distinct climatic regimes and for two subspecies,” and these results “are similar to those reported by Feng (1999) for several coniferous tree species found throughout western North America.” They also note “increasing iWUE has been reported for conifers at other northern hemisphere locations (e.g., Bert *et al.*, 1997; Saurer *et al.*, 2004).” They conclude “future increases in iWUE are likely for

ponderosa pine within our study regions as CO₂ levels increase,” and they state they found “significant improvements in radial growth rates during drought years after 1950.” These findings suggest “increased iWUE associated with rising CO₂ can positively impact tree growth rates in the western United States and is thus an evolving component of forest ecosystem processes.” Soule and Knapp also state, “if potential climate changes lead to increasing aridity in the western United States, additional increases in iWUE associated with future increases in CO₂ might ameliorate growth declines associated with drought conditions.”

Working within lichen woodlands of the forest zone of Eastern Canada between longitudes 70 and 72°W, Girard *et al.* (2011) acquired data enabling them to calculate radial, height, and volume growth rates at every 15 minutes of latitude from 47°30'N to 52°41'N for black spruce (*Picea mariana*) trees ranging in age from 34 to 188 years. Dividing the trees into a young group and an old group, with ages ranging between 34 and 93 years for the young group and between 109 and 188 years for the old group, the three Canadian researchers report same-age “radial, height and volume growth rates of trees in stands younger than 100 years were 46%, 51%, and 38%, respectively, greater than those of trees in stands older than 100 years.” And for the two youngest stands, with mean ages of 34 and 43 years, they state “black spruce showed radial, height and volume growth rates of 66%, 74%, and 71%, respectively, greater than those in woodlands older than 100 years.” Further discussing their findings, Girard *et al.* cite several other studies demonstrating “tree productivity in northern forests of eastern North America has increased significantly since the middle of the 19th century,” namely Payette *et al.* (1985), D'Arrigo *et al.* (1987), D'Arrigo *et al.* (1992), and Lavoie and Payette (1994). They also note “similar trends have been observed in the American West,” citing Graumlich *et al.* (1989) and Peterson *et al.* (1990).

Introducing his study, Parn (2012) writes “the potential productivity of a forest site has been regarded as natural and stable in a long-term perspective (Elfvig *et al.*, 1996),” but “environmental changes such as increase of CO₂ in the atmosphere, deposition of pollutants and climate changes since the 1950s have had various effects on forest ecosystems,” and “the increasing human impact on the environment makes the stability of the site conditions questionable.” Thus the author set out to learn whether these environmental changes may have affected the growth of Scots pine trees. Specifically,

Parn studied the growth history of trees of identical cambial age but two different calendar ages at two different sites: Koiguste on Saaremaa island, the largest of the Estonian islands in the Baltic Sea, and Pirita in North Estonia near the Estonian capital. The age of the old stand at the Koiguste site was 160 years and that of the young stand 55 years, and the ages of the old and young stands at the Pirita site were 155 and 55 years, respectively. At both of these locations, Parn writes, “the differences in the radial growth of successive stand generations were assessed using the average tree-ring widths of the same cambial age of stands at age of 30, 40 and 50 years.”

Parn found “the radial growth of young generations exceeded that of old stands at the same cambial age,” and “approximately similar results were obtained when latewood widths were used instead of the tree-ring widths in the analysis.” In addition, he reports “a fairly strong positive effect of the mean temperatures of the spring months on the latewood width can be observed.” He notes a similar “strong link between the latewood width and spring temperatures was described by Miina (2000) for Scots pines in eastern Finland, by Savva *et al.* (2003) for pines from different provenances in Russia, and by Drobyshev *et al.* (2004) for pines in the Komi Republic.” As for what was responsible for these findings, Parn suggests “it may be assumed that long-term climate change may have caused, at least partly, the increasing growth of young generations of pine” and “the increased nitrogen deposition and elevated CO₂ level during the second half of the 20th century may have had some positive influence.”

References

- Ainsworth, E.A. and Long, S.P. 2005. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytologist* **165**: 351–372.
- Arneth, A., Lloyd, J., Santruckova, H., Bird, M., Grigoryev, S., Kalaschnikov, Y.N., Sukachev, V.N., Gleixner, G., and Schulze, E.-D. 2002. Response of central Siberian Scots pine to soil water deficit and long-term trends in atmospheric CO₂ concentration. *Global Biogeochemical Cycles* **16**: 10.1029/2000GB001374.
- Bergh, J., Freeman, M., Sigurdsson, B., Kellomaki, S., Laitinen, K., Niinisto, S., Peltola, H., and Linder, S. 2003. Modelling the short-term effects of climate change on the productivity of selected tree species in Nordic countries. *Forest Ecology and Management* **183**: 327–340.

Climate Change Reconsidered II: Biological Impacts

- Bernacchi, C.J., Calfapietra, C., Davey, P.A., Wittig, V.E., Scarascia-Mugnozza, G.E., Raines, C.A., and Long, S.P. 2003. Photosynthesis and stomatal conductance responses of poplars to free-air CO₂ enrichment (PopFACE) during the first growth cycle and immediately following coppice. *New Phytologist* **159**: 609–621.
- Berntson, G.M. and Bazzaz, F.A. 1998. Regenerating temperate forest mesocosms in elevated CO₂: belowground growth and nitrogen cycling. *Oecologia* **113**: 115–125.
- Bert, D., Leavitt, S.W., and Dupouey, J.-L. 1997. Variations of wood $\delta^{13}\text{C}$ and water use efficiency of *Abies alba* during the last century. *Ecology* **78**: 1588–1596.
- Bond-Lamberty, B., Wang, C., and Gower, S.T. 2002. Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. *Canadian Journal of Forest Research* **32**: 1441–1450.
- Cole, C.T., Anderson, J.E., Lindroth, R.L., and Waller, D.M. 2010. Rising concentrations of atmospheric CO₂ have increased growth in natural stands of quaking aspen (*Populus tremuloides*). *Global Change Biology* **16**: 2186–2197.
- D'Arrigo, R., Jacoby, G., and Free, R. 1992. Tree-ring width and maximum latewood density at the North-American tree line: Parameters of climatic change. *Canadian Journal of Forest Research* **22**: 1290–1296.
- D'Arrigo, R., Jacoby, G., and Fung, I. 1987. Boreal forests and atmosphere biosphere exchange of carbon dioxide. *Nature* **329**: 321–323.
- Davi, H., Dufrene, E., Francois, C., Le Maire, G., Loustau, D., Bosc, A., Rambal, S., Granier, A., and Moors, E. 2006. Sensitivity of water and carbon fluxes to climate changes from 1960–2100 in European forest ecosystems. *Agricultural and Forest Meteorology* **141**: 35–56.
- DeLucia, E.H., Hamilton, J.G., Naidu, S.L., Thomas, R.B., Andrews, J.A., Finzi, A., Lavine, M., Matamala, R., Mohan, J.E., Hendrey, G.R., and Schlesinger, W.H. 1999. Net primary production of a forest ecosystem with experimental CO₂ enrichment. *Science* **284**: 1177–1179.
- DeLucia, E.H. and Thomas, R.B. 2000. Photosynthetic responses to CO₂ enrichment of four hardwood species in a forest understory. *Oecologia* **122**: 11–19.
- Drobyshev, I., Niklasson, M., and Angelstam, P. 2004. Contrasting tree-ring data with fire record in a pine-dominated landscape in the Komi Republik (Eastern European Russia): recovering a common climate signal. *Silva Fennica* **38**: 43–53.
- Duquesnay, A., Breda, N., Stievenard, M., and Dupouey, J.L. 1998. Changes of tree-ring $\delta^{13}\text{C}$ and water use efficiency of beech (*Fagus sylvatica* L.) in north-eastern France during the past century. *Plant, Cell and Environment* **21**: 565–572.
- Elfving, B., Tegnhammar, L., and Tveite, B. 1996. Studies on growth trends of forests in Sweden and Norway. In: Spiecker, H., Mielikainen, K., Kohl, M., and Skovsgaard, J.P. (Eds.) *Growth Trends in European Forests*. EFI Research Report No. 5. Springer-Verlag, Berlin, Germany, pp. 61–70.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Holle, B.V., and Webster, J.R. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* **3**: 479–486.
- Feng, X. 1999. Trends in intrinsic water use efficiency of natural trees for the past 100–200 years: a response to atmospheric concentration. *Geochimica et Cosmochimica Acta* **63**: 1891–1903.
- Girard, F., Payette, S., and Gagnon, R. 2011. Dendroecological analysis of black spruce in lichen-spruce woodlands of the closed-crown forest zone in eastern Canada. *Ecoscience* **18**: 279–294.
- Graumlich, L.J., Brubaker, L.B., and Grier, C.C. 1989. Long-term trends in forest net primary productivity: Cascade Mountains, Washington. *Ecology* **70**: 405–410.
- Graybill, D.A. and Idso, S.B. 1993. Detecting the aerial fertilization effect of atmospheric CO₂ enrichment in tree-ring chronologies. *Global Biogeochemical Cycles* **7**: 81–95.
- Hamilton, J.G., DeLucia, E.H., George, K., Naidu, S.L., Finzi, A.C., and Schlesinger, W.H. 2002. Forest carbon balance under elevated CO₂. *Oecologia* DOI 10.1007/s00442-002-0884-x.
- Hamilton, J.G., Thomas, R.B., and DeLucia, E.H. 2001. Direct and indirect effects of elevated CO₂ on leaf respiration in a forest ecosystem. *Plant, Cell and Environment* **24**: 975–982.
- Hanson, P.J., Samuelson, L.J., Wullschlegel, S.D., Tabberer, T.A., and Edwards, G.S. 1994. Seasonal patterns of light-saturated photosynthesis and leaf conductance for mature and seedling *Quercus rubra* L. foliage: differential sensitivity to ozone. *Tree Physiology* **14**: 1351–1366.
- Hanson, P.J., Wullschlegel, S.D., Norby, R.J., Tschaplinski, T.J., and Gunderson, C.A. 2005. Importance of changing CO₂, temperature, precipitation, and ozone on carbon and water cycles of an upland-oak forest: incorporating experimental results into model simulations. *Global Change Biology* **11**: 1402–1423.

- Hari, P. and Arovaara, H. 1988. Detecting CO₂ induced enhancement in the radial increment of trees. Evidence from the northern timberline. *Scandinavian Journal of Forest Research* **3**: 67–74.
- Hari, P., Arovaara, H., Raunemaa, T., and Hautojarvi, A. 1984. Forest growth and the effects of energy production: A method for detecting trends in the growth potential of trees. *Canadian Journal of Forest Research* **14**: 437–440.
- Herrick, J.D. and Thomas, R.B. 1999. Effects of CO₂ enrichment on the photosynthetic light response of Sun and shade leaves of canopy sweetgum trees (*Liquidambar styraciflua*) in a forest ecosystem. *Tree Physiology* **19**: 779–786.
- Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., and Johnson, C.A. 2001. Climate Change 2001. In: Maskell, K. and Johnson, C.A. (Eds.) *The Scientific Basis: Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*. Cambridge University Press, Cambridge, United Kingdom.
- Hussain, M., Kubiske, M.E., and Connor, K.F. 2001. Germination of CO₂-enriched *Pinus taeda* L. seeds and subsequent seedling growth responses to CO₂ enrichment. *Functional Ecology* **15**: 344–350.
- Hymus, G.J., Ellsworth, D.S., Baker, N.R., and Long, S.P. 1999. Does free-air carbon dioxide enrichment affect photochemical energy use by evergreen trees in different seasons? A chlorophyll fluorescence study of mature loblolly pine. *Plant Physiology* **120**: 1183–1191.
- Idso, S.B. 1995. *CO₂ and the Biosphere: The Incredible Legacy of the Industrial Revolution*. Department of Soil, Water and Climate, University of Minnesota, St. Paul, Minnesota, USA.
- Johnson, S.E. and Abrams, M.D. 2009. Age class, longevity and growth rate relationships: protracted growth increases in old trees in the eastern United States. *Tree Physiology* **29**: 1317–1328.
- Kellomaki, S. and Wang, K.-Y. 2001. Growth and resource use of birch seedlings under elevated carbon dioxide and temperature. *Annals of Botany* **87**: 669–682.
- Knapp, P.A. and Soule, P.T. 2011. Increasing water use efficiency and age-specific growth responses of old-growth ponderosa pine trees in the Northern Rockies. *Global Change Biology* **17**: 631–641.
- Knapp, P.A., Soule, P.T., and Grissino-Mayer, H.D. 2001. Detecting the potential regional effects of increased atmospheric CO₂ on growth rates of western juniper. *Global Change Biology* **7**: 903–917.
- Knight, C.L., Briggs, J.M., and Nellis, M.D. 1994. Expansion of gallery forest on Konza Prairie Research Natural Area, Kansas, USA. *Landscape Ecology* **9**: 117–125.
- Koutavas, A. 2008. Late 20th century growth acceleration in Greek firs (*Aibes cephalonica*) from Cephalonia Island, Greece: A CO₂ fertilization effect? *Dendrochronologia* **26**: 13–19.
- LaMarche Jr., V.C., Graybill, D.A., Fritts, H.C., and Rose, M.R. 1984. Increasing atmospheric carbon dioxide: Tree ring evidence for growth enhancement in natural vegetation. *Science* **223**: 1019–1021.
- Lavoie, C. and Payette, S. 1994. Recent fluctuations of the lichen spruce forest limit in subarctic Quebec. *Journal of Ecology* **82**: 725–734.
- Leavitt, S.W., Idso, S.B., Kimball, B.A., Burns, J.M., Sinha, A., and Stott, L. 2003. The effect of long-term atmospheric CO₂ enrichment on the intrinsic water use efficiency of sour orange trees. *Chemosphere* **50**: 217–222.
- Liu, X., Shao, X., Liang, E., Zhao, L., Chen, T., Qin, D., and Ren, J. 2007. Species dependent responses of juniper and spruce to increasing CO₂ concentration and to climate in semi-arid and arid areas of northwestern China. *Plant Ecology* **193**: 195–209.
- Lloyd, J. 1999. The CO₂ dependence of photosynthesis, plant growth responses to elevated CO₂ concentrations and their interaction with soil nutrient status, II. Temperate and boreal forest productivity and the combined effects of increasing CO₂ concentrations and increased nitrogen deposition at a global scale. *Functional Ecology* **13**: 439–459.
- Long, S.P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: Has its importance been underestimated? *Plant, Cell and Environment* **14**: 729–739.
- Lupo, A. and Kininmonth, W. 2013. Global climate models and their limitations. In Idso, C.D., Carter, R.M., and Singer, S.F. (Eds.) *Climate Change Reconsidered II: Physical Science*. Chicago, IL: The Heartland Institute.
- Madritch, M.D., Greene, S.G., and Lindroth, R.L. 2009. Genetic mosaics of ecosystem functioning across aspen-dominated landscapes. *Oecologia* **160**: 119–127.
- Martinez-Vilalta, J., Lopez, B.C., Adell, N., Badiella, L., and Ninyerola, M. 2008. Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. *Global Change Biology* **14**: 2868–2881.
- Martinez-Vilalta, J., Vanderklein, D., and Mencuccini, M. 2007. Tree height and age-related decline in growth in Scots pine (*Pinus sylvestris* L.). *Oecologia* **150**: 529–544.
- Matthews, H.D. 2007. Implications of CO₂ fertilization for future climate change in a coupled climate-carbon model. *Global Change Biology* **13**: 1–11.

Climate Change Reconsidered II: Biological Impacts

- McDowell, N., Brooks, J.R., Fitzgerald, S.A., and Bond, B.J. 2003. Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. *Plant, Cell and Environment* **26**: 631–644.
- Medlyn, B.E., Badeck, F.-W., De Pury, D.G.G., Barton, C.V.M., Broadmeadow, M., Ceulemans, R., De Angelis, P., Forstreuter, M., Jach, M.E., Kellomaki, S., Laitat, E., Marek, M., Philippot, S., Rey, A., Strassmeyer, J., Laitinen, K., Liozon, R., Portier, B., Roberntz, P., Wang, K., and Jarvis, P.G. 1999. Effects of elevated [CO₂] on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant, Cell and Environment* **22**: 1475–1495.
- Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B., Vorosmarty, C.J., and Schloss, A.L. 1993. Global climate change and terrestrial net primary production. *Nature* **363**: 234–240.
- Miglietta, F., Peressotti, A., Vaccari, F.P., Zaldei, A., deAngelis, P., and Scarascia-Mugnozza, G. 2001. Free-air CO₂ enrichment (FACE) of a poplar plantation: The POPFACE fumigation system. *New Phytologist* **150**: 465–476.
- Miina, J. 2000. Dependence of tree-ring, earlywood and latewood indices of Scots pine and Norway spruce on climatic factors in eastern Finland. *Ecological Modeling* **132**: 259–273.
- Naidu, S.L. and DeLucia, E.H. 1999. First-year growth response of trees in an intact forest exposed to elevated CO₂. *Global Change Biology* **5**: 609–613.
- National Assessment Synthesis Team (NAST). 2000. *Climate Change Impacts on the United States: The Potential Consequences of Climate Variability and Change*. US Global Change Research Program, Washington, DC.
- Naumburg, E. and Ellsworth, D.S. 2000. Photosynthetic sunfleck utilization potential of understory saplings growing under elevated CO₂ in FACE. *Oecologia* **122**: 163–174.
- Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, S.J., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., De Angelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarascia-Mugnozza, G.E., Schlesinger, W.H., and Oren, R. 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences USA* **102**: 18,052–18,056.
- Norby, R.J., Hanson, P.J., O'Neill, E.G., Tschaplinski, T.J., Weltzin, J.F., Hansen, R.A., Cheng, W., Wullschlegel, S.D., Gunderson, C.A., Edwards, N.T., and Johnson, D.W. 2002. Net primary productivity of a CO₂-enriched deciduous forest and the implications for carbon storage. *Ecological Applications* **12**: 1261–1266.
- Norby, R.J., Todd, D.E., Fults, J., and Johnson, D.W. 2001. Allometric determination of tree growth in a CO₂-enriched sweetgum stand. *New Phytologist* **150**: 477–487.
- Olsson, E.G.A., Austrheim, G., and Grenne, S.N. 2000. Landscape change patterns in mountains, land use and environmental diversity, Mid-Norway 1960–1993. *Landscape Ecology* **15**: 155–170.
- Parker, M.L. 1987. Recent abnormal increase in tree-ring widths: A possible effect of elevated atmospheric carbon dioxide. In: Jacoby Jr., G.C. and Hornbeck, J.W. (Eds.) *Proceedings of the International Symposium on Ecological Aspects of Tree-Ring Analysis*. U.S. Department of Energy, Washington, DC, pp. 511–521.
- Parn, H. 2012. Changes in the radial growth of two consecutive generations of Scots pine (*Pinus sylvestris* L.) stands. *Baltic Forestry* **18**: 12–24.
- Peng, C.H. and Apps, M.J. 1998. Simulating carbon dynamics along the Boreal Forest Transect Case Study (BFTCS) in the Central of Canada: II. Sensitivity to climate change. *Global Biogeochemical Cycles* **12**: 393–402.
- Peng, C.H. and Apps, M.J. 1999. Modeling response of net primary productivity (NPP) of boreal forest ecosystems to changes in climate and fire disturbance regimes. *Ecological Modeling* **122**: 175–193.
- Peng, C., Zhou, X., Zhao, S., Wang, X., Zhu, B., Piao, S., and Fang, J. 2009. Quantifying the response of forest carbon balance to future climate change in Northeastern China: Model validation and prediction. *Global and Planetary Change* **66**: 179–194.
- Peterson, D.L., Arbaugh, M.J., Robinson, L.J., and Derderian, B.R. 1990. Growth trends of whitebark pine and lodgepole pine in a sub-alpine Sierra-Nevada forest, California, USA. *Arctic and Alpine Research* **22**: 233–243.
- Pritchard, S.G., Davis, M.A., Mitchell, R.J., Prior, A.S., Boykin, D.L., Rogers, H.H., and Runion, G.B. 2001. Root dynamics in an artificially constructed regenerating longleaf pine ecosystem are affected by atmospheric CO₂ enrichment. *Environmental and Experimental Botany* **46**: 35–69.
- Rathgeber, C., Nicault, A., Guiot, J., Keller, T., Guibal, F., and Roche, P. 2000. Simulated responses of *Pinus halepensis* forest productivity to climatic change and CO₂ increase using a statistical model. *Global and Planetary Change* **26**: 405–421.
- Rathgeber, C., Nicault, A., Kaplan, J.O., and Guiot, J. 2003. Using a biogeochemistry model in simulating forests productivity responses to climatic change and [CO₂] increase: example of *Pinus halepensis* in Provence (south-east France). *Ecological Modelling* **166**: 239–255.

- Rodrigues, R.R. and Nave, A.G. 2000. Heterogeneidade florística das matas ciliares. In: Rodrigues, R.R. and Leitao Filho, H.F. (Eds.) *Matas Ciliares: Conservação e Recuperação*. Editora da USP/FAPESP, 2000. São Paulo, Brazil, pp. 45–71.
- Ryan, M.G. and Yoder, B.J. 1997. Hydraulic limits to tree height and tree growth. *Bioscience* **47**: 235–242.
- Saurer, M.S., Siegwolf, R.T.W., and Schweingruber, F. 2004. Carbon isotope discrimination indicates improving water use efficiency of trees in northern Eurasia over the last 100 years. *Global Change Biology* **10**: 2109–2120.
- Savva, Y.V., Schweingruber, F.H., Vaganov, E.A., and Milyutin, L.I. 2003. Influence of climate changes on tree-ring characteristics of Scots pine provenances in southern Siberia (forest-steppe). *IAWA Journal* **24**: 371–383.
- Schweitzer, J.A., Madritch, M.D., Bailey, J.K., LeRoy, C.J., Fischer, D.G., Rehill, B.J., Lindroth, R.L., Hagerman, A.E., Wooley, S.C., Hart, S.C., and Whitham, T.G. 2008. The genetic basis of condensed tannins and their role in nutrient regulation in a *Populus* model system. *Ecosystems* **11**: 1005–1020.
- Sefcik, L.T., Zak, D.R., and Ellsworth, D.S. 2007. Seedling survival in a northern temperate forest understory is increased by elevated atmospheric carbon dioxide and atmospheric nitrogen deposition. *Global Change Biology* **13**: 132–146.
- Shaw, M.R., Zavaleta, E.S., Chiariello, N.R., Cleland, E.E., Mooney, H.A., and Field, C.B. 2002. Grassland responses to global environmental changes suppressed by elevated CO₂. *Science* **298**: 1987–1990.
- Soule, P.T. and Knapp, P.A. 2006. Radial growth rate increases in naturally-occurring ponderosa pine trees: a late 20th century CO₂ fertilization effect? *New Phytologist* **171**: 379–390.
- Soule, P.T. and Knapp, P.A. 2011. Radial growth and increased water use efficiency for ponderosa pine trees in three regions in the western United States. *The Professional Geographer* **63**: 379–391.
- Su, H.-X. and Sang, W.-G. 2004. Simulations and analysis of net primary productivity in *Quercus liaotungensis* forest of Donglingshan Mountain Range in response to different climate change scenarios. *Acta Botanica Sinica* **46**: 1281–1291.
- Su, H.-X., Sang, W., Wang, Y., and Ma, K. 2007. Simulating *Picea schrenkiana* forest productivity under climatic changes and atmospheric CO₂ increase in Tianshan Mountains, Xinjiang Autonomous Region, China. *Forest Ecology and Management* **246**: 273–284.
- Tang, K., Feng, X., and Funkhouser, G. 1999. The $\delta^{13}\text{C}$ of trees in full-bark and strip-bark bristlecone pines in the White Mountains of California. *Global Change Biology* **5**: 33–40.
- Tans, P. 2009. An accounting of the observed increase in oceanic and atmospheric CO₂ and an outlook for the future. *Oceanography* **22**: 26–35.
- Voelker, S.L., Muzika, R., Guyette, R.P., and Stambaugh, M.C. 2006. Evidence for historic CO₂ enhancement of tree-ring growth shows a decline through age in *Quercus velutina*, *Quercus coccinea* and *Pinus echinata*. *Ecological Monographs* **76**: 549–564.
- Walker, R.F., Johnson, D.W., Geisinger, D.R., and Ball, J.T. 2000. Growth, nutrition, and water relations of ponderosa pine in a field soil as influenced by long-term exposure to elevated atmospheric CO₂. *Forest Ecology and Management* **137**: 1–11.
- Wang, G.G., Chhin, S., and Baurle, W.L. 2006. Effect of natural atmospheric CO₂ fertilization suggested by open-grown white spruce in a dry environment. *Global Change Biology* **12**: 601–610.
- Waterhouse, J.S., Switsur, V.R., Barker, A.C., Carter, A.H.C., Hemming, D.L., Loader, N.J., and Robertson, I. 2004. Northern European trees show a progressively diminishing response to increasing atmospheric carbon dioxide concentrations. *Quaternary Science Reviews* **23**: 803–810.
- Weiner, J. and Thomas, S.C. 2001. The nature of tree growth and the age-related decline in forest productivity. *Oikos* **94**: 374–376.
- West, D.C. 1988. Detection of forest response to increased atmospheric carbon dioxide. In: Koomanoff, F.A. (Ed.) *Carbon Dioxide and Climate: Summaries of Research in FY 1988*. U.S. Department of Energy, Washington, DC, p. 57.
- Whitham, T.G., Bailey, J.K., and Schweitzer, J.A. 2006. A framework for community and ecosystem genetics from genes to ecosystems. *Nature Reviews Genetics* **7**: 510–523.
- Winnett, S.M. 1998. Potential effects of climate change on US forests: a review. *Climate Research* **11**: 39–49.
- Wullschlegel, S.D. and Norby, R.J. 2001. Sap velocity and canopy transpiration in a sweetgum stand exposed to free-air CO₂ enrichment (FACE). *New Phytologist* **150**: 489–498.

1.2.1.3 Growth Rates of Old vs. Young Trees

- In contrast to frequently stated assumptions, old-growth forests can be significant carbon sinks, and their capacity to sequester carbon in the future will be enhanced as the air's CO₂ content rises.

The planting and preservation of forests has long been acknowledged to be an effective and environmentally friendly means of slowing climate-model-predicted CO₂-induced global warming. This prescription for moderating potential climate change is based on two well-established and very straightforward facts: (1) the carbon that trees use to construct their tissues comes from the air, and (2) its extraction from the atmosphere slows the rate of rise of the air's CO₂ content.

Although simple in concept, this potential partial solution to the putative global warming problem has been under attack for several years by those who want to address the issue solely through forced reductions in anthropogenic CO₂ emissions (see Pearce, 1999). The tack they take in this campaign is to claim carbon sequestration by forests is viable only when forests are young and growing vigorously; as forests age, they assert, they gradually lose their carbon sequestering prowess, so forests more than one hundred years old become essentially useless for removing CO₂ from the air. They further claim such old stands yearly lose as much CO₂ via respiration as they acquire via photosynthesis. Here we examine the validity of such assertions based on actual measurements made on older trees.

In Panama (Condit *et al.*, 1995), Brazil (Chambers *et al.*, 1998; Laurance *et al.*, 2004; Chambers *et al.*, 2001), and many parts of the southwestern United States (Graybill and Idso, 1993), individual trees of a number of different species have been shown to live for nearly one-and-a-half millennia. At a hundred or so years of age, these super-consumers of CO₂ are mere youngsters. In their *really* old age, their appetite for the vital gas, though diminished, is not lost. Chambers *et al.* (1998) note the long-lived trees of Brazil continue to experience protracted slow growth even at 1,400 years of age. The protracted slow growth (evident in yearly increasing trunk diameters) of very old and large trees can absorb a tremendous amount of CO₂ out of the air each year, especially when—as noted by Chambers *et al.* (1998) with respect to the Brazilian forests in the central Amazon—about 50% of forests' aboveground biomass is contained in less than the largest 10% of their trees. Consequently, since the lifespan of these massive, long-lived trees is considerably greater than the projected lifespan of the entire "Age of Fossil Fuels," their cultivation and preservation represents an essentially *permanent* partial solution to the perceived problem of global warming that is ascribed to anthropogenic CO₂ emissions.

As important as are these facts about trees,

however, an even more important fact comes into play in the case of forests and their ability to sequester carbon over long periods of time. This little-acknowledged piece of information is the fact that the forest itself—conceptualized as a huge super-organism—is the unit of primary importance in determining the ultimate amount of carbon that can be sequestered on a unit area of land.

That this difference in perspective can have enormous consequences is demonstrated by Cary *et al.* (2001), who note most models of forest carbon sequestration wrongly assume "age-related growth trends of individual trees and even-aged, monospecific stands can be extended to natural forests." When they compared the predictions of such models against real-world data gathered from northern Rocky Mountain subalpine forests that ranged in age from 67 to 458 years, they found aboveground net primary productivity in 200-year-old natural stands is almost twice as great as in modeled stands, and the difference between the two increases linearly throughout the entire sample age range.

What explains the huge discrepancy? Cary *et al.* suggest long-term recruitment and the periodic appearance of additional late-successional species (increasing biodiversity) may have significant effects on stand productivity, infusing the primary unit of concern (the ever-evolving forest super-organism) with greater vitality than would have been projected on the basis of characteristics possessed by the unit earlier in its life. They also note the failure to include effects of size- or age-dependent decreases in stem and branch respiration per unit of sapwood volume in models of forest growth can cause overestimates of respiration in older stands by a factor of two to five.

How serious are these model shortcomings? For the real-world forests studied by Cary *et al.*, they produce predictions of carbon sequestration only a little over half as large as what is observed in nature for 200-year-old forests, and for 400-year-old forests they produce results only about a third as large as what is characteristic of the real world. As the forests grew older still, the difference between reality and model projections grew right along with them.

Paw U *et al.* (2004) note old-growth forests generally have been considered to "represent carbon sources or are neutral (Odum, 1963, 1965)," stating "it is generally assumed that forests reach maximum productivity at an intermediate age and productivity declines in mature and old-growth stands (Franklin, 1988), presumably as dead woody debris and other respiratory demands increase." Particularly, they report a number of articles have suggested "old-

growth conifer forests are at equilibrium with respect to net ecosystem productivity or net ecosystem exchange (DeBell and Franklin, 1987; Franklin and DeBell, 1988; Schulze *et al.*, 1999), as an age-class end point of ecosystem development.”

To see whether these claims had any merit, Paw U *et al.* used an eddy covariance technique to estimate the CO₂ exchange rate of the oldest forest ecosystem (500 years old) in the AmeriFlux network of carbon-flux measurement stations—the Wind River old-growth forest in southwestern Washington, USA, which is composed mainly of Douglas-fir and western Hemlock—for 16 months, from May 1998 to August 1999. Throughout this period, the 14 scientists report, “there were no monthly averages with net release of CO₂,” and the cumulative net ecosystem exchange showed “remarkable sequestration of carbon, comparable to many younger forests.” They conclude, “in contrast to frequently stated opinions, old-growth forests can be significant carbon sinks,” noting “the old-growth forests of the Pacific Northwest can contribute to optimizing carbon sequestration strategies while continuing to provide ecosystem services essential to supporting biodiversity.”

Binkley *et al.* (2004) also addressed whether old forests gain or lose carbon. They revisited an aging aspen forest in the Tesuque watershed of northern New Mexico, USA—which between 1971 and 1976 (when it was between 90 and 96 years old) was thought to have had a negative net ecosystem production rate of $-2.0 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ —and measured the basal diameters of all trees in the central 0.01 ha of each of 27 plots arrayed across the watershed. They then used the same regression equations employed in the earlier study to calculate live tree biomass as of 2003.

“Contrary to expectation,” Binkley *et al.* write, “live tree mass in 2003 [186 Mg ha^{-1}] was significantly greater than in 1976 [149 Mg ha^{-1}] ($P = 0.02$), refuting the hypothesis that live tree mass declined.” They report the annual net increment of live tree mass was about $1.37 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ from age 96 to age 123 years, only 12% less than the mean annual increment of live tree mass experienced over the forest’s initial 96 years of existence ($149 \text{ Mg ha}^{-1} / 96 \text{ yr} = 1.55 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Consequently, in response to the question they posed when embarking on their study—“Do old forests gain or lose carbon?”—Binkley *et al.* conclude, “old aspen forests continue to accrue live stem mass well into their second century, despite declining current annual increments.”

Hollinger *et al.* (1994) obtained similar results for

a 300-year-old *Nothofagus* site in New Zealand, as did Law *et al.* (2001) for a 250-year-old ponderosa pine site in the northwestern United States, Falk *et al.* (2002) for a 450-year-old Douglas fir/western hemlock site in the same general area, and Knohl *et al.* (2003) for a 250-year-old deciduous forest in Germany. In commenting on these findings, the latter investigators say they found “unexpectedly high carbon uptake rates during two years for an unmanaged ‘advanced’ beech forest, which is in contrast to the widely spread hypothesis that ‘advanced’ forests are insignificant as carbon sinks.” Thus, for the forest they studied, “assimilation is clearly not balanced by respiration, although this site shows typical characteristics of an ‘advanced’ forest at a comparatively late stage of development.”

What has put the planet’s trees on this healthier trajectory of being able to sequester significant amounts of carbon in their old age, when past theory (based on past observations) decreed they should be in a state of no-net-growth or even negative growth? The answer is rather simple. For any tree of age 250 years or more, the greater portion of its life (at least two-thirds of it) was spent in an atmosphere of much-reduced CO₂ content. Up until 1920, for example, the air’s CO₂ concentration had never been above 300 ppm throughout the entire lives of such trees, whereas it is currently 400 ppm, or 33% higher. And older trees spent even greater portions of their lives in air of even lower CO₂ concentration. Thus the phenomenon that has given new life to old trees and allows them to “live long and prosper” is most likely the aerial fertilization effect produced by the flooding of the air with the CO₂ that resulted from the Industrial Revolution and is currently being maintained by its aftermath (Idso, 1995).

Greenep *et al.* (2003) found “the capacity for enhanced photosynthesis in trees growing in elevated CO₂ is unlikely to be lost in subsequent generations.” That finding and the others previously cited suggest Earth’s forests will remain strong sinks for atmospheric carbon far beyond the date at which IPCC’s models indicate they would have given back to the atmosphere most of the carbon they had removed from it over their existence to that point in time. Subsequent reports have validated this assessment.

Zhou *et al.* (2006), for example, also note “old-growth forests have traditionally been considered negligible as carbon sinks because carbon uptake has been thought to be balanced by respiration.” Thus they report “the soil carbon balance of old-growth forests has received little attention.” In an attempt to

rectify this situation, they “conducted a study to measure the long-term (1979 to 2003) dynamics of soil organic carbon stock in old-growth forests (age > 400 years) at the Dinghushan Biosphere Reserve in Guangdong Province, China.” The eight scientists report “soil organic carbon concentration in the top 20-cm soil layer increased between 1979 and 2003 from about 1.4% to 2.35% at an average rate of 0.035% each year,” and “measurements on a total of 230 composite soil samples collected between 1979 and 2003 suggested that soil organic carbon stock in the top 20-cm soil layer increased significantly during that time ($P < 0.0001$), with an average rate of 0.61 Mg C ha⁻¹ year⁻¹.” In discussing their findings, Zhou *et al.* state although “the driving forces for this observed high rate of soil organic carbon increase in the old-growth forests are not clear at present,” their study “suggests that the carbon cycle processes in the belowground system of these forests are changing in response to the changing environment.”

Luyssaert *et al.* (2008) conducted a literature survey to test the hypothesis that forests continue to acquire and sequester carbon from the atmosphere for hundreds of years. They compiled data from 519 plot studies conducted throughout the world’s boreal and temperate forests (30% and 70% of the studies, respectively), skipping the tropics because of the low number of tropical sites that possessed the net ecosystem production (NEP) and forest age estimates needed for their analysis. They report, “in forests between 15 and 800 years old, the NEP is usually positive; that is, the forests are CO₂ sinks.” In fact, they write, “young forests rather than old-growth forests are very often conspicuous sources of CO₂ because the creation of new forests (whether naturally or by humans) frequently follows disturbance to soil and the previous vegetation, resulting in a decomposition rate of coarse woody debris, litter and soil organic matter that exceeds the net primary production of the regrowth.” Discussing the implications of their findings, the team of American, Belgian, British, French, German, and Swiss researchers writes, “because old-growth forests steadily accumulate carbon for centuries, they contain vast quantities of it,” and “they will lose much of this carbon to the atmosphere if they are disturbed, so carbon-accounting rules for forests should give credit for leaving old-growth forests intact” to let them sequester even more carbon.

Phillips *et al.* (2008) note there was “a long held view,” as they describe it, that “old trees exhibit little potential for growth.” They therefore state “it may seem reasonable to conclude that old trees are not

responsive to increased CO₂.” They go on to demonstrate that view was far from correct.

The three researchers begin their analysis of the subject by stating, “hydraulic constraints in tall trees,” such as those of great age, “constitute a fundamental form of water limitation; indeed, one that is indistinguishable from soil water limitations,” citing Koch *et al.* (2004) and Woodruff *et al.* (2004). They also report “recent research indicates that tree size and its hydraulic correlates, rather than age *per se*, controls carbon gain in old trees,” as indicated by Mencuccini *et al.* (2005). These findings imply, in their words, “factors that alleviate internal or external resource constraints on old trees could improve physiological function and ultimately growth,” which is something elevated CO₂ does quite well by increasing plant water use efficiency. They list several phenomena that suggest “a fundamental potential for old growth trees to show greater photosynthesis and growth under industrial age increases in CO₂ than they would under constant, pre-industrial CO₂ levels.”

Drawing from their own work, Phillips *et al.* report “500- and 20-year-old Douglas-fir trees both show high sensitivity of photosynthesis to atmospheric CO₂,” presenting data that clearly demonstrate “under optimal conditions there exists the potential for an approximately 30% increase in photosynthetic rate with an increase in CO₂ from pre-industrial to current levels [i.e., from 280 to 385 ppm] in old trees.” They note “the phenomenon of twentieth-century ring-width increase,” which could thus be expected to accompany the twentieth century increase in the air’s CO₂ concentration, has in fact been detected in several other studies, including LaMarche *et al.*, (1984), Jacoby (1986), Graybill (1987), Kienast and Luxmoore (1988), Graumlich (1991), Knapp *et al.* (2001), Bunn *et al.* (2005), and Soule and Knapp (2006), to which could be added Graybill and Idso (1993).

A year later, Phillips *et al.* (2009) noted, over the past quarter-century of intensive region-wide measurements, the productivity of the Amazon rainforest—even in its extreme old age—has been “increasing with time,” citing the comprehensive observational studies of Phillips *et al.* (1998), Nemani *et al.* (2003), Baker *et al.* (2004), Lewis *et al.* (2004), and Ichii *et al.* (2005). Phillips *et al.* sought to determine what negative effect a severe drought might have on South America’s surprisingly productive tropical mega-forest. What the international team of scientists wanted to know, essentially, was whether such a decline in the

availability of water might wipe out the super ecosystem's biomass gains of prior decades, thereby fulfilling one of the models' worst-case catastrophic scenarios.

Focusing their attention on the Amazonian drought of 2005, which they describe as “one of the most intense droughts of the past 100 years” and “a possible analog of future events,” the 66 researchers, who had monitored a host of forest plots across the Amazon basin over the prior quarter-century, utilized tree diameter, wood density, and allometric models to compute the basin's woody biomass at each time of measurement, both before and after the drought, deriving the results plotted in Figure 1.2.1.3.1.

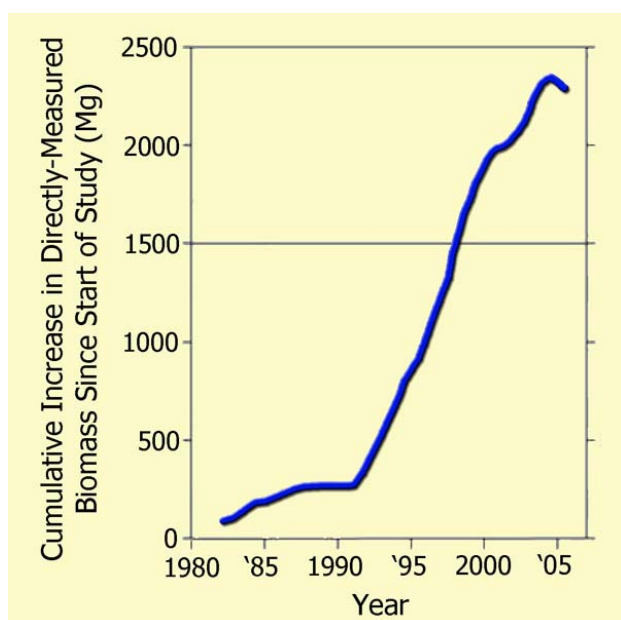


Figure 1.2.1.3.1. The post-1980 cumulative biomass increase of Amazon trees ≥ 10 cm in diameter as a function of the mid-date of each forest-plot census interval, portrayed as a 50-interval moving mean. Adapted from Phillips *et al.* (2009).

As may readily be seen from these real-world measurement-based results, the great Amazonian drought of 2005 resulted in only a slight hiatus in the strong upward trend of tree biomass accumulation exhibited over the prior two decades, which occurred, as Phillips *et al.* note, through a multidecadal period spanning both wet and dry conditions, the latter of which are not even detectable in their wood biomass data. Hence, although extremely severe drought conditions can indeed bring a temporary halt to biomass accumulation in old growth tropical forests—and sometimes even lead to minor

reductions in biomass due to selective tree mortality—the vast majority of the trees are able to regain their photosynthetic capacity and add to their prior store of biomass once the moisture stress subsides, thanks in large measure to the enhanced growth (Lin *et al.*, 1998) and water use efficiency (Hietz *et al.*, 2005) experienced by nearly all woody plants as the air's CO₂ content rises.

Lloyd and Farquhar (2008) provide additional support for this attribution, concluding “the magnitude and pattern of increases in forest dynamics across Amazonia observed over the last few decades are consistent with a CO₂-induced stimulation of tree growth.” Phillips *et al.* (2008) provided still more support for the premise, concluding the simplest explanation for the phenomenon is “improved resource availability has increased net primary productivity, in turn increasing growth rates.” They also note “the only change for which there is unambiguous evidence that the driver has widely changed and that such a change should accelerate forest growth is the increase in atmospheric CO₂,” because of “the undisputed long-term increase in [its] concentration, the key role of CO₂ in photosynthesis, and the demonstrated effects of CO₂ fertilization on plant growth rates.”

Lewis *et al.* (2009) found further support for this view in records of old-growth forests of tropical Africa, where they had invested a great amount of time and effort in documenting changes in aboveground carbon storage in 79 permanent plots spanning 40 years (1968–2007), located in closed-canopy moist forest, spanning West, Central, and Eastern Africa, based on data from more than 70,000 individual trees across ten countries. They found “aboveground carbon storage in live trees increased by $0.63 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ between 1968 and 2007” and “extrapolation to unmeasured forest components (live roots, small trees, necromass) and scaling to the continent implies a total increase in carbon storage in African tropical forest trees of $0.34 \text{ Pg C year}^{-1}$.”

In discussing these results, the 33 researchers write the observed changes in carbon storage were “similar to those reported for Amazonian forests per unit area, providing evidence that increasing carbon storage in old-growth forests is a pan-tropical phenomenon.” They also note “combining all standardized inventory data from this study and from tropical America and Asia together yields a comparable figure of $0.49 \text{ Mg C ha}^{-1} \text{ year}^{-1}$,” which equates to “a carbon sink of $1.3 \text{ Pg C year}^{-1}$ across all tropical forests during recent decades,” accounting for roughly half of the global missing carbon sink. Lewis

et al. conclude, “taxon-specific analyses of African inventory and other data suggest that widespread changes in resource availability, such as increasing atmospheric carbon dioxide concentrations, may be the cause of the increase in carbon stocks, as some theory (Lloyd and Farquhar, 1996) and models (Friedlingstein *et al.*, 2006; Stephens *et al.*, 2007; Ciais *et al.*, 2008) predict.”

Tan *et al.* (2011) report stands of trees with ages greater than 200 years have been demonstrated by several research groups to act as carbon sinks in both coniferous and mixed forests, citing Hollinger *et al.* (1994), Law *et al.* (2001), Roser *et al.* (2002), Knohl *et al.* (2003), Paw U *et al.* (2004), Desai *et al.* (2005), and Guan *et al.* (2006). They buttress this claim with the results of their own study of the subject, in which they employed an eddy covariance technique to examine the carbon balance of a more-than-300-year-old subtropical evergreen broadleaved forest located in the center of the largest subtropical land area of the world in the Ailao Mountain Nature Reserve (24°32'N, 101°01'E) of Yunnan Province in Southwest China.

There, in addition to their micrometeorologically based eddy flux carbon budget estimation, the six scientists conducted a tree inventory of one hectare of forest located within the footprint of the eddy flux tower they employed in November 2003 and again in November 2007. They then compared measurements of tree diameter at breast height (DBH) between the two times and employed site-specific allometric equations to derive mean yearly biomass production. Finally, they assessed aboveground litter production via the amount captured each year in 25 litter traps randomly distributed within the one-hectare plot.

Tan *et al.* thus determined the mean annual net ecosystem production of the forest was approximately 9 tC/ha/year, which suggests, in their words, “this forest acts as a large carbon sink.” In addition, their inventory data indicate about 6 tC/ha/year was contributed by biomass and necromass. And they report approximately 60% of the biomass increment was contributed by the growth of large trees with breast height diameters greater than 60 cm.

The research cited above clearly shows the notion of old trees contributing next to nothing to global carbon sequestration is manifestly invalid.

References

- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Núñez Vargas, P., Pitman, N.C.A., Silva, J.N.M., and Vásquez Martínez, R. 2004. Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* **359**: 353–365.
- Binkley, D., White, C.S., and Gosz, J.R. 2004. Tree biomass and net increment in an old aspen forest in New Mexico. *Forest Ecology and Management* **203**: 407–410.
- Bunn, A.G., Graumlich, L.J., and Urban, D.L. 2005. Trends in twentieth-century tree growth at high elevations in the Sierra Nevada and White Mountains, USA. *The Holocene* **15**: 481–488.
- Carey, E.V., Sala, A., Keane, R., and Callaway, R.M. 2001. Are old forests underestimated as global carbon sinks? *Global Change Biology* **7**: 339–344.
- Chambers, J.Q., Higuchi, N., and Schimel, J.P. 1998. Ancient trees in Amazonia. *Nature* **391**: 135–136.
- Chambers, J.Q., Van Eldik, T., Southon, J., and Higuchi, N. 2001. Tree age structure in tropical forests of central Amazonia. In: Bierregaard, R.O., Gascon, C., Lovejoy, T., and Mesquita, R. (Eds.) *Lessons from Amazonia: Ecology and Conservation of a Fragmented Forest*. Yale University Press, New Haven, CT, USA, pp. 68–78.
- Ciais, P., Piao, S.-L., Cadule, P., Friedlingstein, P., and Chedin, A. 2008. Variability and recent trends in the African carbon balance. *Biogeosciences* **5**: 3497–3532.
- Condit, R., Hubbell, S.P., and Foster, R.B. 1995. Mortality-rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* **65**: 419–439.
- DeBell, D.S. and Franklin, J.S. 1987. Old-growth Douglas-fir and western hemlock: a 36-year record of growth and mortality. *Western Journal of Applied Forestry* **2**: 111–114.
- Desai, A.R., Paw, U.K.T., Cook, B.D., Davis, K.J., and Carey, E.V. 2005. Comparing net ecosystem exchange of carbon dioxide between an old-growth and mature forest in the upper Midwest, USA. *Agricultural and Forest Meteorology* **128**: 33–55.
- Falk, M., Paw, U.K.T., and Schroeder, M. 2002. Interannual variability of carbon and energy fluxes for an old-growth rainforest. In: *Proceedings of the 25th Conference on Agricultural and Forest Meteorology*. American Meteorological Society, Boston, Massachusetts, USA.
- Franklin, J.F. 1988. Pacific Northwest Forests. In: Barbour, M.G. and Billings, W.D. (Eds.) *North American Terrestrial Vegetation*. Cambridge University Press, New York, New York, USA, pp. 104–131.
- Franklin, J.F. and DeBell, D.S. 1988. Thirty-six years of

tree population change in an old-growth Pseudotsuga-Tsuga forest. *Canadian Journal of Forest Research* **18**: 633–639.

Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H.D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K.-G., Schnur, R., Strassmann, K., Weaver, A.J., Yoshikawa, C., and Zeng, N. 2006. Climate-carbon cycle feedback analysis: Results from the (CMIP)-M-4 model intercomparison. *Journal of Climate* **19**: 3337–3353.

Graumlich, L.J. 1991. Subalpine tree growth, climate, and increasing CO₂: an assessment of recent growth trends. *Ecology* **72**: 1–11.

Graybill, D.A. 1987. A network of high elevation conifers in the western US for detection of tree-ring growth response to increasing atmospheric carbon dioxide. In: Jacoby, G.C. and Hornbeck, J.W. (Eds.) *Proceedings of the International Symposium on Ecological Aspects of Tree-Ring Analysis*. U.S. Department of Energy Conference Report DOE/CONF8608144, pp. 463–474.

Graybill, D.A. and Idso, S.B. 1993. Detecting the aerial fertilization effect of atmospheric CO₂ enrichment in tree-ring chronologies. *Global Biogeochemical Cycles* **7**: 81–95.

Greenep, H., Turnbull, M.H., and Whitehead, D. 2003. Response of photosynthesis in second-generation *Pinus radiata* trees to long-term exposure to elevated carbon dioxide partial pressure. *Tree Physiology* **23**: 569–576.

Guan, D., Wu, J.B., Zhao, X.S., Han, S.J., Yu, G.R., Sun, X.M., and Jin, C.J. 2006. CO₂ fluxes over an old temperate mixed forest in northeastern China. *Agricultural and Forest Meteorology* **137**: 138–149.

Hietz, P., Wanek, W., and Dunisch, O. 2005. Long-term trends in cellulose $\delta^{13}\text{C}$ and water use efficiency of tropical *Cedrela* and *Swietenia* from Brazil. *Tree Physiology* **25**: 745–752.

Hollinger, D.Y., Kelliher, F.M., Byers, J.N., Hunt, J.E., McSeveny, T.M., and Weir, P.L. 1994. Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology* **75**: 143–150.

Ichii, K., Hashimoto, H., Nemani, R., and White, M. 2005. Modeling the interannual variability and trends in gross and net primary productivity of tropical forests from 1982 to 1999. *Global and Planetary Change* **48**: 274–286.

Idso, S.B. 1995. *CO₂ and the Biosphere: The Incredible Legacy of the Industrial Revolution*. Department of Soil, Water and Climate, University of Minnesota, St. Paul, Minnesota, USA.

Jacoby G.C. 1986. Long-term temperature trends and a positive departure from the climate-growth response since the 1950s in high elevation lodgepole pine from California. In: Rosenzweig, C. and Dickinson, R. (Eds.) *Proceedings of the NASA Conference on Climate-Vegetation Interactions*. Office for Interdisciplinary Earth Studies (OIES), University Corporation for Atmospheric Research (UCAR), Boulder, Colorado, USA, pp. 81–83.

Kienast, F. and Luxmoore, R.J. 1998. Tree-ring analysis and conifer growth responses to increased atmospheric CO₂ levels. *Oecologia* **76**: 487–495.

Knapp, P.A., Soule, P.T., and Grissino-Mayer, H.D. 2001. Detecting potential regional effects of increased atmospheric CO₂ on growth rates of western juniper. *Global Change Biology* **7**: 903–917.

Knohl, A., Schulze, E.-D., Kolle, O., and Buchmann, N. 2003. Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany. *Agricultural and Forest Meteorology* **118**: 151–167.

Koch, G.W., Sillett, S.C., Jennings, G.M., and Davis, S.D. 2004. The limits to tree height. *Nature* **428**: 851–854.

LaMarche Jr., V.C., Graybill, D.A., Fritts, H.C., and Rose, M.R. 1984. Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. *Science* **225**: 1019–1021.

Laurance, S.G.W., Laurance, W.F., Nascimento, H.E.M., Andrade, A., Fearnside, P.M., Rebello, E.R.G., and Condit, R. 2009. Long-term variation in Amazon forest dynamics. *Journal of Vegetation Science* **20**: 323–333.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Condit, R., D'Angelo, S., and Andrade, A. 2004. Inferred longevity of Amazonian rainforest trees based on a long-term demographic study. *Forest Ecology and Management* **190**: 131–143.

Law, B.E., Goldstein, A.H., Anthoni, P.M., Unsworth, M.H., Panek, J.A., Bauer, M.R., Fracheboud, J.M., and Hultman, N. 2001. Carbon dioxide and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer. *Tree Physiology* **21**: 299–308.

Lewis, S.L., Lopez-Gonzalez, G., Sonke, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo K, M.-N., Ewango, C.E.N., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J.C., Makana, J.-R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K. S.-H., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R., and Woll, H. 2009. Increasing carbon storage in intact African tropical forests. *Nature* **457**: 1003–1006.

Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W.F., Neill, D.A.,

Climate Change Reconsidered II: Biological Impacts

- Silva, J.N.M., Terborgh, J., Lezama, A.T., Vásquez Martinez, R., Brown, S., Chave, J., Kuebler, C., Núñez Vargas, P., and Vinceti, B. 2004. Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* **359**: 421–436.
- Lin, G., Marino, B.D.V., Wei, Y., Adams, J., Tubiello, F., and Berry, J.A. 1998. An experimental and modeling study of responses in ecosystems carbon exchanges to increasing CO₂ concentrations using a tropical rainforest mesocosm. *Australian Journal of Plant Physiology* **25**: 547–556.
- Lloyd, J. and Farquhar, G.D. 1996. The CO₂ dependence of photosynthesis, plant growth responses to elevated atmospheric CO₂ concentrations and their interaction with soil nutrient status. 1. General principles and forest ecosystems. *Functional Ecology* **10**: 4–32.
- Lloyd, J. and Farquhar, G.D. 2008. Effects of rising temperatures and [CO₂] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B* **363**: 1811–1817.
- Luyssaert, S., Schulze, E.-D., Borner, A., Knohl, A., Hessenmoller, D., Law, B.E., Ciais, P., and Grace, J. 2008. Old-growth forests as global carbon sinks. *Nature* **455**: 213–215.
- Mencuccini, M., Martinez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., and Lee, S. 2005. Size-mediated ageing reduces vigor in trees. *Ecology Letters* **8**: 1183–1190.
- Nemani, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneni, R.B., and Running, S.W. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* **300**: 1560–1563.
- Odum, E.P. 1963. *Ecology*. Holt, Rinehart and Winston, New York, New York, USA.
- Odum, E.P. 1965. *Fundamentals of Ecology*. Saunders, Philadelphia, Pennsylvania, USA.
- Paw U, K.T., Falk, M., Suchanek, T.H., Ustin, S.L., Chen, J., Park, Y.-S., Winner, W.E., Thomas, S.C., Hsiao, T.C., Shaw, R.H., King, T.S., Pyles, R.D., Schroeder, M., and Matista, A.A. 2004. Carbon dioxide exchange between an old-growth forest and the atmosphere. *Ecosystems* **7**: 513–524.
- Phillips, O.L., Aragao, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., Lopez-Gonzalez, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Banki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., de Oliveira, A.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jimenez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patino, S., Penuela, M.C., Prieto, A., Ramirez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., ter Steege, H., Stropp, J., Vasquez, R., Zelazowski, P., Davila, E.A., Andelman, S., Andrade, A., Chao, K.-J., Erwin, T., Di Fiore, A., Euradice Honorio C., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C.A., Vargas, P.N., Ramirez-Angulo, H., Rudas, A., Salamao, R., Silva, N., Terborgh, J., and Torres-Lezama, A. 2009. Drought sensitivity of the Amazon rainforest. *Science* **323**: 1344–1347.
- Phillips, N.G., Buckley, T.N., and Tissue, D.T. 2008. Capacity of old trees to respond to environmental change. *Journal of Integrative Plant Biology* **50**: 1355–1364.
- Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Nunez, P.V., Vasquez, R.M., Laurance, S.G., Ferreira, L.V., Stern, M., Brown, S., and Grace, J. 1998. Changes in the carbon balance of tropical forests: Evidence from long-term plots. *Science* **282**: 439–442.
- Roser, C., Montagnani, L., Schulze, E.D., Mollicone, D., Kolle, O., Meroni, M., Papale, D., Marchesini, L.B., Federici, S., and Valetini, R. 2002. Net CO₂ exchange rates in three different successional stages of the “Dark Taiga” of central Siberia. *Tellus* **54**: 642–654.
- Schulze, E.-D., Lloyd, J., Kelliher, F.M., Wirth, C., Rebmann, C., Luhker, B., Mund, M., Knohl, A., Milyukova, I.M., and Schulze, W. 1999. Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink: a synthesis. *Global Change Biology* **5**: 703–722.
- Soule, P.T. and Knapp, P.A. 2006. Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century CO₂ fertilization effect? *New Phytologist* **171**: 379–390.
- Stephens, B.B., Gurney, K.R., Tans, P.P., Sweeney, C., Peters, W., Bruhwiler, L., Ciais, P., Ramonet, M., Bousquet, P., Nakazawa, T., Aoki, S., Machida, T., Inoue, G., Vinnichenko, N., Lloyd, J., Jordan, A., Heimann, M., Shibistova, O., Langenfelds, R.L., Steele, L.P., Francey, R.J., and Denning, A.S. 2007. Weak northern and strong tropical land carbon uptake from vertical profiles of atmospheric CO₂. *Science* **316**: 1732–1735.
- Tan, Z.-H., Zhang, Y.-P., Schaefer, D., Yu, G.-R., Liang, N., and Song, Q.-H. 2011. An old-growth subtropical Asian evergreen forest as a large carbon sink. *Atmospheric Environment* **45**: 1548–1554.
- Woodruff, D.R., Bond, J.B., and Meinzer, F.C. 2004. Does turgor limit growth in tall trees? *Plant, Cell and Environment* **27**: 229–236.

1.2.1.4 Carbon Sequestration

As the CO₂ content of the air increases, nearly all plants, including those of various forest ecosystems, respond by increasing their photosynthetic rates and producing more biomass. These phenomena allow long-lived perennial species characteristic of forest ecosystems to sequester large amounts of carbon within their trunks and branches aboveground and their roots belowground for extended periods of time. These processes, in turn, significantly counterbalance CO₂ emissions produced by mankind's use of fossil fuels. The subsections below review information about forest-species sequestration of the carbon they remove from the atmosphere in response to rising atmospheric CO₂ and rising temperature.

1.2.1.4.1 The Influence of CO₂

- Elevated CO₂ enhances photosynthetic rates and biomass production in forest trees, and both of these phenomena lead to greater amounts of carbon sequestration. Elevated CO₂ also enhances carbon sequestration by reducing carbon losses arising from plant respiration and in some cases from decomposition. Thus, as the air's CO₂ content rises, the ability of forests to sequester carbon rises along with it, appropriately tempering the rate of rise of the air's CO₂ content.

In reviewing studies of individual trees, it is clear elevated levels of atmospheric CO₂ increase photosynthesis and growth in both broad-leaved and coniferous species (see Section 1.1.3.1). When broad-leaved trembling aspen (*Populus tremuloides*) were exposed to twice-ambient levels of atmospheric CO₂ for 2.5 years, for example, Pregitzer *et al.* (2000) reported 17 and 65% increases in fine root biomass at low and high levels of soil nitrogen, respectively, and Zak *et al.* (2000) observed 16 and 38% CO₂-induced increases in total tree biomass when subjected to the same respective levels of soil nitrogen.

Also focusing on a broad-leaved species, Marek *et al.* (2001) constructed open-top chambers around 30-year-old mature oak (*Quercus ilex*) trees growing naturally in perennial evergreen stands in central Italy, where they were continually exposed to atmospheric CO₂ concentrations of either 350 or 700 ppm for five years, to determine the long-term effects of elevated CO₂ on photosynthesis in this important tree species. The researchers found the elevated CO₂ increased rates of net photosynthesis in Sun-exposed

and shaded leaves by 68 and 59%, respectively, in comparison with control rates measured on similar leaves of trees exposed to ambient air. In addition, after measuring short-term photosynthetic rates at various atmospheric CO₂ concentrations, the four researchers found photosynthetic acclimation was not apparent in leaves of these mature trees exposed to long-term atmospheric CO₂ enrichment. They also report the CO₂ light compensation point—the light level at which photosynthetic carbon uptake is equivalent to respiratory carbon loss—was 24 and 30% lower in the Sun-exposed and shaded leaves, respectively, of the CO₂-enriched trees than what was measured in corresponding leaves of the ambient-air trees.

As the air's CO₂ content increases, therefore, it is likely the stimulatory effect of elevated CO₂ on photosynthesis in oak seedlings will persist in the long term within mature trees, without showing any signs of photosynthetic acclimation. And because elevated CO₂ significantly lowers the light compensation point in mature oak trees, which allows them to exhibit net carbon gains earlier in the mornings and maintain them later into the evenings, the stimulatory effect of elevated CO₂ on daily carbon uptake should be further enhanced. Together, these two observations suggest carbon sequestration by this and perhaps other tree species may be more substantial in future CO₂-enriched atmospheres than what had long been thought to be the case.

In a FACE study conducted at the Oak Ridge National Environmental Research Park in Roane County, Tennessee, USA, Norby *et al.* (2004) planted one-year-old bare-rooted sweetgum (*Liquidambar styraciflua* L.) seedlings in the ground in 1988 to create an experimental forest. Eight years later, five 25m-diameter FACE rings were constructed to enclose about 90 trees each. A year after that, when pretreatment measurements were made, the trees were about 2 m tall with an average diameter of 11 cm. At this point, the trees were in a linear growth phase and the canopy was no longer expanding. A year later, in April 1998, exposure to elevated CO₂ was begun in two of the plots and was continued each year thereafter throughout each subsequent growing season (April to November).

Over the last four years of the study (years 3–6), the atmospheric CO₂ concentrations of the ambient and CO₂-enriched plots averaged 391 ppm and 544 ppm (39% more than ambient), respectively. During this period, the net primary production of the CO₂-enriched plots averaged 22% more than the ambient plots, but there was no discernible “bulking up” of the

trees. So where had the extra biomass attributable to the extra CO₂ been going?

In July 1997, the Oak Ridge scientists installed five mini-rhizotron tubes in each FACE plot. These transparent tubes extended to a depth of 60 cm below the soil surface and were inclined at a 60-degree angle from the vertical. Each was equipped with a video recorder collecting images biweekly throughout the growing season, and the data were digitized and used to calculate a number of different root parameters on the same biweekly basis. In analyzing the images, Norby *et al.* report “the CO₂ effect on annual [root] production was highly significant, with production 2.2-fold higher in CO₂-enriched plots from 2000–2003.” They also state “CO₂ enrichment significantly increased peak-standing root crop by altering allocation such that the potential for root occupancy of the soil volume was increased,” noting “this response was manifested especially in the deeper distribution of roots in the soil profile.” In particular, they say the peak-standing root crop exhibited “3-fold more length at 30–45 cm and 4-fold more at 45–60 cm,” impressive considering the enhancement of the air’s CO₂ concentration employed in this study was only 39%.

The Oak Ridge investigators also determined the mass of fine roots produced in a given year accounted for 11–34% of forest net primary production. They remark this “preferential allocation to fine roots should significantly reduce the potential for additional carbon (C) sequestration in trees in elevated CO₂,” which was proven true in their study. However, as they continue, “sequestration of some of that C in the forest remains a possibility” because “as fine roots die, their C enters the soil system where there is the potential for movement into long-lived organic matter pools.” They note “soil analysis indicates that there is increased accumulation of new C in CO₂-enriched plots, particularly in micro-aggregate fractions that facilitate movement of C into pools with long residence times.” And they state “it may become especially important that the greatest increases in root production in elevated CO₂ occur in deeper soil, where sequestration into longer-lived pools may be more likely.”

Norby *et al.* further note “the CO₂-induced increase in fine-root standing crop in summer could also be an important mechanism for conferring increased resistance to late-season droughts,” and “the stimulation of root growth in deeper soil could be particularly important in buffering trees against seasonal droughts.” This being the case, the huge allocation of net primary production the CO₂-enriched

trees send belowground and distribute to greater depths may enable them to sequester more biomass in their aboveground woody tissues, if it helps them remain able to produce biomass during droughty periods that might otherwise bring to a halt the net productivity of trees growing in ambient air.

Karberg *et al.* (2005) describe how “free air CO₂ and O₃ enrichment technology was used at the Aspen FACE project in Rhinelander, Wisconsin [USA] to understand how elevated atmospheric CO₂ and O₃ interact to alter pCO₂ and DIC [dissolved inorganic carbon] concentrations in the soil.” The experimental setting consisted of three blocks of four treatments—control, elevated CO₂, elevated O₃, and elevated CO₂ + O₃—where ambient CO₂ was 360 ppm, elevated CO₂ was 542 ppm, ambient O₃ was 33 ppb, and elevated O₃ was 49 ppb. Half of each FACE ring was planted with trembling aspen, a quarter with a 1:1 mix of trembling aspen and paper birch, and a quarter with a mix of trembling aspen and sugar maple. In this setting, the researchers applied the CO₂ and O₃ treatments over the 2002 growing season, which ran from 28 May to 11 October, and retrieved biweekly samples of the soil air and solution from depths of 15, 30, and 125 cm for various chemical analyses in the laboratory.

The authors found “measured concentrations of soil CO₂ and calculated concentrations of DIC increased over the growing season by 14 and 22%, respectively, under elevated atmospheric CO₂ and were unaffected by elevated tropospheric O₃.” In addition, Karberg *et al.* write, “the increased concentration of DIC altered inorganic carbonate chemistry by increasing system total alkalinity by 210%, likely due to enhanced chemical weathering [of primary minerals],” and they note a mixing model they employed “showed that new atmospheric CO₂ accounted for approximately 90% of the C leaving the system as DIC.”

In discussing their findings, the Michigan scientists state the CO₂-induced increase in soil solution DIC, which ultimately makes its way to rivers that reach oceans, “represents a potential long-lived sequestration reservoir in deep ocean sediments,” noting further it suggests “aggrading forest ecosystems may be used to capture and sequester atmospheric CO₂ through inorganic processes,” which can transfer it to the bottoms of faraway seas, as also has been demonstrated and discussed by Raymond and Cole (2003) and Wang and Cai (2004). And, of course, increases in the air’s CO₂ concentration can significantly increase this phenomenon.

Rasineni *et al.* (2011) write, “carbon sequestration as a climate change mitigation policy has received significant attention over the past several years,” and planting young fast-growing trees to absorb excess atmospheric CO₂ “has recently gained potentiality, leading to identification of tree species with high CO₂ sequestration capacity.” As their contribution, they grew well-watered and well-fertilized five-week-old fast-growing *Gmelina arborea* trees out-of-doors at the University of Hyderabad, India, in open-top chambers maintained at ambient and ambient plus 100 ppm atmospheric CO₂ concentrations throughout the 120 days of that region’s spring and summer seasons, while they periodically made numerous measurements of the trees’ physical properties and physiological performance.

At the conclusion of the spring and summer growing seasons, the three researchers found the trees in the modestly elevated CO₂ chambers exhibited net photosynthetic rates 38% greater than trees growing in ambient air. Aided by a significant CO₂-induced reduction in leaf transpiration rates, the mean instantaneous water use efficiency of the leaves of the CO₂-enriched trees was 87% greater than the ambient-treatment trees. These CO₂-induced plant physiological benefits raised the aboveground biomass of the CO₂-enriched trees at the end of the growing season to be 45% greater than trees growing in ambient air, and their total biomass (above and below ground) was 53% higher.

Discussing their findings, Rasineni *et al.* note elevated atmospheric CO₂ “persistently enhanced all the growth characteristics in *Gmelina*, including plant height, number of branches, internodes, internodal distance, aerial biomass and total plant biomass.” They suggest “high sink demand and better growth dynamics” led to the huge sustained increase in carbon sequestration in the tropical deciduous tree. Thus, they conclude their findings point to the likelihood “there are management options for creating short-rotation deciduous tree plantations to achieve increased sequestration of carbon in a future elevated CO₂ environment.”

Barton and Jarvis (1999) report fumigating branches of Sitka spruce (*Picea sitchensis*) with air of 700 ppm CO₂ for four years raised rates of net photosynthesis in current and second-year needles to be 100 and 43% higher, respectively, than photosynthetic rates of needles exposed to ambient air. In addition, ponderosa pine (*Pinus ponderosa*) grown at 700 ppm CO₂ for close to 2.5 years exhibited rates of net photosynthesis in current-year

needles 49% greater than those of needles exposed to air containing 350 ppm CO₂ (Houpis *et al.*, 1999). As to biomass production, Saxe *et al.* (1998) reviewed the then-existent literature on the topic, finding “close to a doubling” of the air’s CO₂ concentration led to an approximate 50% increase in the biomass production of angiosperm trees and a 130% increase in the biomass production of coniferous species.

Pritchard *et al.* (2001) reconstructed ecosystems representative of regenerating longleaf pine communities of the southeastern USA in large soil bins placed in open-top chambers maintained at CO₂ concentrations of 365 and 720 ppm for 18 months, while they studied the effects of elevated CO₂ on root dynamics and growth in this important forest community. The five species included in the regenerating forest stands were longleaf pine (*Pinus palustris* Mill.), sand post oak (*Quercus margaretta*), a C₄ bunch grass called wiregrass (*Aristida stricta* Michx.), a C₄ perennial legume called rattlebox (*Crotalaria rotundifolia* Walt. Ex Genmel), and a herbaceous C₃ perennial called butterfly weed (*Asclepias tuberosa* L.).

They report the elevated CO₂ increased the total aboveground biomass of the longleaf pine and sand post oak by approximately 20 and 50%, respectively. It had no effect on the aboveground biomass produced by the three non-woody herbaceous species. Thus, at the ecosystem level, elevated CO₂ increased total aboveground biomass by an average of 35%, and belowground it increased the root biomass of longleaf pine by 62%. In contrast, sand post oak, which was very responsive to elevated CO₂ aboveground, exhibited no significant CO₂-induced changes belowground, and the three herbaceous species displayed an average CO₂-induced reduction in root biomass of 28%. At the whole-community level, therefore, the CO₂-enriched plots displayed 37% greater root length production per day and 47% greater root length mortality per day at soil depths between 10 and 30 cm than was observed in control plots exposed to ambient CO₂ concentrations.

Consequently, as the air’s CO₂ content increases, the ability of longleaf pine trees to compete for soil moisture and nutrients in regenerating stands of longleaf pine savannahs will likely be enhanced by the large preferential CO₂-induced increases in the trees’ root systems. This phenomenon likely will give longleaf pine a significant edge over its primary competitors—sand post oak and wiregrass. Pritchard *et al.* remark these competitive shifts suggest “longleaf pine savannahs may flourish in a future CO₂-enriched world.” If that happens, the trees and

the soil beneath them likely will become a major repository of sequestered carbon. Sand post oak also should do well as the air's CO₂ content increases, significantly enhancing the carbon-sequestering power of the total community, which should undergo a shift from savannah to forest, with a consequent greater storage of both above- and below-ground carbon.

Another study of the suitability of forests as long-term carbon sinks was conducted by Lou *et al.* (2003). They analyzed data from the Duke Forest FACE experiment, in which three 30-meter-diameter plots within a 13-year-old forest (composed primarily of loblolly pines with sweetgum and yellow poplar trees as sub-dominants, together with numerous other trees, shrubs, and vines that occupied still-smaller niches) began to be enriched with an extra 200 ppm of CO₂ in August 1996, while three similar plots were maintained at the ambient atmospheric CO₂ concentration. A number of papers describing different facets of this long-term study have been published, and as recounted by Lou *et al.* they have revealed the existence of a CO₂-induced "sustained photosynthetic stimulation at leaf and canopy levels [Myers *et al.*, 1999; Ellsworth, 2000; Luo *et al.*, 2001; Lai *et al.*, 2002], which has resulted in sustained stimulation of wood biomass increment [Hamilton *et al.*, 2002] and a larger carbon accumulation in the forest floor at elevated CO₂ than at ambient CO₂ [Schlesinger and Lichter, 2001]."

Based on these findings and what they imply about rates of carbon removal from the atmosphere and its different residence times in plant, litter, and soil carbon pools, Luo *et al.* developed a model for studying the sustainability of forest carbon sequestration. Applying this model to a situation where the atmospheric CO₂ concentration gradually rises from a value of 378 ppm in 2000 to a value of 710 ppm in 2100, they calculated the carbon sequestration rate of the Duke Forest would rise from an initial value of 69 g m⁻² yr⁻¹ to a final value of 201 g m⁻² yr⁻¹. That is a far cry from the model-based IPCC projections, which have long suggested forests will have released much of the carbon they had previously absorbed as early as the year 2050 (Pearce, 1999).

The preceding findings fit well with the work of Fan *et al.* (1998), who used atmospheric measurements to calculate the broad-leaf forested region of North America between 15° and 51°N latitude possesses a current carbon sink that can annually remove all the CO₂ emitted into the air from fossil fuel combustion in both Canada and the United

States. Looking to the future, White *et al.* (2000) calculated coniferous and mixed forests north of 50°N latitude likely will expand their northern and southern boundaries by about 50% as a result of the combined effects of increasing atmospheric CO₂, rising temperature, and nitrogen deposition.

Nitrogen deposition is an important variable. White *et al.* (2000) note it can play an interactive role with increasing atmospheric CO₂ to increase plant growth and carbon sequestration. Some researchers, however, have questioned the magnitude of that role. Nadelhoffer *et al.* (1999), for example, conclude nitrogen deposition from human activities is "unlikely to be a major contributor" to the large CO₂ sink that exists in northern temperate forests. Houghton *et al.* (1998), however, suggest nitrogen deposition holds equal weight with CO₂ fertilization in the production of terrestrial carbon sinks; and Lloyd (1999) demonstrates simultaneous CO₂ and nitrogen increases lead to greater modeled forest productivity than what is predicted by the sum of the individual contributions of these two variables.

Thomas *et al.* (2010) used "spatially extensive forest inventory data to discern [1] the effect of nitrogen deposition on the growth and survival of the 24 most common tree species of the northeastern and north-central United States, as well as [2] the effect of nitrogen deposition on carbon sequestration in trees across the breadth of the northeastern US." The four researchers found "nitrogen deposition (which ranged from 3 to 11 kg ha⁻¹ yr⁻¹) enhanced the growth of eleven species and decreased the growth of three species," and "enhanced [the] growth of all tree species with arbuscular mycorrhizal fungi associations." That led to "a 40% enhancement over pre-industrial conditions," which "includes the direct effects of nitrogen deposition on tree growth through soil fertilization, foliar nitrogen uptake and other potential interactions between nitrogen deposition and other environmental changes, including CO₂ fertilization." To give some feeling for the significance of the size of this response, they note it "exceeds the 23% enhancement of net primary production anticipated for the year 2050 from a doubling of atmospheric CO₂ over preindustrial levels, as estimated using free-air CO₂ enrichment studies," citing Norby *et al.* (2005).

Thomas *et al.* thus conclude "nitrogen deposition is an important mechanism contributing to carbon sequestration within these temperate forests," but they maintain this phenomenon is still "unlikely to explain all of the observed terrestrial carbon sink." Nevertheless, it goes a long way toward doing so,

while demonstrating the major benefits of the concomitant increases in the air's CO₂ content and the temperature with which it has interacted over the course of the Industrial Revolution and after, the latter increases of which IPCC characterizes as negatively affecting the biosphere. Clearly, these CO₂ increases are not doing harm, and neither is the concomitant increase in anthropogenic nitrogen deposition. These phenomena have interacted with each other in such a way as to greatly increase the productivity of Earth's forests, both in temperate latitudes, as demonstrated by Thomas *et al.*, and in tropical regions, as revealed by many of the other studies reviewed in this section and chapter.

On a related note, woody plant encroachment upon arid and semiarid grasslands and savannas has been a ubiquitous natural phenomenon experienced throughout the world over the past century or more (Idso, 1995), driven—at least partially, many believe—by the contemporaneous rise in the air's CO₂ concentration (Knapp and Soule, 1998; Soule and Knapp, 1999). This phenomenon may be responsible for sequestering much of the planet's so-called missing carbon, an unidentified but growing repository of organic matter needed to explain the less-than-predicted rate-of-rise of the air's CO₂ content calculated on the basis of known sources and sinks of this important greenhouse gas, as demonstrated by Hibbard *et al.* (2001).

Working in the La Copita Research Area southwest of Alice, Texas, Hibbard *et al.* analyzed several chemical and physical properties of the top ten centimeters of soils in remnant herbaceous areas and patches of woody vegetation in various stages of invasive development. Compared to soils beneath herbaceous vegetation, the soils beneath the tree/shrub areas were found to have much greater concentrations of both carbon (C) and nitrogen (N). A companion study of soil C and N across woody patches ranging in age from 10 to 110 years revealed these variables had experienced a linear increase through time.

The source of these C and N increases was woody plant roots. The authors write they “were surprised by the magnitude of root biomass in surficial soils of woody patches, which greatly exceeded that of herbaceous patches and which greatly exceeded that of foliar litter inputs.” Citing a number of studies of rates of root turnover in herbaceous and woody-plant ecosystems, they conclude “the role of belowground inputs in fueling changes in surficial soil C and N stocks ... accompanying shifts from grass to woody plant domination may therefore be more substantial

than previously appreciated.”

As to how much more substantial such changes might be, the researchers note “the contrasts between woody and herbaceous patches reported here are conservative in that they do not include an assessment of whole plant C and N stocks,” i.e., root biomass below ten centimeters depth and woody biomass aboveground. With respect to the first of these factors, they cite several studies that have detected greater soil C concentrations beneath woody vs. herbaceous vegetation to depths of 100 to 400 centimeters. With respect to the second factor, they likewise cite evidence suggesting “plant C mass has increased tenfold with the conversion of grassland to savanna woodland over the past 100 years.”

As to what their findings imply about the world as a whole, Hibbard *et al.* note since “woody plant expansion into drylands has been geographically widespread over the past century,” and “40% of the terrestrial biosphere consists of arid and semiarid savanna, shrubland, and grassland ecosystems, this type of vegetation change may be of significance to the global C and N cycle.” However, they say, a full understanding of the significance of this phenomenon will require better information on “the historic or modern rate, areal extent, and pattern of woody plant expansion in the world's drylands.”

McCarron *et al.* (2003) measured the effects of shrub encroachment in a mesic grassland on soil CO₂ flux, extractable inorganic N, and N mineralization beneath isolated C₃ shrub communities (islands) of *Cornus drummondii* and surrounding undisturbed native tallgrass prairie at the Konza Prairie Biological Station in northeast Kansas, USA, during the 1999 and 2000 growing seasons. They determined—as had Norris (2000) and Smith (2001) before them—the invasion of mesic grasslands by woody plants leaves soil carbon stores essentially unaltered while greatly boosting aboveground inventories of sequestered carbon. Those observations provide more evidence the invasion of mesic grasslands by shrubs and trees enhances the biological sequestration of carbon in these widespread and globally dispersed ecosystems that cover vast areas of the Earth's surface.

Hyvonen *et al.* (2007) led an international team of forest researchers—22 scientists from nine countries (Belgium, Denmark, France, Finland, Iceland, Italy, Sweden, the United Kingdom, and the United States)—investigating “whether the mature forests that are C sinks today will continue to be sinks as the climate changes.” One way of addressing this question is to look at what has happened to forests that matured several decades ago and have

experienced the concurrent increases in air temperature and atmospheric CO₂ concentration of the past half-century or more, a period over which IPCC claims both of these factors rose at unprecedented rates and to unprecedented levels.

Good candidates for this assessment are old-growth forests, such as those of Amazonia, which for most of the past century were believed to be close to dynamic equilibrium. In one of the first studies to dispel this long-held notion, Phillips and Gentry (1994) analyzed the turnover rates—which are close correlates of net productivity (Weaver and Murphy, 1990)—of 40 tropical forests around the world. They found the growth rates of these forests had been increasing steadily since at least 1960 and had undergone an apparent acceleration in growth rate some time after 1980. A few years later, Phillips *et al.* (1998) analyzed forest growth rate data for the period 1958 to 1996 for several hundred plots of mature tropical trees around the world. They found tropical forest biomass, as a whole, increased substantially over the period of record. The increase in the Neotropics was equivalent to approximately 40% of the missing terrestrial carbon sink of the entire globe. Laurance *et al.* (2004a) reported accelerated growth in the 1990s relative to the 1980s for the large majority (87%) of tree genera in 18 one-hectare plots spanning an area of about 300 km² in central Amazonia, and Laurance *et al.* (2004b) observed similarly accelerated tree community dynamics in the 1990s relative to the 1980s.

This wealth of pertinent positive findings provides strong reason to reject the model-based view of forest carbon sinks turning into forest carbon sources in the decades ahead. If anything, real-world observations suggest today's forest carbon sinks may become even stronger carbon sinks as air temperatures and atmospheric CO₂ concentrations continue to rise.

Agren *et al.* (2007) used official forestry statistics on standing tree volumes and harvests to estimate the standing stock of tree components for each year between 1926 and 2000 throughout all of Sweden for the country's two most dominant tree species—Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*)—which together constituted 80.6% of the country's standing tree stock. For each of these tree components they estimated annual litter production, the decomposition of different litter fractions in the soil, and ultimate turnover rates, with soil carbon stocks for all sites evaluated to a depth of one meter or to bedrock, if bedrock was encountered at less than a meter depth.

Agren *et al.* report “there was a steady increase in carbon stocks in Swedish forests in the period 1926–2000,” such that forest ecosystems in 2000 contained 35% more carbon than they did in 1926, with tree biomass being responsible for nearly three-quarters of the total increase in carbon stocks. For comparative purposes, they note the total amount of carbon sequestered amounted to just under half that emitted to the air by the burning of fossil fuels in Sweden.

With respect to the soil component of the carbon sequestered, the Swedish scientists arrived at a value of 1.7 Tg/year, or just under a quarter of the total sequestered carbon (7.1 Tg/year). In addition, they write, “the current soil carbon stock is not in equilibrium with the current rate of litter production,” as “the increase in soil carbon stocks since 1926 is only 33% of what would be required to be in equilibrium with current tree biomass.” This state of affairs, however, was only to be expected, as Agren and Bosatta (1998) calculate, for forest litter typical of coniferous needles and Swedish climatic conditions, “50% of the steady state value is reached after ca. 200 years but 15,000 years are required to reach 80%.”

Clearly, carbon stocks in Swedish forests have been growing significantly faster than expected, especially considering that from 1951 to 2000, the forested area of the country actually declined by 1%. Modern global warming, atmospheric CO₂ enrichment, nitrogen deposition, and management factors all probably contributed to the increase, which as noted above has compensated for just under half the country's carbon emissions from the burning of fossil fuels. In addition, forest extraction of carbon from the air likely will continue well into the future in Sweden, as Agren *et al.* opine “the time since the last glaciation has probably not been long enough to reach a steady state,” and since the factors that determine steady state appear to be changing in ways that continue to increase the magnitude of the equilibrium condition.

Smittenberg *et al.* (2006) begin their paper by noting “refractory organic matter makes up approximately half of the SOC [soil organic carbon] pool because of its resistance to degradation, and it is this pool that is ultimately responsible for long-term terrestrial carbon storage.” However, they suggest current ideas about the long-term buildup of SOC are questionable because our understanding of the phenomenon is largely derived from studies of present-day soils, due to a paucity of long-term records of SOC dynamics.

To provide more information about this

phenomenon, the scientists worked with high-temporal-resolution sediments of Saanich Inlet, Canada, obtained from seven well-dated cores that contained layers ranging in age from recent to 5,500 years before present, as well as layers just below the well-dated section and a late Pleistocene layer. Smittenberg *et al.* analyzed the distribution, stable carbon isotopic composition, and radiocarbon composition of long-chain *n*-alkanes derived predominantly from C₃ vascular plant material produced upon boreal-forest-covered watersheds that drain into rivers that empty into the inlet. These *n*-alkanes may thus serve as proxies for recalcitrant terrigenous organic matter produced upon the watersheds.

The scientists found the average *n*-alkane ages have been increasing in a near-linear fashion toward the present, strongly suggesting any loss due to mineralization or erosion is still largely outpaced by the accumulation. They interpret this finding to imply “the accumulation of refractory organic carbon in soils that developed after the deglaciation of the American Pacific Northwest is ongoing and may still be far from equilibrium with mineralization and erosion rates.” This further suggests, in their words, “the turnover time of this carbon pool is 10,000 to 100,000 years or more and not 1,000 to 10,000 years as is often used in soil carbon models.”

Smittenberg *et al.* therefore conclude their findings “challenge the notion that the current production of refractory organic matter is balanced by decomposition and erosion after a few thousand years, as inferred via chrono-sequences or soil respiration measurements.” They also state their findings place the terrestrial biosphere “in a more prominent position as a slow but progressively important atmospheric carbon sink on geologic time scales,” and it “may even influence current predictions about carbon cycling and soil carbon storage in response to elevated atmospheric CO₂ levels,” hinting the potential for refractory organic carbon sequestration in a world with a CO₂-accreting atmosphere may be greater than what previously has been believed, but with the effect having its main impact on time scales of more than a thousand years.

Ciais *et al.* (2008a) analyzed national forest inventory data and timber harvest statistics of the EU-15 countries excluding Luxembourg, plus Norway and Switzerland, for the period AD 1950–2000. They found over this half-century interval, the net primary productivity (NPP) of Europe’s forests rose by about 67%, while their biomass carbon stocks rose by approximately 75%. This build-up of forest carbon

stocks, in the words of the 13 researchers, “appears to result from woody NPP exceeding losses by timber harvest and natural disturbances such as fire and wind throw,” and they note their analyses suggests 70–80% of the observed increase in NPP has likely been due to “changes in climate and to the fertilizing effect of CO₂.”

Buttressing their conclusions in this regard, Ciais *et al.* note “another independent model-based analysis that accounted for changing age-classes, management and land use (Zaehle *et al.*, 2006) further indicates that forest NPP increases were mainly driven by climate change and CO₂.” In addition, they note “real increases of biomass increment have occurred and are still occurring,” as “corroborated by tree-ring studies and by measurements of long-term permanent sample plots (Becker *et al.*, 1995; Nicolussi *et al.*, 1995; Spiecker, 1996; Rolland *et al.*, 1998; Motta and Nola, 2001).”

The international group of scientists (from Belgium, China, Finland, France, Germany, Italy, the Netherlands, Romania, and the United States) write, “European forests still have the potential to realize a build-up of their carbon stocks by a factor of two, within the next century.” However, they state this “potential CO₂ sink is threatened by the proposal of the European Commission to increase the share of renewable energy to 20% of the total energy consumption by 2020,” and “this will almost double the wood demand for biomass energy (Ragwitz *et al.*, 2005) in the EU-15 from 55% of harvested wood in 2001 to 100% in 2020 at current harvest levels.” Summing up this latter situation, Ciais *et al.* conclude “a return to using wood as biofuel ... could cancel out the benefits of carbon storage over the past five decades.”

Lewis *et al.* (2009) invested a great amount of time and effort in documenting changes in aboveground carbon storage in “79 permanent sample plots spanning 40 years (1968–2007), located in closed-canopy moist forest, spanning West, Central and Eastern Africa,” based on data from more than 70,000 individual trees across ten countries. They found “aboveground carbon storage in live trees increased by 0.63 Mg C ha⁻¹ year⁻¹ between 1968 and 2007,” and “extrapolation to unmeasured forest components (live roots, small trees, necromass) and scaling to the continent implies a total increase in carbon storage in African tropical forest trees of 0.34 Pg C year⁻¹.”

The 33 researchers say the observed changes in carbon storage “are similar to those reported for Amazonian forests per unit area, providing evidence

that increasing carbon storage in old-growth forests is a pan-tropical phenomenon,” and “combining all standardized inventory data from this study and from tropical America and Asia together yields a comparable figure of 0.49 Mg C ha⁻¹ year⁻¹.” This equates to “a carbon sink of 1.3 Pg C year⁻¹ across all tropical forests during recent decades,” which can account for roughly half of the so-called missing carbon sink.

In identifying the driving force that breathed new life into old trees, Lewis *et al.* write in the concluding sentence of the abstract of their paper, “taxon-specific analyses of African inventory and other data suggest that widespread changes in resource availability, such as increasing atmospheric carbon dioxide concentrations, may be the cause of the increase in carbon stocks, as some theory (Lloyd and Farquhar, 1996) and models (Friedlingstein *et al.*, 2006; Stephens *et al.*, 2007; Ciais *et al.*, 2008b) predict.”

All these findings indicate elevated CO₂ enhances photosynthetic rates and biomass production in forest trees, both of which lead to greater amounts of carbon sequestration. Elevated CO₂ also enhances carbon sequestration by reducing carbon losses arising from plant respiration. Karnosky *et al.* (1999), for example, report aspen seedlings grown for one year at 560 ppm CO₂ displayed dark respiration rates 24% lower than rates exhibited by trembling aspen grown at 360 ppm CO₂. Also, elevated CO₂ has been shown to decrease maintenance respiration, which it did by 60% in western hemlock seedlings exposed to an atmospheric CO₂ concentration of nearly 1,600 ppm (McDowell *et al.*, 1999).

In a thorough review of these topics, Drake *et al.* (1999) conclude, on average, a doubling of the atmospheric CO₂ concentration reduces plant respiration rates by approximately 17%. This finding contrasts strikingly with the much smaller effects reported by Amthor (2000), who found an average reduction in dark respiration of only 1.5% for nine deciduous tree species exposed to 800 ppm CO₂. The period of CO₂ exposure in his much-shorter experiments, however, was but a mere 15 minutes. Thus, if the air’s CO₂ content doubles, plants will likely sequester something on the order of 17% more carbon than ambiently grown plants, solely as a consequence of CO₂-induced reductions in respiration. This stored carbon is in addition to that sequestered as a result of CO₂-induced increases in plant photosynthetic rates.

Still, some researchers have expressed concern about the fate of the extra carbon stored in plant tissues as a consequence of atmospheric CO₂

enrichment, fearing it may rapidly return to the atmosphere following tissue senescence and decomposition, as opposed to being locked away for long periods of time.

In addressing such concerns, it is important to note atmospheric CO₂ enrichment typically reduces, or has no effect upon, decomposition rates of senesced plant material. De Angelis *et al.* (2000), for example, note when leaf litter from Mediterranean forest species exposed to 710 ppm CO₂ for 3.5 years was collected and allowed to decompose at 710 ppm CO₂ for approximately one year, it decomposed at a rate 4% less than leaf litter produced and incubated at ambient CO₂ for one year. Similarly, leaf litter collected from yellow-poplar (*Liriodendron tulipifera*) seedlings exposed to 700 ppm CO₂ for four years contained 12% more biomass than leaf litter collected from seedlings grown at ambient CO₂, following two years of decomposition at their respective CO₂ growth concentrations (Scherzel *et al.*, 1998). Hirschel *et al.* (1997) found no significant CO₂-induced effects on decomposition rates in tropical rainforest species, as Scherzel *et al.* (1998) also found for eastern white pine (*Pinus strobes*). Others have reported similar findings.

Cotrufo *et al.* (1998) grew two-year-old ash and sycamore seedlings for one growing season in closed-top chambers maintained at atmospheric CO₂ concentrations of 350 and 600 ppm. The high-CO₂ air increased lignin contents in the litter produced from both tree species, which likely contributed to the decreased litter decomposition rates observed in the CO₂-enriched chambers. After one year of incubation, for example, litter bags from the CO₂-enriched trees of both species had about 30 percent more dry mass remaining in them than litter bags from the ambient trees. In addition, woodlouse arthropods consumed 16 percent less biomass when fed litter generated from seedlings grown at 600 ppm CO₂ than when fed litter generated from seedlings grown in ambient air.

Cotrufo and Ineson (2000) grew beech seedlings for five years in open-top chambers fumigated with air containing either 350 or 700 ppm CO₂. Subsequently, woody twigs from each CO₂ treatment were collected and incubated in native forest soils for 42 months. They determined there was no significant effect of the differential CO₂ exposure during growth on subsequent woody twig decomposition, although the mean decomposition rate of the CO₂-enriched twigs was 5 percent less than the ambient-treatment twigs.

Conway *et al.* (2000) grew two-year-old ash tree seedlings in solar domes maintained at atmospheric

CO₂ concentrations of 350 and 600 ppm, after which naturally senesced leaves were collected, inoculated with various fungal species, and incubated for 42 days. They found the elevated CO₂ significantly reduced the amount of nitrogen in the senesced leaves, thus giving the CO₂-enriched leaf litter a higher carbon-to-nitrogen ratio than the litter collected from the seedlings growing in ambient air. This change likely contributed to the observed reductions in the amount of fungal colonization present on the senesced leaves from the CO₂-enriched treatment, which would be expected to result in reduced rates of leaf decomposition.

King *et al.* (2001) grew aspen seedlings for five months in open-top chambers receiving atmospheric CO₂ concentrations of 350 and 700 ppm. At the end of this period, they collected naturally senesced leaf litter, analyzed it, and allowed it to decompose under ambient conditions for 111 days. Although the elevated CO₂ slightly lowered leaf litter nitrogen content, it had no effect on litter sugar, starch, or tannin concentrations. With little to no CO₂-induced effects on leaf litter quality, there was no CO₂-induced effect on litter decomposition.

Dilustro *et al.* (2001) erected open-top chambers around portions of a regenerating oak-palmetto scrub ecosystem in Florida, USA and maintained them at CO₂ concentrations of either 350 or 700 ppm. They then incubated ambient- and elevated-CO₂-produced fine roots for 2.2 years in the chamber soils, which were nutrient-poor and often water-stressed. They found the elevated CO₂ did not significantly affect the decomposition rates of the fine roots originating from either the ambient or CO₂-enriched environments.

Thus it would appear the ongoing rise in the air's CO₂ content will not materially alter the rate of decomposition of the world's soil organic matter. This means the rate at which carbon is sequestered in forest soils should continue to increase as the productivity of Earth's plants is increased by the aerial fertilization effect of the rising atmospheric CO₂ concentration.

Another concern, which for a time was thought to limit the sequestering power of forests under rising atmospheric CO₂ but which has been thoroughly debunked, is what has come to be known as the progressive nitrogen limitation hypothesis. Some researchers suggested the striking CO₂-induced growth enhancements initially experienced by woody plants in scientific studies would disappear gradually over time, as the plants slowly deplete the soils in which they are growing of their initial store of nitrogen.

Long-term atmospheric CO₂-enrichment experiments show this progressive nitrogen limitation hypothesis is not supported by real-world data, as even soils low in nitrogen at the start of many long-term atmospheric CO₂ enrichment experiments have continued to supply sufficient nitrogen to maintain the initial high level of the CO₂-induced stimulation of plant growth.

In the introduction to a paper on the subject that summarizes nine years of work at the Duke Forest FACE experiment in North Carolina (USA), where portions of an aggrading loblolly pine (*Pinus taeda*) plantation had been continuously exposed to an extra 200 ppm of CO₂ since 1996, Lichter *et al.* (2008) note progressive nitrogen limitation (PNL) may “accompany C sequestration in plants and soils stimulated by CO₂ fertilization, gradually attenuating the CO₂ response.” They then describe what they learned about this PNL hypothesis over the nine years of the Duke Forest experiment.

First, the nine researchers report their data pertaining to forest-floor carbon pools indicate the existence of “a long-term steady-state sink” of about 30 g C per m² per year, which represents “a substantial increase in forest-floor C storage under elevated CO₂ (i.e. 29%),” and which they attribute to “increased litterfall and root turnover during the first 9 years of the study.” Second, below the forest floor, they say, of the mineral soil C formed during the past nine years, “approximately 20% has been allocated to stable pools that will likely remain protected from microbial activity and associated release as CO₂.”

The research team also found “a significant widening of the C:N ratio of soil organic matter in the upper mineral soil under both elevated and ambient CO₂,” which suggests, as they describe it, “enhanced rates of soil organic matter decomposition are increasing mineralization and uptake to provide the extra N required to support the observed increase in primary productivity under elevated CO₂.” Pritchard *et al.* (2008) report this CO₂-induced increase in productivity amounts to approximately 30% annually, and they add there is “little evidence to indicate a diminished response through time,” citing Finzi *et al.* (2007), who found the same to be true at the long-term forest FACE studies being conducted at Rhinelander, Wisconsin (USA), Oak Ridge National Laboratory (USA), and Tuscania (Italy).

Thus, contrary to the PNL hypothesis, in the case of North Carolina's Duke Forest, “even after nine years of experimental CO₂ fertilization,” as Lichter *et al.* describe it, “attenuation of the CO₂-induced productivity enhancement has not been observed.”

This finding at this location is extremely significant, because the growth of pine-hardwood forests in the southeastern United States often removes so much nitrogen from the soils in which they grow that they induce what Finzi and Schlesinger (2003) describe as “a state of acute nutrient deficiency that can only be reversed with fertilization.” No fertilization was done during the Duke Forest FACE study.

Langley *et al.* (2009) note “it has been suggested that stimulation of productivity with elevated CO₂ ties up nitrogen in plant litter, which, if not offset by increases in N-use efficiency or N supply, will limit the ecosystem CO₂ response,” citing Reich *et al.* (2006). The six scientists “employed an acid-hydrolysis-incubation method and a net nitrogen-mineralization assay to assess stability of soil carbon pools and short-term nitrogen dynamics in a Florida scrub-oak ecosystem after six years of exposure to elevated CO₂,” at a multiple open-top-chamber facility on a barrier island located at NASA’s Kennedy Space Center on the east coast of central Florida, USA. Langley *et al.* report elevated atmospheric CO₂ (to 350 ppm above ambient concentrations) tended to increase net N mineralization in the top 10 cm of the soil, but it also decreased total soil organic carbon content there by 21%. That loss of carbon mass was equivalent to only “roughly one-third of the increase in plant biomass that occurred in the same experiment.” In addition, the strongest increases in net N mineralization were observed in the 10–30 cm depth increment, and “release of N from this depth may have allowed the sustained CO₂ effect on productivity in this scrub-oak forest,” which over the four years leading up to their study “increased litterfall by 19–59%,” according to Hungate *et al.* (2006).

Much more information rebutting the PNL hypothesis is presented in Chapter 3, Section 3.11, where it is demonstrated atmospheric CO₂ enrichment generally enables plants to find the extra nitrogen they need to take full advantage of the aerial fertilization effect of elevated atmospheric CO₂ concentrations, which increases total ecosystem carbon content, resulting in a negative feedback to anthropogenic CO₂ emissions. As the air’s CO₂ content rises, the ability of forests to sequester carbon rises along with it, while tempering the rate of rise of the air’s CO₂ content.

References

- Agren, G.I. and Bosatta, E. 1998. *Theoretical Ecosystem Ecology—Understanding Element Cycles*. Cambridge University Press, Cambridge, UK.
- Agren, G.I., Hyvonen, R., and Nilsson, T. 2007. Are Swedish forest soils sinks or sources for CO₂—model analyses based on forest inventory data. *Biogeochemistry* **82**: 217–227.
- Amthor, J.S. 2000. Direct effect of elevated CO₂ on nocturnal in situ leaf respiration in nine temperate deciduous tree species is small. *Tree Physiology* **20**: 139–144.
- Barton, C.V.M. and Jarvis, P.G. 1999. Growth response of branches of *Picea sitchensis* to four years exposure to elevated atmospheric carbon dioxide concentration. *New Phytologist* **144**: 233–243.
- Becker, M., *et al.* 1995. In: Landmann, G. and Bonneau, M. (Eds.) *Forest Decline and Atmospheric Deposition Effects in the French Mountains*. Springer-Verlag, Berlin, Germany, pp. 120–142.
- Chambers, J.Q., Higuchi, N., and Schimel, J.P. 1998. Ancient trees in Amazonia. *Nature* **391**: 135–136.
- Ciais, P., Piao, S.-L., Cadule, P., Friedlingstein, P., and Chedin, A. 2008b. Variability and recent trends in the African carbon balance. *Biogeosciences* **5**: 3497–3532.
- Ciais, P., Schelhaas, M.J., Zaehle, S., Piao, S.L., Cescatti, A., Liski, J., Luyssaert, S., Le-Maire, G., Schulze, E.-D., Bouriaud, O., Freibauer, A., Valentini, R., and Nabuurs, G.J. 2008a. Carbon accumulation in European forests. *Nature Geoscience* **1**: 425–429.
- Conway, D.R., Frankland, J.C., Saunders, V.A., and Wilson, D.R. 2000. Effects of elevated atmospheric CO₂ on fungal competition and decomposition of *Fraxinus excelsior* litter in laboratory microcosms. *Mycology Research* **104**: 187–197.
- Cotrufo, M.F. and Ineson, P. 2000. Does elevated atmospheric CO₂ concentration affect wood decomposition? *Plant and Soil* **224**: 51–57.
- Cotrufo, M.F., Briones, M.J.I., and Ineson, P. 1998. Elevated CO₂ affects field decomposition rate and palatability of tree leaf litter: importance of changes in substrate quality. *Soil Biology and Biochemistry* **30**: 1565–1571.
- De Angelis, P., Chigwerewe, K.S., and Mugnozza, G.E.S. 2000. Litter quality and decomposition in a CO₂-enriched Mediterranean forest ecosystem. *Plant and Soil* **224**: 31–41.
- Dilustro, J.J., Day, F.P., and Drake, B.G. 2001. Effects of

elevated atmospheric CO₂ on root decomposition in a scrub oak ecosystem. *Global Change Biology* **7**: 581–589.

Drake, B.G., Azcon-Bieto, J., Berry, J., Bunce, J., Dijkstra, P., Farrar, J., Gifford, R.M., Gonzalez-Meler, M.A., Koch, G., Lambers, H., Siedow, J., and Wullschlegel, S. 1999. Does elevated atmospheric CO₂ inhibit mitochondrial respiration in green plants? *Plant, Cell and Environment* **22**: 649–657.

Ellsworth, D.S. 2000. Seasonal CO₂ assimilation and stomatal limitations in a *Pinus taeda* canopy with varying climate. *Tree Physiology* **20**: 435–444.

Fan, S., Gloor, M., Mahlman, J., Pacala, S., Sarmiento, J., Takahashi, T., and Tans, P. 1998. A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. *Science* **282**: 442–446.

Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., and Ceulemans, R. 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂. *Proceedings of the National Academy of Sciences, USA* **104**: 14,014–14,019.

Finzi, A.C. and Schlesinger, W.H. 2003. Soil-nitrogen cycling in a pine forest exposed to 5 years of elevated carbon dioxide. *Ecosystems* **6**: 444–456.

Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H.D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K.-G., Schnur, R., Strassmann, K., Weaver, A.J., Yoshikawa, C., and Zeng, N. 2006. Climate-carbon cycle feedback analysis: Results from the (CMIP)-M-4 model intercomparison. *Journal of Climate* **19**: 3337–3353.

Hamilton, J.G., DeLucia, E.H., George, K., Naidu, S.L., Finzi, A.C., and Schlesinger, W.H. 2002. Forest carbon balance under elevated CO₂. *Oecologia* DOI 10.1007/s00442-002-0884-x.

Hibbard, K.A., Archer, S., Schimel, D.S., and Valentine, D.W. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* **82**: 1999–2011.

Hirschel, G., Körner, C., and Arnone III, J.A. 1997. Will rising atmospheric CO₂ affect leaf litter quality and in situ decomposition rates in native plant communities? *Oecologia* **110**: 387–392.

Houghton, R.A., Davidson, E.A., and Woodwell, G.M. 1998. Missing sinks, feedbacks, and understanding the role of terrestrial ecosystems in the global carbon balance. *Global Biogeochemical Cycles* **12**: 25–34.

Houpis, J.L.J., Anderson, P.D., Pushnik, J.C., and Anschel, D.J. 1999. Among-provenance variability of gas exchange and growth in response to long-term elevated CO₂ exposure. *Water, Air, and Soil Pollution* **116**: 403–412.

Hungate, B.A., Johnson, D.W., Dijkstra, P., Hymus, G., Stiling, P., Megonigal, J.P., Pagel, A.L., Moan, J.L., Day, F., Li, J., Hinkle, C.R., and Drake, B.G. 2006. Nitrogen cycling during seven years of atmospheric CO₂ enrichment in a scrub oak woodland. *Ecology* **87**: 26–40.

Hyvonen, R., Agren, G.I., Linder, S., Persson, T., Cotrufo, M.F., Ekblad, A., Freeman, M., Grelle, A., Janssens, I.A., Jarvis, P.G., Kellomaki, S., Lindroth, A., Loustau, D., Lundmark, T., Norby, R.J., Oren, R., Pilegaard, K., Ryan, M.G., Sigurdsson, B.D., Stromgren, M., van Oijen, M., and Wallin, G. 2007. The likely impact of elevated [CO₂], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytologist* **173**: 463–480.

Idso, S.B. 1995. *CO₂ and the Biosphere: The Incredible Legacy of the Industrial Revolution*. Special Publication, Kuehnast Lecture Series. Department of Soil, Water & Climate, University of Minnesota, St. Paul, Minnesota, USA.

Karberg, N.J., Pregitzer, K.S., King, J.S., Friend, A.L., and Wood, J.R. 2005. Soil carbon dioxide partial pressure and dissolved inorganic carbonate chemistry under elevated carbon dioxide and ozone. *Oecologia* **142**: 296–306.

Karnosky, D.F., Mankovska, B., Percy, K., Dickson, R.E., Podila, G.K., Sober, J., Noormets, A., Hendrey, G., Coleman, M.D., Kubiske, M., Pregitzer, K.S., and Isebrands, J.G. 1999. Effects of tropospheric O₃ on trembling aspen and interaction with CO₂: results from an O₃-gradient and a FACE experiment. *Water, Air, and Soil Pollution* **116**: 311–322.

King, J.S., Pregitzer, K.S., Zak, D.R., Kubiske, M.E., Ashby, J.A., and Holmes, W.E. 2001. Chemistry and decomposition of litter from *Populus tremuloides* Michaux grown at elevated atmospheric CO₂ and varying N availability. *Global Change Biology* **7**: 65–74.

Knapp, P.A. and Soule, P.T. 1998. Recent *Juniperus occidentalis* (Western Juniper) expansion on a protected site in central Oregon. *Global Change Biology* **4**: 347–357.

Lai, C.T., Katul, G., Butnor, J., Ellsworth, D., and Oren, R. 2002. Modeling nighttime ecosystem respiration by a constrained source optimization method. *Global Change Biology* **8**: 124–141.

Langley, J.A., McKinley, D.C., Wolf, A.A., Hungate, B.A., Drake, B.G., and Megonigal, J.P. 2009. Priming depletes soil carbon and releases nitrogen in a scrub-oak ecosystem exposed to elevated CO₂. *Soil Biology & Biochemistry* **41**: 54–60.

Climate Change Reconsidered II: Biological Impacts

- Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Condit, R., D'Angelo, S., and Andrade, A. 2004b. Inferred longevity of Amazonian rainforest trees based on a long-term demographic study. *Forest Ecology and Management* **190**: 131–143.
- Laurance, W.F., Oliveira, A.A., Laurance, S.G., Condit, R., Nascimento, H.E.M., Sanchez-Thorin, A.C., Lovejoy, T.E., Andrade, A., D'Angelo, S., and Dick, C. 2004a. Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* **428**: 171–175.
- Lewis, S.L., Lopez-Gonzalez, G., Sonke, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo K., M.-N., Ewango, C.E.N., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J.C., Makana, J.-R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K. S.-H., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R., and Woll, H. 2009. Increasing carbon storage in intact African tropical forests. *Nature* **457**: 1003–1006.
- Lichter, J., Billings, S.A., Ziegler, S.E., Gaindh, D., Ryals, R., Finzi, A.C., Jackson, R.B., Stemmler, E.A., and Schlesinger, W.H. 2008. Soil carbon sequestration in a pine forest after 9 years of atmospheric CO₂ enrichment. *Global Change Biology* **14**: 2910–2922.
- Lloyd, J. 1999. The CO₂ dependence of photosynthesis, plant growth responses to elevated CO₂ concentrations and their interaction with soil nutrient status, II. Temperate and boreal forest productivity and the combined effects of increasing CO₂ concentrations and increased nitrogen deposition at a global scale. *Functional Ecology* **13**: 439–459.
- Lloyd, J. and Farquhar, G.D. 1996. The CO₂ dependence of photosynthesis, plant growth responses to elevated atmospheric CO₂ concentrations and their interaction with soil nutrient status. 1. General principles and forest ecosystems. *Functional Ecology* **10**: 4–32.
- Luo, Y., Medlyn, B., Hui, D., Ellsworth, D., Reynolds, J., and Katul, G. 2001. Gross primary productivity in the Duke Forest: Modeling synthesis of the free-air CO₂ enrichment experiment and eddy-covariance measurements. *Ecological Applications* **11**: 239–252.
- Luo, Y., White, L.W., Canadell, J.G., DeLucia, E.H., Ellsworth, D.S., Finzi, A., Lichter, J., and Schlesinger, W.H. 2003. Sustainability of terrestrial carbon sequestration: A case study in Duke Forest with inversion approach. *Global Biogeochemical Cycles* **17**: 10.1029/2002GB001923.
- Marek, M.V., Sprtova, M., De Angelis, P., and Scarascia-Mugnozza, G. 2001. Spatial distribution of photosynthetic response to long-term influence of elevated CO₂ in a Mediterranean *macchia* mini-ecosystem. *Plant Science* **160**: 1125–1136.
- McCarron, J.K., Knapp, A.K., and Blair, J.M. 2003. Soil C and N responses to woody plant expansion in a mesic grassland. *Plant and Soil* **257**: 183–192.
- McDowell, N.G., Marshall, J.D., Qi, J., and Mattson, K. 1999. Direct inhibition of maintenance respiration in western hemlock roots exposed to ambient soil carbon dioxide concentrations. *Tree Physiology* **19**: 599–605.
- Motta, R. and Nola, P. 2001. Growth trends and dynamics in sub-alpine forest stands in the Varaita Valley (Piedmont, Italy) and their relationships with human activities and global change. *Journal of Vegetation Science* **12**: 219–230.
- Myers, D.A., Thomas, R.B., and DeLucia, E.H. 1999. Photosynthetic capacity of loblolly pine (*Pinus taeda* L.) trees during the first year of carbon dioxide enrichment in a forest ecosystem. *Plant, Cell and Environment* **22**: 473–481.
- Nadelhoffer, K.J., Emmett, B.A., Gundersen, P., Kjonaas, O.J., Koopmans, C.J., Schleppi, P., Tietema, A., and Wright, R.F. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature* **398**: 145–148.
- Nicolussi, K., Bortenschlager, S., and Körner, C. 1995. Increase in tree-ring width in subalpine *Pinus cembra* from the central Alps that may be CO₂-related. *Trees* **9**: 181–189.
- Norris, M. 2000. *Biogeochemical Consequences of Land Cover Change in Eastern Kansas*. In: Division of Biology, Kansas State University, Manhattan, Kansas, USA.
- Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, S.J., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., De Angelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarasci-Mugnozza, G.E., Schlesinger, W.H., and Oren, R. 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences* **102**: 18,052–18,056.
- Norby, R.J., Ledford, J., Reilly, C.D., Miller, N.E., and O'Neill, E.G. 2004. Fine-root production dominates response of a deciduous forest to atmospheric CO₂ enrichment. *Proceedings of the National Academy of Sciences USA* **101**: 9689–9693.
- Pearce, F. 1999. That sinking feeling. *New Scientist* **164** (2209): 20–21.
- Phillips, O.L. and Gentry, A.H. 1994. Increasing turnover through time in tropical forests. *Science* **263**: 954–958.
- Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Nunez, P.V., Vasquez, R.M., Laurance, S.G., Ferreira, L.V., Stern, M., Brown, S., and Grace, J. 1998. Changes in the carbon balance of tropical forests: Evidence from long-term plots. *Science* **282**: 439–442.

- Pregitzer, K.S., Zak, D.R., Maziasz, J., DeForest, J., Curtis, P.S., and Lussenhop, J. 2000. Interactive effects of atmospheric CO₂ and soil-N availability on fine roots of *Populus tremuloides*. *Ecological Applications* **10**: 18–33.
- Pritchard, S.G., Davis, M.A., Mitchell, R.J., Prior, A.S., Boykin, D.L., Rogers, H.H., and Runion, G.B. 2001. Root dynamics in an artificially constructed regenerating longleaf pine ecosystem are affected by atmospheric CO₂ enrichment. *Environmental and Experimental Botany* **46**: 35–69.
- Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., and Oren, R. 2008. Mycorrhizal and rhizomorph dynamics in a loblolly pine forest during 5 years of free-air-CO₂-enrichment. *Global Change Biology* **14**: 1–13.
- Ragwitz et al. 2005. FORRES Analysis of the Renewable Energy Sources' Evolution up to 2020. Final Report. (Karlsruhe, 2005).
- Rasineni, G.K., Guha, A., and Reddy, A.R. 2011. Responses of *Gmelina arborea*, a tropical deciduous tree species, to elevated atmospheric CO₂: Growth, biomass productivity and carbon sequestration efficacy. *Plant Science* **181**: 428–438.
- Raymond, P.A. and Cole, J.J. 2003. Increase in the export of alkalinity from North America's largest river. *Science* **301**: 88–91.
- Reich, P.B., Hungate, B.A., and Luo, Y. 2006. Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology, Evolution and Systematics* **37**: 611–636.
- Rolland, C., Petitcolas, V., and Michalet, R. 1998. Changes in radial tree growth for *Picea abies*, *Larix deciduas*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline since 1750. *Trees* **13**: 40–50.
- Saxe, H., Ellsworth, D.S., and Heath, J. 1998. Tree and forest functioning in an enriched CO₂ atmosphere. *New Phytologist* **139**: 395–436.
- Scherzel, A.J., Rebbeck, J., and Boerner, R.E.J. 1998. Foliar nitrogen dynamics and decomposition of yellow-poplar and eastern white pine during four seasons of exposure to elevated ozone and carbon dioxide. *Forest Ecology and Management* **109**: 355–366.
- Schlesinger, W.H. and Lichter, J. 2001. Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO₂. *Nature* **411**: 466–469.
- Smith, D. 2001. Changes in Carbon Cycling as Forests Expand into Tallgrass Prairie: Mechanisms Driving Low Soil Respiration Rates in Juniper Forests. In: Division of Biology, Kansas State University, Manhattan, Kansas, USA.
- Smittenberg, R.H., Eglinton, T.I., Schouten, S., and Damste, J.S.S. 2006. Ongoing buildup of refractory organic carbon in boreal soils during the Holocene. *Science* **314**: 1283–1286.
- Soule, P.T. and Knapp, P.A. 1999. Western juniper expansion on adjacent disturbed and near-relict sites. *Journal of Range Management* **52**: 525–533.
- Spiecker, H. 1996. *Growth Trends in European Forests*. European Forest Institute Research Report 5. Springer-Verlag, Berlin, Germany.
- Stephens, B.B., Gurney, K.R., Tans, P.P., Sweeney, C., Peters, W., Bruhwiler, L., Ciais, P., Ramonet, M., Bousquet, P., Nakazawa, T., Aoki, S., Machida, T., Inoue, G., Vinnichenko, N., Lloyd, J., Jordan, A., Heimann, M., Shibistova, O., Langenfelds, R.L., Steele, L.P., Francey, R.J., and Denning, A.S. 2007. Weak northern and strong tropical land carbon uptake from vertical profiles of atmospheric CO₂. *Science* **316**: 1732–1735.
- Thomas, R.Q., Canham, C.D., Weathers, K.C., and Goodale, C.L. 2010. Increased tree carbon storage in response to nitrogen deposition in the US. *Nature Geoscience* **3**: 13–17.
- Wang, Z.A. and Cai, W.-J. 2004. Carbon dioxide degassing and inorganic carbon export from a marsh-dominated estuary (the Duplin River): A marsh CO₂ pump. *Limnology and Oceanography* **49**: 341–354.
- Weaver, P.L. and Murphy, P.G. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica* **22**: 69–82.
- White, A., Cannell, M.G.R., and Friend, A.D. 2000. The high-latitude terrestrial carbon sink: a model analysis. *Global Change Biology* **6**: 227–245.
- Zaehle, S., Sitch, S., Prentice, I.C., Liski, J., Cramer, W., Erhard, M., Hickler, T., and Smith, B. 2006. The importance of age-related decline in forest NPP for modeling regional carbon balances. *Ecological Applications* **16**: 1555–1574.
- Zak, D.R., Pregitzer, K.S., Curtis, P.S., Vogel, C.S., Holmes, W.E., and Lussenhop, J. 2000. Atmospheric CO₂, soil-N availability, and allocation of biomass and nitrogen by *Populus tremuloides*. *Ecological Applications* **10**: 34–46.

1.2.1.4.2 The Influence of Temperature

- If air temperatures rise in the future they likely will have a positive effect on carbon storage in forests and their associated soils.

The planting of forests with the objective of removing CO₂ from the atmosphere and sequestering its carbon

in soil organic matter—which tends to slow the rate of rise of the air's CO₂ content—has come under fire as being only a stopgap measure in the quest to moderate global warming. Pearce (1999) even referred to the concept as a dangerous delusion, saying “planned new forests, called ‘carbon sinks,’ will swiftly become saturated with carbon and begin returning most of their carbon to the atmosphere.”

The rationale for this contention was that rising temperatures will increase rates of soil respiration, thereby causing forest ecosystems to return CO₂ to the air at a faster rate than they remove it from the atmosphere via photosynthesis. Proponents of the theory argue future rates of photosynthesis will “flatten out,” according to Pearce, and respiration rates will “soar.” Much like the theory of CO₂-induced global warming, however, a number of studies have shown quite conclusively this theory is not supported by real-world observations, which in fact directly contradict the theory.

A data-driven analysis by Fan *et al.* (1998) revealed the carbon-sequestering abilities of North America's forests between 15 and 51°N latitude are so robust they can yearly remove from the atmosphere all of the CO₂ annually released to it by fossil fuel consumption in both the United States and Canada—and this calculation was done during a time said to have the warmest temperatures on record. Similarly, Phillips *et al.* (1998) demonstrate carbon sequestration in tropical forests has increased substantially over the past 42 years in spite of any temperature increases during that time.

Liski *et al.* (1999) studied soil carbon storage across a temperature gradient in a modern-day Finnish boreal forest, reporting carbon sequestration in the soil of this forest increased with temperature. Contemporaneously, King *et al.* (1999) showed aspen seedlings increased their photosynthetic rates and biomass production as temperatures rose from 10 to 29°C, putting to rest the idea that high-temperature-induced increases in respiration rates would cause net losses in carbon fixation.

Giardina and Ryan (2000) analyzed organic carbon decomposition data derived from forest soils of 82 sites on five continents. Based on this worldwide assemblage of real-world data, they state carbon decomposition rates “are not controlled by temperature limitations to microbial activity, and that increased temperature alone will not stimulate the decomposition of forest-derived carbon in mineral soil.” They report, “despite a 20°C gradient in mean annual temperature,” soil carbon mass loss was “insensitive to temperature.”

A group of 30 scientists (Valentini *et al.*, 2000) collected data on net ecosystem carbon exchange in 15 European forests, and they report their results “confirm that many European forest ecosystems act as carbon sinks.” Their data also demonstrate the warmer forests of southern Europe annually sequester far more carbon than the cooler forests of northern Europe, again in direct contradiction of claims warmer temperatures must inevitably lead to forest carbon loss.

Grace and Rayment (2000) present still more evidence refuting the claim forests “will swiftly become saturated with carbon and begin returning most of their carbon to the atmosphere.” Specifically, they cite a number of additional studies that “show quite clearly,” as they put it, “that old undisturbed forests, as well as middle-aged forests, are net absorbers of CO₂.” They also note these real-world observations mean “forests are serving as a carbon sink, providing a global environmental service by removing CO₂ from the atmosphere and thus reducing the rate of CO₂-induced warming.” Further commenting on the work of Giardina and Ryan (2000) and Valentini *et al.* (2000), Grace and Rayment unequivocally state, “the results from these two papers should send a powerful message to those working with models of global vegetation change,” namely, “that the doomsday view of runaway global warming now seems unlikely.”

One of the simpler ways Earth's deciduous forests increase their storage of carbon is to leaf out progressively earlier each spring and remain photosynthetically active increasingly later every fall. This gradual lengthening of the growing season allows trees to remove more carbon dioxide from the atmosphere each succeeding year. This phenomenon, in turn, reduces the annual rate of rise of the air's CO₂ content, completing a negative feedback loop that slows the CO₂-induced portion of the warming that originally set the whole process in motion.

White *et al.* (1999) investigated in detail several aspects of this multistage phenomenon in a study of 88 years of data spanning the period 1900 to 1987, obtained from 12 locations in the eastern U.S. deciduous forest from Charleston, SC (32.8°N latitude) to Burlington, VT (44.5°N latitude). They determined a 1°C increase in mean annual air temperature increased the length of the forest's growing season by approximately five days. In addition, they demonstrated this relationship was linear over the entire mean annual air temperature range investigated, which stretched from 7 to 19°C and included growing seasons ranging in length from

150 to 210 days.

The second step of White *et al.*'s analysis was a bit more complicated, as they had to determine how much extra CO₂ was removed from the air for each day's temperature-induced extension of the growing season. They began by using an ecosystem process model that had previously been validated in other studies to predict carbon fluxes for the 12 forest sites. Using daily meteorological data, the model first calculated annual dates of the appearance and disappearance of "greenness"—the length of the photosynthetically active growing season—for each of the 88 years of records at each site. Then it calculated the net ecosystem production (NEP = gross primary production minus the sum of autotrophic and heterotrophic respiration) for each day of the 88 growing seasons at each site and summed each year's results to obtain 88 annual NEP totals for each site.

Plotting these yearly totals of net CO₂ removal from the atmosphere as functions of yearly growing season length for each site, White *et al.* report a one-day extension in growing season increased the mean forest NEP of the 12 sites by 1.6%, with greater increases in the colder northern sites (1.9% for Burlington, VT) and smaller increases in the warmer southern sites (1.4% for Charleston, SC).

As for how significant these numbers are, if Earth were to undergo a mean global warming of 1°C, according to the first of the two relationships derived by White *et al.*, this temperature increase would result in the eastern U.S. deciduous forest increasing the length of its growing season by approximately five days. Their second relationship suggests this growing season expansion would lead to an 8% increase in total carbon sequestration (5 days x 1.6% per day = 8%).

Moreover, this temperature-driven phenomenon may be much stronger than is implied by this simple exercise. In a study of 30 years of phenological data derived from observations of identical clones of trees and shrubs maintained by the European network of the International Phenological Gardens—located in the area bounded by latitudes 42 and 69° N and by longitudes 10° W and 27° E—Menzel and Fabian (1999) report the mean date of spring bud-break had increased by fully six days "since the early 1960s," and leaf senescence in the fall was delayed by an average of 4.8 days over the same period. Using the northernmost NEP enhancement factor derived by White *et al.*—which in all likelihood is a conservative choice, as White *et al.*'s northernmost forest site is at about the same latitude as the southernmost part of the latitudinal gradient spanned by Menzel and

Fabian's study area—the 10.8 extra warming-induced growing-season days produce a 20.5% increase in annual carbon sequestration (10.8 days x 1.9% per day = 20.5%).

Melillo *et al.* (2002) studied an even-aged mixed hardwood stand of the Harvard Forest in central Massachusetts, USA, where they installed buried heating cables at 10cm depths, spaced 20cm apart, in 6m by 6m plots, half of which were not operated to produce any heat (serving as "disturbance control" plots) and half of which maintained the average soil temperature approximately 5°C above ambient. At monthly intervals from April through November of each year of their 10-year study, the researchers measured CO₂ evolution rates from the soils of both sets of plots.

Over the first six years of the study, Melillo *et al.* observed an approximate 28% increase in CO₂ emissions from the heated plots relative to the non-heated plots. However, "over the last four years of the study, the 'stimulatory' effect of warming on soil respiration markedly decreased"; so much so, in fact, that from 1998 through 2000 there was "only about a 5% increase in soil respiration in the warmed versus disturbance control plots," and by the tenth year of the study "soil respiration showed no significant response to warming."

This exemplary study showed just how important it is to do experiments ... and to do *long-term* experiments. Most prior theoretical studies, for example, had tended to predict what the scientists observed over the first six years of their measurement program—a large warming-induced increase in respiratory carbon loss from the forest soil—which likely would have been accepted as the long-term truth if they had terminated their work at any time during that period. Continuing their measurements for four more years, however, the scientists discovered what is likely the true long-term response—no significant change in soil respiratory carbon loss. That was but the beginning of what they learned.

Concurrent with their soil CO₂ evolution measurements, Melillo *et al.* measured rates of net nitrogen mineralization, finding "over the entire 10-year study period, warming resulted in a cumulative increase in net nitrogen mineralization." Also, partially overlapping Melillo *et al.*'s long-term warming experiment was a long-term nitrogen fertilization study of a similar hardwood stand in the Harvard Forest described by Magill *et al.* (2000), where after nine years, they report, "12.7% of the total amount of nitrogen fertilizer added ended up in the woody tissue of the stand's trees."

Assuming an identical portion of the increased nitrogen made available by the warming of their experiment ended up in the woody tissues of the trees they studied, Melillo *et al.* calculate this phenomenon “would result in an additional 1560 g m⁻² of carbon storage in the vegetation over the decade of warming.” Hence, having previously determined the soil carbon loss stimulated by their applied warming for the entire 10-year period was 944 g m⁻², the net result of the two competing phenomena for the complete forest ecosystem was a net carbon gain on the order of 600 g m⁻².

In discussing the significance of this unexpected but positive finding, Melillo *et al.* note there is other independent “direct field evidence that soil warming enhances carbon storage in trees.” Citing Bergh *et al.* (1999) and Jarvis and Linder (2000), they say in a similar long-term study these investigators also found “there was a significant (more than 50%) increase in stem-wood growth of the trees on the heated plots relative to the controls.”

These independent experimental observations suggest claims to the contrary have no backing in empirical science. Both the aerial fertilization effect of atmospheric CO₂ enrichment and the soil fertilization effect of the increase in nitrogen mineralization induced by global warming increase carbon sequestration in forest ecosystems, providing a strong, double-barreled, negative-feedback brake on the impetus for warming created by the enhanced greenhouse effect of the ongoing rise in the air’s CO₂ content.

Perfors *et al.* (2003) utilized overhead infrared radiative heaters to continuously warm five plots of ungrazed montane meadow at the Rocky Mountain Biological Laboratory in Gunnison County, Colorado, USA. Five similar but unheated plots served as controls. In the heated plots, the extra downward flux of infrared radiation warmed the top 15 cm of soil by about 1.5°C and dried it by about 15% on a gravimetric basis during the growing season, prolonging the snow-free season at each end by a total of approximately 20 days. The scientists also developed and applied a method for extracting the age-detrended growth rate of common sagebrush—*Artemisia tridentata* (Nutt.), ssp. *vaseyana*, a perennial shrub that is abundant throughout much of the semiarid western United States—to determine the effect of a modest warming on the distribution of this common woody plant.

The scientists found annual sagebrush growth rates in the heated plots were approximately 50% greater than those in the control plots, due primarily

to the warming-induced increase in the length of the snow-free season. The three researchers report their observations and analysis “suggest that global climate change, which is expected to result in a contracted period of snow accumulation in the montane west, will result in increased growth and range expansion of sagebrush near high-elevation range boundaries in the western US.” And although Saleska *et al.* (2002) had demonstrated the experimental warming treatment decreased soil organic carbon content, Perfors *et al.* suggest, over the long term, “because sagebrush litter is more recalcitrant to decomposition than is the litter from the forb species that are in decline in the heated plots of our climate manipulation experiment, enhanced sagebrush growth could also contribute to a negative feedback [to CO₂-induced warming] by increasing the turnover time of soil carbon.”

Monson *et al.* (2006) studied the effect of changes in snow cover on soil carbon cycling during natural climatic variations over a six-year period at the Niwot Ridge AmeriFlux site in the U.S. Rocky Mountains (40°1’58”N, 105°32’47”W). They used eddy covariance measurements to assess the net CO₂ exchange of a subalpine montane forest ecosystem, special chambers for measuring soil respiration beneath snow, various instruments to characterize a number of snow properties, and standard techniques for identifying soil microbial populations and assessing their growth kinetics and substrate-use. They report “microbes collected from under the snowpack could grow exponentially at 0°C,” and “their growth rates increased rapidly with increasing temperature,” so anything that decreased the temperature of their environment decreased forest soil respiration in winter, as they typically observed to be the case. They also note “a shallower snowpack has less insulation potential, causing colder soil temperatures,” and “long-term monitoring of mountain snow packs in the western USA and Europe have shown trends towards decreasing depth, with several mountain ranges experiencing 50–75% decreases, and these have been attributed to positive temperature anomalies (Latenser and Schneebeli, 2003; Scherrer *et al.*, 2004; Mote *et al.*, 2005).”

Because rising air temperatures cause decreases in snow depth, decreases in snow depth in turn lead to colder soil temperatures, and colder soil temperatures lead to reduced microbial respiration, global warming may actually lead to greater quantities of carbon being trapped in the soils of montane forest ecosystems. As Monson *et al.* describe it, “decreases in the winter snow pack will generally cause decreases in the loss of respired CO₂ from the soils of

forest ecosystems, thus enhancing the potential for soil carbon sequestration.” Thus their work reveals yet another negative feedback mechanism whereby Earth’s biosphere acts to resist changes in temperature caused by thermal pressures exerted by independent climate forcing factors.

Chen *et al.* (2006) note “CO₂ fluxes measured on micrometeorological towers in many flux networks worldwide (Baldocchi *et al.*, 2001) ... can only sample a very small fraction of the land surface as each can only represent a footprint area of about 1 km².” Hence they sought “ways to retrieve carbon cycle information from atmospheric CO₂ concentration measurements, which have much larger footprints (10³–10⁴ km²) (Lin *et al.*, 2003) than flux towers.” They analyzed a 13-year (1990–1996, 1999–2004) hourly averaged atmospheric CO₂ concentration database obtained from a 40 m tower at Fraserdale, Ontario, Canada (together with temperature, humidity, and wind speed measured at 20 and 40 meters and precipitation at ground level). They compared their results with a marine boundary layer CO₂ dataset representing the free troposphere above the tower.

The eight researchers report in warmer years the planetary boundary layer over their measurement site was more depleted of CO₂, which suggests the 10³–10⁴ km² land area of the boreal ecosystem upwind of the tower sequestered more carbon in such years. They say this finding “suggests that gross primary productivity increased considerably faster with temperature than did ecosystem respiration,” a relationship they found to be true for both annual temperatures (from year to year) and 10-day mean temperatures (throughout the growing season). These findings led them to conclude “the fact that the temperature sensitivity of gross primary productivity is larger than that of ecosystem respiration suggests that global warming could lead to increased carbon sequestration in boreal ecosystems.”

Burton *et al.* (2008) note “increases in terrestrial ecosystem respiration as temperatures warm could create a positive feedback that causes atmospheric CO₂ concentration, and subsequently global temperature, to increase more rapidly,” but they also note “if plant tissue respiration acclimates to temperature over time, this feedback loop will be weakened, reducing the potential temperature increase.” In an attempt to determine which of these scenarios is more likely to occur, the three researchers employed published values of annual root respiration rates to assess “the cross-ecosystem rate of increase with temperature.” They then examined “the potential

for trade-offs between root metabolic capacity and biomass in regulating ecosystem root respiration, using published values for mid-growing season root specific respiration rates and root biomass.” Finally, they determined whether “relationships that occur across ecosystems adapted to different climates might also exist within an ecosystem that is subjected to warming,” by analyzing data obtained “from soil warming studies, including recent measurements of fine root respiration made at three warming experiments at Harvard Forest.”

Burton *et al.* report their analyses of the pertinent scientific literature show “a clear trend for decreasing root metabolic capacity (respiration rate at a standard temperature) with increasing mean annual temperature”; “no instances of high growing season respiration rates and high root biomass occurring together”; and in the soil warming experiments at Harvard Forest, “decreases in metabolic capacity for roots from the heated plots.” Thus Burton *et al.* conclude “these findings clearly suggest that modeling efforts that allow root respiration to increase exponentially with temperature, with Q₁₀ values of 2 or more, may over-predict root contributions to ecosystem CO₂ efflux for future climates and underestimate the amount of carbon available for other uses, including net primary productivity,” rebuffing long-espoused claims to the contrary.

The studies cited above indicate rising air temperatures likely would have a positive effect on carbon storage in forests and their associated soils, instead of exerting a negative influence on forest carbon sequestration.

References

- Baldocchi, D., Falge, E., Gu, L.H., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law B., Lee, X.H., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw U, K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., and Wofsy, S. 2001. FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society* **82**: 2415–2434.
- Bergh, J., Linder, S., Lundmark, T., and Elfving, B. 1999. The effect of water and nutrient availability on the productivity of Norway spruce in northern and southern Sweden. *Forest Ecology and Management* **119**: 51–62.
- Burton, A.J., Melillo, J.M., and Frey, S.D. 2008.

Climate Change Reconsidered II: Biological Impacts

- Adjustment of forest ecosystem root respiration as temperature warms. *Journal of Integrative Plant Biology* **50**: 1467–1483.
- Chen, J.M., Chen, B., Higuchi, K., Liu, J., Chan, D., Worthy, D., Tans, P., and Black, A. 2006. Boreal ecosystems sequestered more carbon in warmer years. *Geophysical Research Letters* **33**: 10.1029/2006GL025919.
- Fan, S., Gloor, M., Mahlman, J., Pacala, S., Sarmiento, J., Takahashi, T., and Tans, P. 1998. A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. *Science* **282**: 442–446.
- Giardina, C.P. and Ryan, M.G. 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature* **404**: 858–861.
- Grace, J. and Rayment, M. 2000. Respiration in the balance. *Nature* **404**: 819–820.
- Jarvis, P. and Linder, S. 2000. Constraints to growth of boreal forests. *Nature* **405**: 904–905.
- King, J.S., Pregitzer, K.S., and Zak, D.R. 1999. Clonal variation in above- and below-ground responses of *Populus tremuloides* Michaux: Influence of soil warming and nutrient availability. *Plant and Soil* **217**: 119–130.
- Laternser, M. and Schneebeli, M. 2003. Long-term snow climate trends of the Swiss Alps (1931–99). *International Journal of Climatology* **23**: 733–750.
- Lin, C., Gerbig, C., Wofsy, S.C., Andrews, A.E., Daube, B.C., Davis, K.T., and Grainger, C.A. 2003. A near-field tool for simulating the upstream influence of atmospheric observations: The Stochastic Time-Inverted Lagrangian Transport (STILT) model. *Journal of Geophysical Research* **108**: 10.1029/2002JD003161.
- Liski, J., Ilvesniemi, H., Makela, A., and Westman, C.J. 1999. CO₂ emissions from soil in response to climatic warming are overestimated—The decomposition of old soil organic matter is tolerant of temperature. *Ambio* **28**: 171–174.
- Magill, A.H., Aber, J.D., Berntson, G.M., McDowell, W.H., Nadelhoffer, K.J., Melillo, J.M., and Steudler, P. 2000. Long-term nitrogen additions and nitrogen saturation in two temperate forests. *Ecosystems* **3**: 238–253.
- Melillo, J.M., Steudler, P.A., Aber, J.D., Newkirk, K., Lux, H., Bowles, F.P., Catricala, C., Magill, A., Ahrens, T., and Morrisseau, S. 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* **298**: 2173–2176.
- Menzel, A. and Fabian, P. 1999. Growing season extended in Europe. *Nature* **397**: 659.
- Monson, R.K., Lipson, D.L., Burns, S.P., Turnipseed, A.A., Delany, A.C., Williams, M.W., and Schmidt, S.K. 2006. Winter forest soil respiration controlled by climate and microbial community composition. *Nature* **439**: 711–714.
- Mote, P.W., Hamlet, A.F., Clark, M.P., and Lettenmaier, D.T. 2005. Declining mountain snow pack in Western North America. *Bulletin of the American Meteorological Society* **86**: 39–49.
- Pearce, F. 1999. That sinking feeling. *New Scientist* **164** (2209): 20–21.
- Perfors, T., Harte, J., and Alter, S.E. 2003. Enhanced growth of sagebrush (*Artemisia tridentata*) in response to manipulated ecosystem warming. *Global Change Biology* **9**: 736–742.
- Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Nunez, P.V., Vasquez, R.M., Laurance, S.G., Ferreira, L.V., Stern, M., Brown, S., and Grace, J. 1998. Changes in the carbon balance of tropical forests: Evidence from long-term plots. *Science* **282**: 439–442.
- Saleska, S.R., Shaw, M.R., Fischer, M.L., Dunne, J.A., Still, C.J., Holman, M.L., and Harte, J. 2002. Plant community composition mediates both large transient decline and predicted long-term recovery of soil carbon under climate warming. *Global Biogeochemical Cycles* **16**: 10.1029/2001GB001573.
- Scherrer, S.C., Appenzeller, C., and Laternser, M. 2004. Trends in Swiss alpine snow days—The role of local and large-scale climate variability. *Geophysical Research Letters* **31**: 10.1029/2004GL020255.
- Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.-D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grunwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, U., Berbigier, P., Loustau, D., Gudmundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., and Jarvis, P.G. 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* **404**: 861–865.
- White, M.A., Running, S.W., and Thornton, P.E. 1999. The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *International Journal of Biometeorology* **42**: 139–145.

1.2.2 Grasslands

Most of Earth's terrestrial plant life evolved around 500 to 400 million years ago, when the atmospheric CO₂ concentration was possibly 10 to 20 times higher than it is today. As a consequence, the biochemical

pathways and enzymes involved in carbon fixation should be better adapted to significantly higher-than-present atmospheric CO₂ levels, which has in fact been demonstrated to be the case. As the atmosphere's CO₂ content has dropped from that early point in time, it has caused most of Earth's vegetation to become less efficient at extracting carbon dioxide from the air. However, the recent ongoing rise in atmospheric CO₂ concentration is gradually increasing photosynthetic rates and stimulating vegetative productivity and the terrestrial sequestration of carbon around the globe. The subsections below review some of the recent evidence for these phenomena in various grassland species.

1.2.2.1 General Responses to Elevated CO₂

- As the air's CO₂ concentration increases, the productivity of Earth's grassland species also should increase, even under unfavorable growing conditions characterized by less-than-adequate soil moisture, inadequate soil nutrition, elevated air temperature, and physical stress imposed by herbivory.

Wand *et al.* (1999) provided an overview of the effects of elevated atmospheric CO₂ concentrations on photosynthesis in grasses by analyzing the pertinent peer-reviewed literature published between 1980 and 1997. These authors report a doubling of the air's CO₂ content increases photosynthetic rates of C₃ and C₄ grasses by 33 and 25%, respectively. Importantly, their results also demonstrate, contrary to some circulating opinions, C₄ plants can—and do—respond positively to increases in the air's CO₂ content.

Another good summary of grassland community responses to atmospheric CO₂ enrichment followed a year later in the comprehensive review of Campbell *et al.* (2000), who compiled and analyzed more than 165 peer-reviewed scientific journal articles dealing with pastures and rangelands. Although their review includes many responses of individual species, it provides a conservative estimate of community responses as well: an average 17% increase for a doubling of the air's CO₂ content. Therefore, as the atmospheric CO₂ concentration increases, it is likely grassland communities will exhibit increases in photosynthesis and biomass production, which will invariably lead to enhanced carbon sequestration in the soils beneath them. This conclusion is borne out in many additional studies.

Szente *et al.* (1998) grew two grass and two

broad-leaved species common to loess grasslands of Budapest in open-top chambers for 231 days at atmospheric CO₂ concentrations of 350 and 700 ppm. The elevated CO₂ caused photosynthetic enhancements of 136 and 486% in the grass and broad-leaved species, respectively. After growing microcosms of the C₃ grass *Danthonia richardsonii* for four years in glasshouses receiving atmospheric CO₂ concentrations of 360 and 720 ppm, Lutze and Gifford (1998) report the elevated CO₂ increased total microcosm biomass by an average of 24%. Similarly, in the four-year study of Leadley *et al.* (1999), species-rich Swiss grasslands exposed to atmospheric CO₂ concentrations of 600 ppm in open-top and open-bottom chambers produced 29% more community biomass than control grasslands exposed to air of 350 ppm CO₂. And tallgrass prairie ecosystems in Kansas, USA, exposed to twice-ambient levels of atmospheric CO₂ displayed significant CO₂-induced enhancements of biomass, but only during relatively dry years (Owensby *et al.*, 1999).

Cotrufo and Gorissen (1997) grew three grasses (*Lolium perenne*, *Agrostis capillaries*, and *Festuca ovina*) at atmospheric CO₂ concentrations of 350 and 700 ppm for approximately two months before harvesting. On average, atmospheric CO₂ enrichment increased plant biomass by approximately 20%, with greater carbon partitioning to roots, as opposed to shoots. Also, in a much shorter two-week study performed on tall fescue (*Festuca ovina*), Newman *et al.* (1999) report twice-ambient levels of atmospheric CO₂ increased plant biomass by 37% relative to plants grown in ambient air.

In two additional studies, researchers grew perennial ryegrass (*Lolium perenne*) in controlled environmental chambers receiving atmospheric CO₂ concentrations of 350 and 700 ppm for approximately 14 weeks. After assessing plant growth, the authors reported CO₂-induced increases in shoot (van Ginkel and Gorissen, 1998) and root (van Ginkel *et al.*, 2000) biomass of 28 and 41%, respectively. Hodge *et al.* (1998) also report, for the same species, plants grown at an atmospheric CO₂ concentration of 720 ppm for a mere 21 days exhibited total biomass values 175% greater than those observed for control plants exposed to air of 450 ppm CO₂.

Lüscher *et al.* (1998) collected nine to 14 genotypes for each of 12 native grassland species from two permanent meadows near Zurich, Switzerland, and transplanted them into artificial gaps created in well-fertilized swards of *Lolium perenne* growing in FACE arrays maintained at 350 and 700 ppm CO₂, to determine inter- and intraspecific species

growth responses to elevated CO₂ by harvesting aboveground biomass several times over a three-year period. CO₂-induced biomass increases varied with plant type, being greatest for legumes followed by non-legume dicotyledonous species and, last, monocotyledonous grasses. There were no significant differences in CO₂ responsiveness within genotypes for any of the 12 species.

Suter *et al.* (2002) grew perennial ryegrass (*Lolium perenne* L.) in field plots, as part of a FACE experiment, and in controlled-environment chambers, to compare growth and carbon allocation responses of this important forage crop to elevated atmospheric CO₂ concentrations under different experimental protocols. In both regimes, the control and elevated CO₂ concentrations were maintained for approximately two months at 350 and 600 ppm, respectively. The overall growth response of perennial ryegrass to elevated CO₂ was consistently greater for plants grown in the FACE experiment than for plants grown in the controlled-environment chambers. Elevated CO₂, for example, increased total dry matter production by 65 and 54% in the FACE and controlled-environment chambers, respectively. In addition, it enhanced root dry weights by 109 and 47% for plants grown in the FACE and controlled-environment chambers, respectively.

Bhatt *et al.* (2007) transplanted 30-day-old seedlings of *Cenchrus ciliaris* to open-top chambers—maintained at either the ambient atmospheric CO₂ concentration (360 ppm) or at an elevated CO₂ concentration (600 ppm)—in which the plants were grown for an additional 120 days, “using recommended agronomical practices” and with irrigation “given as and when required.” During this time of outdoor field growth, the researchers measured numerous plant properties and physiological processes. At the end of the experiment, the plants were harvested and other pertinent measurements made. Among other things, Bhatt *et al.* report the extra 240 ppm of CO₂ employed in their experiment increased several plant parameters by the following percentages: plant height (44%), number of tillers (33%), leaf length (23%), leaf width (51%), leaf area index (234%), net photosynthetic rate per unit leaf area (25%), net photosynthetic rate per unit ground area (316%), total fresh weight (134%), total dry weight (193%), and whole-crop photosynthetic water use efficiency (34%). The three Indian researchers conclude “*C. ciliaris* grown in elevated CO₂ throughout the crop season may produce more fodder in terms of green biomass.”

Several researchers have examined the effects of

CO₂ enrichment on grasslands under varying soil nitrogen and fertility regimes. In a model-based study, Cannell and Thornley (1998) used the Hurley Pasture Model to simulate growth responses of perennial ryegrass (*Lolium perenne* L.) to a step increase in atmospheric CO₂ concentration (350 to 700 ppm) under conditions of low and high soil nitrogen. At high soil nitrogen conditions, elevated CO₂ stimulated net primary productivity and plant biomass by approximately 30% within a few years. Under low soil nitrogen conditions, elevated CO₂ caused a much greater stimulation of approximately 114%, although it took longer (five to ten years) to attain this greater degree of growth enhancement.

Navas *et al.* (1999) grew mixed communities of two grasses and two legumes across a range of soil nitrogen contents at ambient (357ppm) and enriched (712 ppm) atmospheric CO₂ concentrations for two months. Although soil nitrogen content had a much greater influence on community productivity than did atmospheric CO₂ concentration, communities fumigated with CO₂-enriched air tended to produce greater amounts of biomass than those exposed to ambient air. Likewise, Jongen and Jones (1998) report an eight-month exposure to twice-ambient levels of atmospheric CO₂ increased the community biomass of semi-natural grasslands characteristic of the Irish lowlands by 26%.

Reich *et al.* (2001) grew 16 perennial grassland species as monocultures in FACE plots maintained at atmospheric CO₂ concentrations of 360 and 560 ppm and low and high levels of soil nitrogen for two years. Interestingly, they found no interactions between atmospheric CO₂ concentration and soil nitrogen for any measured plant parameter. Nonetheless, elevated CO₂ increased total plant biomass for forbs, legumes, and C₃ grasses by 31, 18, and 9%, respectively, and it decreased the growth of C₄ grasses by 4%.

In a two-year study, Stocklin *et al.* (1999) grew simulated low-fertility Swiss grasslands in glass-houses receiving atmospheric CO₂ concentrations of 360 and 600 ppm. The authors report elevated CO₂ concentrations stimulated total biomass production by an average of 23% in these nutrient-poor grassland communities. And in another two-year experiment, Niklaus *et al.* (1998) note swards of calcareous grasslands exposed to atmospheric CO₂ concentrations of 600 ppm displayed total biomass values 25% greater than those exhibited by control swards grown in ambient air of 350 ppm CO₂.

Zaller and Arnone (1999) established open-top chambers in a species-rich grassland located near Basel, Switzerland and fumigated them continuously

with atmospheric CO₂ concentrations of 350 and 600 ppm, except during winter months, for nearly one-and-a-half years, to see whether graminoids, non-legume forbs, and legumes growing near earthworm surface casts were more responsive to atmospheric CO₂ enrichment than those growing further away from these nutrient-rich microsites. Generally, plants growing in close proximity to earthworm casts produced more biomass than similar plants growing further away, regardless of CO₂ concentration. When assessing the influence of earthworm casts on plant responsiveness to atmospheric CO₂ enrichment, no statistically significant results were detected. Nonetheless, the average growth response of graminoids to elevated CO₂ was greater for those plants growing closer to earthworm casts than for those growing further away from them. This finding suggests plant growth responses to atmospheric CO₂ enrichment may be increased if local plant niches are closely associated with earthworm casts, which provide limiting nutrients to facilitate greater plant growth.

Also working in Switzerland, Niklaus *et al.* (2003) enriched the air above plots of a nutrient-poor, species-rich calcareous grassland in the northwestern portion of the country with an extra 240 ppm of CO₂ via a set of novel windscreens that “operated around the clock” except during midwinter (December–February). Among several other findings, the authors report during the six years of their experiment, aboveground plant biomass accumulation increased in response to CO₂ by an average of 21%. Simultaneously, there was an increase in soil moisture due to CO₂-induced reductions in plant transpiration. They also report microbial nitrogen (N) pools did not change, “indicating that elevated CO₂ did not stimulate net microbial immobilization of N which could have imposed a negative feedback on plant growth [but didn’t].”

Contemporaneously, in a paper produced from the same experimental site, Ebersberger *et al.* (2003) assessed the impact of the extra CO₂ after six growing seasons on N-mineralization in the grassland soil and the activities of the soil microbial enzymes invertase, xylanase, urease, protease, arylsulfatase, and alkaline phosphatase in both the spring and summer. Results indicate the extra CO₂ increased N-mineralization significantly ($P = 0.02$, *a priori* linear contrast) by 30% in the spring and insignificantly ($P = 0.6$) by 3% in the summer. In addition, at both sampling times all measured enzyme activities were higher in the CO₂-enriched treatment, with the single exception of xylanase in summer. The strongest responder in the spring was alkaline phosphatase (up 32%, $P = 0.02$),

followed by urease (up 21%, $P = 0.13$). In the summer, the best responder was urease (up 21%, $P = 0.2$), followed by protease (up 17%, $P = 0.09$) and invertase (up 14%, $P = 0.07$). The authors attribute the increased N-mineralization and enzyme activity of the soil biota to the higher moisture content of the soil in the CO₂-enriched plots (due to a CO₂-induced decrease in stand transpiration) and/or the CO₂-induced increase in root biomass (up 24%, $P = 0.02$, in June 1999).

The observations of Ebersberger *et al.* are significant because soil microorganisms hold a key position in terrestrial ecosystems, as they mineralize organic matter and make its nitrogen available for use by plants. Hence, it is encouraging to note, in the words of the authors, “that elevated CO₂ will enhance below-ground C- and N-cycling in grasslands,” even nutrient-poor grasslands such as the one they studied.

Morgan *et al.* (2001) grew the C₃ grass *Pascopyrum smithii*, the C₄ grass *Bouteloua gracilis*, and the C₃ legume *Medicago sativa* for 20 days post-defoliation in growth chambers receiving atmospheric CO₂ concentrations of 355 and 700 ppm and low or high levels of soil nitrogen, to determine how these factors affect the regrowth of these forage species. After 20 days post-defoliation, *Medicago sativa* plants grown in elevated CO₂ had attained total dry weights about 62% greater than those reached by ambiently grown plants, regardless of soil nitrogen, the scientists report. *Pascopyrum smithii* plants were more sensitive to soil nitrogen; whole plant regrowth was stimulated by 150 and 68% under conditions of high and low soil nitrogen, respectively. Elevated CO₂ had no positive effect on the regrowth of the C₄ grass, which fared better under high vs. low soil nitrogen conditions.

As the CO₂ concentration of the air increases, C₃ forage species subjected to natural or mechanical defoliation likely will respond by increasing their regrowth biomass in a plant-dependent and soil-nitrogen-dependent manner. Leguminous nitrogen-fixing C₃ species, for example, likely will exhibit enhanced regrowth irrespective of soil nitrogen content, and non-nitrogen-fixing C₃ species likely will exhibit greater regrowth on soils containing more, rather than less, nitrogen. Moreover, the regrowth of C₄ species may be less responsive to atmospheric CO₂ enrichment than C₃ species. Thus, future increases in the air’s CO₂ content should promote, or at the very least not impair, prairie regrowth following defoliation by either animals or machinery.

Edwards *et al.* (2005) grew well-watered mixtures of two plants—the legume white clover

(*Trifolium repens* L.) and C₄ buffalo grass (*Stenotaphrum secundatum* (Walt.) Kuntze)—which were initially equal in plantlet size, number, and spatial distribution—for 15 months in sand placed in large plastic containers located in greenhouses maintained at different atmospheric CO₂ concentrations (360 and 700 ppm) under three sand nutrient conditions (zero-N/low-P, zero-N/high-P, plus-N/high-P). Ten harvests were made of all plant biomass over a height of 5 cm above the sand surface, after which the scientists determined the total carbon contents of the whole plants and their respective soils. The slightly less than a doubling of the air's CO₂ concentration employed in this study led to increases of 27%, 55%, and 23% in final-harvest whole plant biomass in the zero-N/low-P, zero-N/high-P, and plus-N/high-P soil treatments, respectively.

Hartwig *et al.* (2002) grew perennial ryegrass (*Lolium perenne* L.) in environmental chambers receiving atmospheric CO₂ concentrations of 350 and 600 ppm for 60 days. In addition, they subjected plants to low and high levels of soil nitrogen and inoculated some with arbuscular mycorrhizal fungi. Thus the authors studied the interactive effects of elevated CO₂, soil nitrogen, and arbuscular mycorrhizal fungi on growth in this important grassland species. They found elevated CO₂ increased plant biomass by 10 and 17% at low and high levels of soil nitrogen, respectively. When plants were inoculated with the arbuscular mycorrhizal fungi, elevated CO₂ enhanced plant biomass only by 3% at low soil nitrogen, but it increased it by 41% at high soil nitrogen. Thus, at high soil nitrogen, the presence of this symbiotic fungi more than doubled the plant growth response to atmospheric CO₂ enrichment. In addition, the amount of root colonization by the arbuscular mycorrhizal fungi increased by 56% in the high CO₂ treatment.

Arbuscular mycorrhizal fungi are important because nearly all grassland species form symbiotic relationships with mycorrhizal fungi. Arbuscular mycorrhizal fungi commonly colonize roots of grasses and form symbiotic structures known as arbuscules, short-lived organs that facilitate carbon and nutrient exchange between the fungi and their host plants. The presence of these symbiotic relationships often increases grassland vitality and productivity, and several other researchers have set out to understand how rising atmospheric CO₂ concentrations may affect these relationships.

In an earlier study, Wilson and Hartnett (1998) grew 36 grass species common to tallgrass prairie ecosystems with and without the presence (induced

by inoculation) of arbuscular mycorrhizae. They report fungal inoculation increased the average dry mass of perennial C₄ species by 85%. Fungal inoculation had no significant effects on dry mass production in perennial C₃ species or in any annual grasses, regardless of their photosynthetic physiology. Thus, a large number of plant-fungal interactions exist at ambient CO₂ concentrations that may be modified by exposure to elevated CO₂.

In a similar study, Rillig *et al.* (1998a) grew monocultures of three grasses and two herbs that co-occur in Mediterranean annual grasslands, in pots placed in open-top chambers receiving ambient and twice-ambient concentrations of atmospheric CO₂ for four months. They report elevated CO₂ significantly increased the percent root colonization by arbuscular mycorrhizal fungal hyphae in all five species, which ultimately could lead to greater biomass production in these annual grassland plants.

In another four-month study using the same experimental enclosures, Rillig *et al.* (1998b) grew the annual grass *Bromus hordeaceus* at ambient and elevated atmospheric CO₂ concentrations. In this study, elevated CO₂ did not increase the percent root colonized by fungal hyphae, but it did significantly increase the percent root colonized by arbuscules, indicating elevated CO₂ can enhance fungal-plant interactions by modifying fungal structures other than hyphae.

In two related long-term studies, Rillig *et al.* (1999a,b) constructed open-top chambers on two adjacent serpentine and sandstone grassland communities in California, USA, fumigating them with air containing 350 and 700 ppm of CO₂ for six years. In corroboration of their earlier short-term results, they report elevated CO₂ did not increase the percent root colonized by fungal hyphae (Rillig *et al.*, 1999a) but it enhanced the percent root colonized by arbuscules in serpentine and sandstone grasslands by three- and ten-fold, respectively (Rillig *et al.*, 1999b). Such observations suggest increases in the air's CO₂ concentration will positively impact plant-fungal interactions on grasslands by increasing percent root colonization by either mycorrhizal fungal hyphae or arbuscules, both of which aid in carbon and nutrient exchanges between the two interacting symbionts. Earth's grasslands thus should exhibit increased productivity—even above and beyond that normally caused by atmospheric CO₂ enrichment—due to these enhanced relationships that can make soil nutrients more available for plant uptake and use.

Johnson *et al.* (2003) grew communities of 14 common prairie plants in 12 greenhouse chambers at

Flagstaff, Arizona, USA. Six of the chambers were maintained at an atmospheric CO₂ concentration of 450 ppm, and six were maintained at 688 ppm (equivalent to 368 and 560 ppm at sea level, respectively) during daylight hours. Each of the CO₂ treatments also was subdivided into treatments possessing living or dead arbuscular mycorrhizal (AM) fungal inoculum and low or enriched soil nitrogen (N) content. After one growing season under these conditions, Johnson *et al.* write, “plant species richness was highest in mesocosms with elevated CO₂, +AM fungi, and low soil N.” They conclude, “in some plant species elevated CO₂ can increase the net benefits of mycorrhizae by reducing their relative carbon cost.” Thus, not only did the extra CO₂ directly help the various plant species involved in the study, it also helped them indirectly—by promoting the growth of AM fungi that provided additional benefits to the plants. This study also suggests increases in the air’s CO₂ content should have a tendency to maintain, and possibly even increase, the species richness of prairie ecosystems, especially those where soil nitrogen content is less than optimal.

Also focusing on species richness, or biodiversity, Edwards *et al.* (2001) conducted a FACE experiment utilizing atmospheric CO₂ concentrations of 360 and 475 ppm on a sheep-grazed dry-land pasture located in Manawatu, New Zealand. In each of the two years of their study, elevated CO₂ increased seed production and dispersal in seven of the eight most abundant pasture species: the grasses *Anthoxanthum odoratum*, *Lolium perenne*, and *Poa pratensis*; the legumes *Trifolium repens* and *Trifolium subterranean*; and the herbs *Hypochaeris radicata* and *Leontodon saxatilis*. In some of these species, the elevated CO₂ increased the number of seeds produced per reproductive structure, and in all of the species it increased the number of reproductive structures per unit ground area.

These CO₂-induced increases in seed production contributed to the increase in the numbers of species observed in the CO₂-enriched experimental plots. In addition, atmospheric CO₂ enrichment helped maintain biodiversity by increasing the number of *H. radicata*, *L. saxatilis*, *T. repens*, and *T. subterranean* seedlings that survived for at least seven months in both study years, and it additionally lengthened the survival time of *A. odoratum* and *L. perenne* in the initial year of experimentation. As the atmospheric CO₂ concentration increases further, therefore, it should help to maintain, and maybe even increase, the biodiversity of these dry-land pasture communities by increasing the numbers of both common and

uncommon species they contain.

Teyssonneyre *et al.* (2002) grew three C₃ grasses (*Lolium perenne*, *Festuca arundinacea*, and *Holcus lanatus*) as monocultures and two-species mixtures for five months in plastic tunnels maintained at atmospheric CO₂ concentrations of 350 and 700 ppm, cutting the grasses either frequently or infrequently to stimulate competition for light. In monoculture, the high-CO₂ treatment increased total aboveground biomass by 22%, 22%, and 4% in *Festuca*, *Holcus*, and *Lolium*, respectively. In two-species mixtures, elevated CO₂ caused a 22% reduction in the amount of *Lolium* in the *Lolium* x *Festuca* mixture under the infrequent cutting regime, and it caused 30% and 67% reductions in the amount of *Lolium* in the *Lolium* x *Holcus* mixture under the frequent and infrequent cutting regimes, respectively.

De Deyn *et al.* (2003) begin their study by noting aboveground vertebrate herbivores “can indirectly benefit subdominant plant species through selective feeding on dominants (Crawley, 1997; Olff and Ritchie, 1998).” They then note root symbionts below the soil surface “can enhance plant species diversity by improving the nutrient uptake and growth of subdominants (van der Heijden *et al.*, 1998),” further noting root pathogens “can do so by suppressing dominant host plant species (Bever, 1994).” They then expanded the scope of these types of interactions by exploring the impact of invertebrate soil fauna on plant biodiversity.

De Deyn *et al.* established 32 microcosms of plant species mixtures characteristic of recently abandoned grassland (early succession), grassland under restoration for 20 years (mid-succession), and species-rich natural grassland (the ultimate target state). These microcosms were inoculated with soil fauna from one of the three grassland successional stages. The density and composition of the soil fauna added to the microcosms were the same as those of the three grassland successional stages and included microfauna (nematodes), mesofauna (microarthropods), and macrofauna (beetle larvae). After four and six months of these treatments, the researchers clipped the microcosm plants at 4 cm above the soil surface and determined the harvested dry weights of all individual plant species. After 12 months they clipped the plants at the soil surface and determined their root dry weights again.

De Deyn *et al.* report “the soil fauna decreased the shoot biomass of the early succession plant species after 6 months, as well as plant species from the mid-succession stage, whereas the shoot biomass of the target plant species was increased.” Hence,

they note, “addition of the soil fauna also enhanced plant species diversity.” Results obtained at the end of the experiment further suggest “the invertebrate root herbivores were selectively feeding on roots of dominant plants,” which “provided an indirect advantage for the subdominant plant species, which were only marginally suppressed in the presence of soil fauna.” The researchers also report the positive contributions of soil fauna and mycorrhizal fungi seemed to be additive. Such findings suggest the ongoing rise in the air’s CO₂ content may enhance ecosystem species richness, as a consequence of the tendency for atmospheric CO₂ enrichment to increase both mycorrhizal fungi and soil fauna populations.

Working in central Texas (USA) with elongated field chambers designed to expose tallgrass prairie vegetation comprised of a mix of seven different species—four C₄ grasses (*Bouteloua curtipendula*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Tridens albescens*) and three forbs (*Salvia azurea*, *Solidago canadensis*, and *Desmanthus illinoensis*)—to a continuous atmospheric CO₂ gradient spanning the preindustrial to elevated CO₂ concentration range of 250 to 500 ppm, Polley *et al.* (2011) measured the concentrations of ten elements found in the above-ground tissues of three of the C₄ grasses (*B. curtipendula*, *S. scoparium*, and *S. nutans*) that are common competitive dominants in assemblages of tallgrass prairie vegetation, which they grew on three soil types over three growing seasons. Polley *et al.* report “the CO₂ effect on relative abundances of *Bouteloua* and *Sorghastrum* had far greater impact on element concentrations in grass stands than did change in element levels of individual species,” and “elements that were most limiting relative to the nutritional requirements of cattle generally occurred at lowest concentrations in *Bouteloua*, the species most strongly disadvantaged at elevated CO₂.” Also, “CO₂ enrichment favored a grass, *Sorghastrum*, with relatively high concentrations of these elements, thereby increasing mean concentrations of several elements in grass assemblages.”

The four researchers say their results “highlight the importance of accounting for change in species abundances and composition when predicting CO₂ effects on ecosystem functioning and services,” as is also indicated by Polley *et al.* (2010), who conclude, “by favoring one grass species over another, CO₂ enrichment from pre-industrial to elevated levels increased concentrations of several nutritionally important elements in prairie grasses,” further noting this “improvement in the nutritional quality of plants for herbivores” represents an “underappreciated

impact that CO₂ enrichment may have on ecosystem functioning by changing plant composition.”

Isbell *et al.* (2013) write, “anthropogenic drivers of environmental change often have multiple effects, including changes in biodiversity, species composition, and ecosystem functioning,” but “it remains unknown whether such shifts in biodiversity and species composition may, themselves, be major contributors to the total, long-term impacts of anthropogenic drivers on ecosystem functioning.” To discover how this phenomenon may operate, Isbell *et al.* set out to analyze temporal trends in the effects of nitrogen enrichment on the productivity, plant diversity, and species compositions of naturally assembled grasslands in a long-term nitrogen-addition experiment conducted at the Cedar Creek Ecosystem Science Reserve in central Minnesota (USA), where they measured aboveground peak biomass and the number and abundances of plant species in each plot from 1982 to 2008. They then similarly analyzed data from the BioCON (Biodiversity, CO₂ and N) experiment located at the same reserve, “to quantify the extent to which N enrichment and elevated CO₂ influence productivity by non-randomly changing grassland plant diversity,” which they did in the latter instance from 1998 to 2011.

The six scientists report “although chronic nitrogen enrichment initially increased productivity, it also led to loss of plant species, including initially dominant species, which then caused substantial diminishing returns from nitrogen fertilization.” In contrast, they report, “elevated CO₂ did not decrease grassland plant diversity” but “consistently promoted productivity over time,” both by its direct aerial fertilization effect and by its non-significant yet real tendency to enhance species diversity.

Greer *et al.* (2000) studied the effects of elevated air temperature and CO₂ concentration on photosynthesis in five pasture species grown for approximately one month in controlled environment chambers. They found the CO₂-induced photosynthetic enhancement rose with increasing air temperature. At twice-ambient levels of atmospheric CO₂, average photosynthetic rates were 36 and 70% greater than for control plants grown under ambient CO₂ concentrations at air temperatures of 18 and 28°C, respectively.

Kudernatsch *et al.* (2008) conducted a warming-only (no change in CO₂) experiment on species-rich *Carex sempervirens* (CS) and species-poor *Carex firma* (CF) calcareous grasslands in the Berchtesgaden National Park of Southeast Germany. They installed several open-top chambers on the

plants in each of three successive years just after snowmelt was complete in the spring and removed them just before snowfall commenced in the autumn. This led to snow-free-season increases in mean daily air temperature of 0.7°C in the CS grasslands and 1.4°C in the CF grasslands, along with corresponding mean daily soil temperature increases of 0.2 and 0.8°C. The authors report “growth and/or reproduction of 12 of the 14 studied species were significantly stimulated by warming,” “only two species showed no response,” and “none of the species experienced decreases in growth or reproduction.” They also found “a significant effect of warming on nutrient availability could not be detected,” leading them to conclude “the observed response of vegetation is therefore mainly caused by direct and not by indirect temperature effects.”

In 1982–1984, Madsen *et al.* (2011) “studied the ecology of non-breeding moulting geese in Jameson Land, low Arctic East Greenland,” finding the geese “consumed most of the graminoid production in available moss fens,” leading them to conclude “the geese had filled up the available habitat.” Nevertheless, they came back in 2008 to see what had happened over the intervening period of significant global—and local—warming.

Madsen *et al.* replicated what they had done in their earlier study in terms of both methodology and analysis. In addition, they determined the above-ground biomass of the graminoid marsh vegetation, to compare it with what it had been determined to be in 1983 and 1984 by Madsen and Mortensen (1987). The researchers report the data they obtained in late July 2008 yielded a standing crop biomass of 98.2 g/m², which was 2.34 times greater than what had been measured in the same location in late July 1984. After listing three lines of evidence for concluding from their original field studies in 1982–1984 the “habitat capacity of Jameson Land for moulting geese was close to being reached,” they now report, between that earlier time and 2008, “the number of moulting geese in Jameson Land tripled.”

In further support of their observations, they note, “on Bylot Island, northeast Canada, graminoid above-ground production in wetlands has increased by 84% between 1990 and 2007, most likely as a consequence of climate warming,” citing Cadieux *et al.* (2008). Also, they write, “on Svalbard, it is known that early snow melt has a dramatic positive effect on the density of nesting geese and their fecundity,” citing Madsen *et al.* (2007) and noting “the climate in East Greenland has been warming during the last 30 years.”

Other researchers have investigated the impact of elevated CO₂ and water stress on grasslands.

Szente *et al.* (1998) studied two grasses and two broad-leaved species common to loess grasslands in the vicinity of Budapest in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm. After 231 days, the grasses and broad-leaved species exhibited CO₂-induced increases in seasonal plant water use efficiencies of 72 and 366%, respectively, the scientists report. Clark *et al.* (1999) likewise note mixed grassland species from a New Zealand pasture exposed to an atmospheric CO₂ concentration of 700 ppm consistently displayed greater water use efficiencies than species growing in ambient air, due mostly to CO₂-induced increases in photosynthesis. In a two-year CO₂-enrichment study of a tallgrass prairie ecosystem located in Kansas, USA, Adams *et al.* (2000) found plants in open-top chambers fumigated with twice-ambient levels of atmospheric CO₂ exhibited significantly reduced rates of stomatal conductance and transpirational water loss, which also enhanced plant daily average water use efficiency throughout the entire study, but via reduced water loss as opposed to the enhanced photosynthesis observed by Clark *et al.*

In an eight-year CO₂-enrichment study of a tallgrass prairie ecosystem located in Kansas, USA, Owensby *et al.* (1999) report prairie communities in open-top chambers fumigated with twice-ambient levels of atmospheric CO₂ maintained greater amounts of soil moisture than communities exposed to ambient air in every year of the study. Likewise, in an experiment lasting four years, Lutze *et al.* (1998) grew swards of *Danthonia richardsonii* at various soil nitrogen contents in glasshouses receiving atmospheric CO₂ concentrations of 360 and 720 ppm. Averaged across all nitrogen regimes, CO₂-enriched swards used about 25% less water than swards grown at 360 ppm CO₂, which consequently allowed the CO₂-enriched microcosms to maintain greater soil water contents throughout the study.

In a two-year experiment, Arnone and Bohlen (1998) grew intact monoliths of calcareous grasslands in controlled environments fumigated with air containing 350 and 600 ppm CO₂. They found CO₂-induced reductions in transpirational water loss were likely responsible for the higher soil moisture contents observed in the CO₂-enriched monoliths, which were 10 to 20% greater than those observed in monoliths exposed to ambient air. And Zaller *et al.* (1997) established open-top and open-bottom chambers in a species-rich grassland located near Basel, Switzerland, subjecting them to atmospheric

CO₂ concentrations of 350 and 600 ppm. They report mean annual soil moisture contents in the CO₂-enriched chambers were 10% greater than those observed in control chambers treated with air containing 350 ppm CO₂.

Grunzweig and Körner (2001) constructed model grasslands representative of the Negev of Israel and placed them in growth chambers with atmospheric CO₂ concentrations of 280, 440, and 600 ppm for five months, to determine the effects of elevated CO₂ on these semi-arid plant communities. They found elevated CO₂ reduced rates of evapotranspiration and increased soil moisture contents in model grassland communities exposed to atmospheric CO₂ concentrations of 440 and 600 ppm. Between two periods of imposed drought, soil moisture was 22 and 27% higher in communities exposed to 440 and 600 ppm CO₂, respectively, than in control communities exposed to pre-industrial levels of atmospheric CO₂. Such increases in soil moisture content may have contributed to peak ecosystem CO₂ uptake rates 21 and 31% greater at 400 and 600 ppm CO₂ than at 280 ppm CO₂. In addition, atmospheric CO₂ enrichment had no effect on nighttime respiratory carbon losses from the ecosystems. Thus, these semi-arid grasslands were acting as carbon sinks under CO₂-enriched conditions. Elevated CO₂ (440 and 600 ppm) increased total community biomass by 14% over that produced by communities exposed to the subambient CO₂ concentration. Also, when the total biomass produced was related to the total amount of water loss via evapotranspiration, communities grown at atmospheric CO₂ concentrations of 440 and 600 ppm exhibited CO₂-induced increases in water use efficiency 17 and 28% higher than those displayed by control communities exposed to air of 280 ppm CO₂.

As atmospheric CO₂ concentrations increase, semi-arid grasslands common to the Negev of Israel likely will exhibit increases in photosynthesis and biomass production, as the study shows. Moreover, such increases in biomass likely will occur while using less water. Model ecosystems exposed to elevated atmospheric CO₂ concentrations lost less water through evapotranspiration and consequently had greater soil moisture contents than ecosystems that were not CO₂-enriched. Thus it would appear the water-use efficiencies of these grasslands likely will increase in future years as the air's CO₂ content increases further. Most importantly, the gas exchange measurements—including the null effect of elevated CO₂ on dark respiration—and the biomass data obtained for the ecosystems demonstrate these

grasslands likely will become increasingly effective carbon sinks, removing ever-greater amounts of carbon from the air.

Derner *et al.* (2001) grew two C₄ grasses (*Schizachyrium scoparium* Nash and *Andropogon gerardii* Vitman.) common to tallgrass prairies in pots placed in a 38-meter-long controlled environment chamber located in a ventilated glasshouse. This chamber was composed of five 7.6m lengths of a 0.76m-deep and 0.45m-wide soil container topped with a transparent and tunnel-shaped polyethylene cover attached to its upper edges. Various other plants placed in this tunnel served as photosynthetic “sinks” for CO₂ as a commercial blower moved air through the chamber sections. Thus a CO₂ gradient was created through the “long and winding tunnel,” from near 350 ppm at its entrance to approximately 200 ppm at its end. In addition, these two C₄ grasses were subjected to relative soil water contents 90 or 50% of their total soil water holding capacities. Thus the authors were able to study how the historical rise in the air's CO₂ content has influenced growth in these grasses under different soil moisture conditions.

Data from the two C₄ grasses were pooled, as there were no significant differences between species. With respect to aboveground growth, shoot biomass was 57% greater at the ambient (350 ppm), rather than the subambient (200 ppm), atmospheric CO₂ concentration, and the increase in relative water content enhanced shoot biomass by 82%. Root growth (root length, mass, surface area, and volume) was 15–27% greater at the ambient, as opposed to the subambient, atmospheric CO₂ concentration, and 40–51% greater at high, versus low, soil water content.

Since the 150 ppm increase in atmospheric CO₂ concentration employed in this study is actually less than the rise in this parameter that has occurred since the end of the last great ice age, Derner *et al.* state “C₄ grasses may have already experienced an augmentation in root growth which is comparable to that experienced with a doubling of current CO₂ concentrations.” There is every reason to conclude such grasses will continue to respond positively to future increases in the air's CO₂ content. In addition, as the atmospheric CO₂ concentration rises, it likely will decrease water use in these prairie grasses, due to CO₂-induced reductions in stomatal conductance, causing the indirect effects of greater soil moisture to enhance their growth further.

Working with open-top chambers maintained at ambient and twice-ambient atmospheric CO₂ concentrations, Ferretti *et al.* (2003) investigated “the dynamics of soil water isotopes and water cycling in a

mixed C₃/C₄ grassland in the western Great Plains region of the USA,” which is predominantly carpeted by the C₄ grass *Bouteloua gracilis* (H.B.K.) Lag. (blue grama) and the C₃ grasses *Stipa comata* Trin and Rupr. (needle-and-thread grass) and *Pascopyrum smithii* (Rydb.) A. Love (western wheatgrass). In addition to documenting a mean plant biomass increase of 50% in the elevated CO₂ treatment over the two years of their study, the authors observed significantly wetter soils in the elevated CO₂ treatment, which they say were “most likely a result of improved soil-water conservation as a result of reduced stomatal conductance under elevated CO₂.”

Noting “elevated CO₂ had the effect of increasing soil-water conservation as has been previously found (e.g., Morgan *et al.*, 2001; Volk *et al.*, 2000),” and “reduced evaporation was mainly responsible for greater soil water content under elevated CO₂,” Ferretti *et al.* remark “the most significant effect of elevated CO₂ on the hydrologic budget in water limited ecosystems is likely to be an increase in soil water storage (Jackson *et al.*, 1998),” as was found in their study. It is likely this phenomenon contributed significantly to the growth enhancement observed in the CO₂-enriched treatment, which was more than what might have been expected from the aerial fertilization effect of elevated CO₂ operating alone.

Also focusing on water stress, Niklaus and Körner (2004) used screen-aided CO₂ control (SACC) technology to enrich the air above a water-limited and phosphorus-poor temperate calcareous grassland in Switzerland with an extra 235 ppm of CO₂ for a total of six years, over which period they measured several individual and community plant parameters. They report peak percentage increases in biomass production in years 1 through 6 of the experiment were, respectively, 5%, 20%, 22%, 27%, 31%, and 18%, for an average of 23.6% over the last five years of the study. Year-to-year variability in this factor was best predicted by precipitation and resulting soil moisture differences, with the “obvious mechanism,” the authors write, being “soil moisture savings due to reduced stomatal conductance under elevated CO₂,” which would tend to “alleviate effects of water limitation more in dry years.” In addition, although Niklaus and Körner note “low available phosphorous ultimately limited community productivity and responses to CO₂,” this deficiency—coupled with a deficiency of water—was not sufficient to counter the growth-promoting effect of atmospheric CO₂ enrichment, which in this case was equivalent to a 30% increase in growth in response to a standard 300 ppm increase in the air’s CO₂ concentration.

Because many grasslands are subject to grazing pressure from herbivores, it is also important to see how this stress phenomenon affects photosynthetic responses to atmospheric CO₂ enrichment. Rogers *et al.* (1998) grew swards of perennial ryegrass in a FACE experiment utilizing atmospheric CO₂ concentrations of 360 and 600 ppm. In addition, they supplied swards with low and high levels of soil nitrogen and subjected them to cutting treatments to simulate herbivory. Under these conditions, elevated CO₂ stimulated photosynthetic rates by approximately 35%, regardless of soil nitrogen supply or cutting treatment. In a similar FACE experiment, two forbs and one grass species common to chalk grassland swards of Europe were grown for 14 months at 355 and 600 ppm CO₂ to study the influence of simulated grazing on their photosynthetic responses to atmospheric CO₂ enrichment (Bryant *et al.*, 1998). Prior to simulated grazing, the CO₂-induced photosynthetic response of the grass and one forb species were both around 28%, and the other forb was non-responsive to elevated CO₂. After grazing, however, both forbs exhibited a much larger 40% increase in photosynthesis, and the grass slightly increased its positive response to 30%. The data from these two studies suggest grazing pressure from herbivores will not reduce CO₂-induced increases in photosynthesis, and may in fact cause them to rise.

The studies reviewed above suggest increases in the air’s CO₂ concentration lead to rising productivity of Earth’s grassland species, even under unfavorable growing conditions characterized by less-than-adequate soil moisture, inadequate soil nutrition, elevated air temperature, and physical stress imposed by herbivory.

References

- Adams, N.R., Owensby, C.E., and Ham, J.M. 2000. The effect of CO₂ enrichment on leaf photosynthetic rates and instantaneous water use efficiency of *Andropogon gerardii* in the tallgrass prairie. *Photosynthesis Research* 65: 121–129.
- Arnone III, J.A. and Bohlen, P.J. 1998. Stimulated N₂O flux from intact grassland monoliths after two growing seasons under elevated atmospheric CO₂. *Oecologia* 116: 331–335.
- Bever, J.D. 1994. Feedback between plants and their soil communities in an old field community. *Ecology* 75: 1965–1977.
- Bhatt, R.K., Baig, M.J., and Tiwari, H.S. 2007. Growth, biomass production, and assimilatory characters in

Climate Change Reconsidered II: Biological Impacts

- Cenchrus ciliaris* L. under elevated CO₂ condition. *Photosynthetica* **45**: 296–298.
- Bryant, J., Taylor, G., and Frehner, M. 1998. Photosynthetic acclimation to elevated CO₂ is modified by source:sink balance in three component species of chalk grassland swards grown in a free air carbon dioxide enrichment (FACE) experiment. *Plant, Cell and Environment* **21**: 159–168.
- Cadieux, M.C., Gauthier, G., Gagnon, C.A., Bety, J., and Berteaux, D. 2008. Monitoring the Environmental and Ecological Impacts of Climate Change on Bylot Island, Sirmilik National Park. Université Laval, Quebec, Canada.
- Campbell, B.D., Stafford Smith, D.M., Ash, A.J., Fuhrer, J., Gifford, R.M., Hiernaux, P., Howden, S.M., Jones, M.B., Ludwig, J.A., Manderscheid, R., Morgan, J.A., Newton, P.C.D., Nosberger, J., Owensby, C.E., Soussana, J.F., Tuba, Z., and ZuoZhong, C. 2000. A synthesis of recent global change research on pasture and rangeland production: reduced uncertainties and their management implications. *Agriculture, Ecosystems and Environment* **82**: 39–55.
- Cannell, M.G.R. and Thornley, J.H.M. 1998. N-poor ecosystems may respond more to elevated [CO₂] than N-rich ones in the long term. A model analysis of grassland. *Global Change Biology* **4**: 431–442.
- Clark, H., Newton, P.C.D., and Barker, D.J. 1999. Physiological and morphological responses to elevated CO₂ and a soil moisture deficit of temperate pasture species growing in an established plant community. *Journal of Experimental Botany* **50**: 233–242.
- Cotrufo, M.F. and Gorissen, A. 1997. Elevated CO₂ enhances below-ground C allocation in three perennial grass species at different levels of N availability. *New Phytologist* **137**: 421–431.
- Crawley, M.J. 1997. *Plant Ecology*. Blackwell Science, Oxford, UK.
- De Deyn, G.B., Raaijmakers, C.E., Zoomer, H.R., Berg, M.P., de Rulter, P.C., Verhoef, H.A., Bezemer, T.M., and van der Putten, W.H. 2003. Soil invertebrate fauna enhances grassland succession and diversity. *Nature* **422**: 711–713.
- Derner, J.D., Polley, H.W., Johnson, H.B., and Tischler, C.R. 2001. Root system response of C₄ grass seedlings to CO₂ and soil water. *Plant and Soil* **231**: 97–104.
- Ebersberger, D., Niklaus, P.A., and Kandeler, E. 2003. Long term CO₂ enrichment stimulates N-mineralisation and enzyme activities in calcareous grassland. *Soil Biology & Biochemistry* **35**: 965–972.
- Edwards, E.J., McCaffery, S., and Evans, J.R. 2005. Phosphorus status determines biomass response to elevated CO₂ in a legume: C₄ grass community. *Global Change Biology* **11**: 1968–1981.
- Edwards, G.R., Clark, H., and Newton, P.C.D. 2001. The effects of elevated CO₂ on seed production and seedling recruitment in a sheep-grazed pasture. *Oecologia* **127**: 383–394.
- Ferretti, D.F., Pendall, E., Morgan, J.A., Nelson, J.A., LeCain, D., and Mosier, A.R. 2003. Partitioning evapotranspiration fluxes from a Colorado grassland using stable isotopes: Seasonal variations and ecosystem implications of elevated atmospheric CO₂. *Plant and Soil* **254**: 291–303.
- Greer, D.H., Laing, W.A., Campbell, B.D., and Halligan, E.A. 2000. The effect of perturbations in temperature and photon flux density on the growth and photosynthetic responses of five pasture species. *Australian Journal of Plant Physiology* **27**: 301–310.
- Grunzweig, J.M. and Körner, C. 2001. Growth, water and nitrogen relations in grassland model ecosystems of the semi-arid Negev of Israel exposed to elevated CO₂. *Oecologia* **128**: 251–262.
- Hartwig, U.A., Wittmann, P., Braun, R., Hartwig-Raz, B., Jansa, J., Mozafar, A., Luscher, A., Leuann, A., Frossard, E., and Nosberger, J. 2002. Arbuscular mycorrhiza infection enhances the growth response of *Lolium perenne* to elevated atmospheric pCO₂. *Journal of Experimental Botany* **53**: 1207–1213.
- Hodge, A., Paterson, E., Grayston, S.J., Campbell, C.D., Ord, B.G., and Killham, K. 1998. Characterization and microbial utilisation of exudate material from the rhizosphere of *Lolium perenne* grown under CO₂ enrichment. *Soil Biology and Biochemistry* **30**: 1033–1043.
- Isbell, F., Reich, P.B., Tilman, D., Hobbie, S.E., Polasky, S., and Binder, S. 2013. Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proceedings of the National Academy of Sciences USA* **110**: 11,911–11,916.
- Jackson, R.B., Sala, O.E., Paruelo, J.M., and Mooney, H.A. 1998. Ecosystem water fluxes for two grasslands in elevated CO₂: A modeling analysis. *Oecologia* **113**: 537–546.
- Johnson, N.C., Wolf, J., and Koch, G.W. 2003. Interactions among mycorrhizae, atmospheric CO₂ and soil N impact plant community composition. *Ecology Letters* **6**: 532–540.
- Jongen, M. and Jones, M.B. 1998. Effects of elevated carbon dioxide on plant biomass production and competition in a simulated neutral grassland community. *Annals of Botany* **82**: 111–123.
- Kudernatsch, T., Fischer, A., Bernhardt-Romermann, M., and Abs, C. 2008. Short-term effects of temperature

- enhancement on growth and reproduction of alpine grassland species. *Basic and Applied Ecology* **9**: 263–274.
- Leadley, P.W., Niklaus, P.A., Stocker, R., and Körner, C. 1999. A field study of the effects of elevated CO₂ on plant biomass and community structure in a calcareous grassland. *Oecologia* **118**: 39–49.
- Lüscher, A., Hendrey, G.R., and Nosberger, J. 1998. Long-term responsiveness to free air CO₂ enrichment of functional types, species and genotypes of plants from fertile permanent grassland. *Oecologia* **113**: 37–45.
- Lutze, J.L. and Gifford, R.M. 1998. Carbon accumulation, distribution and water use of *Danthonia richardsonii* swards in response to CO₂ and nitrogen supply over four years of growth. *Global Change Biology* **4**: 851–861.
- Madsen, J., Jaspers, C., Tamstorf, M., Mortensen, C.E., and Riget, F. 2011. Long-term effects of grazing and global warming on the composition and carrying capacity of graminoid marshes for moulting geese in East Greenland. *Ambio* **40**: 638–649.
- Madsen, J. and Mortensen, C.E. 1987. Habitat exploitation and interspecific competition of moulting geese in East-Greenland. *Ibis* **129**: 25–44.
- Madsen, J., Tamstorf, M., Klaassen, M., Eide, N., Glahder, C., Riget, F., Nyegaard, H., and Cottaar, F. 2007. Effects of snow cover on the timing and success of reproduction in high-Arctic pink-footed geese *Anser brachyrhynchus*. *Polar Biology* **30**: 1363–1372.
- Morgan, J., LeCain, D., Mosier, A., and Milchunas, D. 2001. Elevated CO₂ enhances water relations and productivity and affects gas exchange in C₃ and C₄ grasses of the Colorado shortgrass steppe. *Global Change Biology* **7**: 451–466.
- Morgan, J.A., Skinner, R.H., and Hanson, J.D. 2001. Nitrogen and CO₂ affect regrowth and biomass partitioning differently in forages of three functional groups. *Crop Science* **41**: 78–86.
- Navas, M.-L., Garnier, E., Austin, M.P., and Gifford, R.M. 1999. Effect of competition on the responses of grasses and legumes to elevated atmospheric CO₂ along a nitrogen gradient: differences between isolated plants, monocultures and multi-species mixtures. *New Phytologist* **143**: 323–331.
- Newman, J.A., Gibson, D.J., Hickam, E., Lorenz, M., Adams, E., Bybee, L., and Thompson, R. 1999. Elevated carbon dioxide results in smaller populations of the bird cherry-oat aphid *Rhopalosiphum padi*. *Ecological Entomology* **24**: 486–489.
- Niklaus, P.A., Alpehi, J., Ebersberger, D., Kampichlers, C., Kandeler, E., and Tschirko, D. 2003. Six years of in situ CO₂ enrichment evoke changes in soil structure and soil biota of nutrient-poor grassland. *Global Change Biology* **9**: 585–600.
- Niklaus, P.A. and Körner, C. 2004. Synthesis of a six-year study of calcareous grassland responses to *in situ* CO₂ enrichment. *Ecological Monographs* **74**: 491–511.
- Niklaus, P.A., Leadley, P.W., Stocklin, J., and Körner, C. 1998. Nutrient relations in calcareous grassland under elevated CO₂. *Oecologia* **116**: 67–75.
- Olf, H. and Ritchie, M.E. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* **13**: 261–265.
- Owensby, C.E., Ham, J.M., Knapp, A.K., and Auen, L.M. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO₂. *Global Change Biology* **5**: 497–506.
- Polley, H.W., Fay, P.A., Jin, V.L., and Combs Jr., G.F. 2011. CO₂ enrichment increases element concentrations in grass mixtures by changing species abundances. *Plant Ecology* **212**: 945–957.
- Polley, H.W., Morgan, J.A., and Fay, P.A. 2010. Application of a conceptual framework to interpret variability in rangeland responses to atmospheric CO₂ enrichment. *Journal of Agricultural Science* **149**: 1–14.
- Reich, P.B., Tilman, D., Craine, J., Ellsworth, D., Tjoelker, M.G., Knops, J., Wedin, D., Naeem, S., Bahauddin, D., Goth, J., Bengtson, W., and Lee, T.A. 2001. Do species and functional groups differ in acquisition and use of C, N and water under varying atmospheric CO₂ and N availability regimes? A field test with 16 grassland species. *New Phytologist* **150**: 435–448.
- Rillig, M.C., Allen, M.F., Klironomos, J.N., Chiariello, N.R., and Field, C.B. 1998a. Plant species-specific changes in root-inhabiting fungi in a California annual grassland: responses to elevated CO₂ and nutrients. *Oecologia* **113**: 252–259.
- Rillig, M.C., Allen, M.F., Klironomos, J.N., and Field, C.B. 1998b. Arbuscular mycorrhizal percent root infection and infection intensity of *Bromus hordeaceus* grown in elevated atmospheric CO₂. *Mycologia* **90**: 199–205.
- Rillig, M.C., Field, C.B., and Allen, M.F. 1999a. Fungal root colonization responses in natural grasslands after long-term exposure to elevated atmospheric CO₂. *Global Change Biology* **5**: 577–585.
- Rillig, M.C., Field, C.B., and Allen, M.F. 1999b. Soil biota responses to long-term atmospheric CO₂ enrichment in two California annual grasslands. *Oecologia* **119**: 572–577.
- Rogers, A., Fischer, B.U., Bryant, J., Frehner, M., Blum, H., Raines, C.A., and Long, S.P. 1998. Acclimation of photosynthesis to elevated CO₂ under low-nitrogen nutrition is affected by the capacity for assimilate utilization. Perennial ryegrass under free-air CO₂ enrichment. *Plant Physiology* **118**: 683–689.

Stocklin, J. and Körner, Ch. 1999. Interactive effects of elevated CO₂, P availability and legume presence on calcareous grassland: results of a glasshouse experiment. *Functional Ecology* **13**: 200–209.

Suter, D., Frehner, M., Fischer, B.U., Nosberger, J., and Lüscher, A. 2002. Elevated CO₂ increases carbon allocation to the roots of *Lolium perenne* under free-air CO₂ enrichment but not in a controlled environment. *New Phytologist* **154**: 65–75.

Szente, K., Nagy, Z., and Tuba, Z. 1998. Enhanced water use efficiency in dry loess grassland species grown at elevated air CO₂ concentration. *Photosynthetica* **35**: 637–640.

Teyssonneyre, F., Picon-Cochard, C., and Soussana, J.F. 2002. How can we predict the effects of elevated CO₂ on the balance between perennial C₃ grass species competing for light? *New Phytologist* **154**: 53–64.

van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., and Sanders, I.R. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**: 69–72.

van Ginkel, J.H., Gorissen, A., and Polci, D. 2000. Elevated atmospheric carbon dioxide concentration: effects of increased carbon input in a *Lolium perenne* soil on microorganisms and decomposition. *Soil Biology & Biochemistry* **32**: 449–456.

van Ginkel, J.H. and Gorissen, A. 1998. In situ decomposition of grass roots as affected by elevated atmospheric carbon dioxide. *Soil Science Society of America Journal* **62**: 951–958.

Volk, M., Niklaus, P.A., and Körner, C. 2000. Soil moisture effects determine CO₂ responses of grassland species. *Oecologia* **125**: 380–388.

Wand, S.J.E., Midgley, G.F., Jones, M.H., and Curtis, P.S. 1999. Responses of wild C₄ and C₃ grass (Poaceae) species to elevated atmospheric CO₂ concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology* **5**: 723–741.

Wilson, G.W.T. and Hartnett, D.C. 1998. Interspecific variation in plant responses to mycorrhizal colonization in tallgrass prairie. *American Journal of Botany* **85**: 1732–1738.

Zaller, J.G. and Arnone III, J.A. 1999. Interactions between plant species and earthworm casts in a calcareous grassland under elevated CO₂. *Ecology* **80**: 873–881.

Zaller, J.G. and Arnone III, J.A. 1997. Activity of surface-casting earthworms in a calcareous grassland under elevated atmospheric CO₂. *Oecologia* **111**: 249–254.

1.2.2.2 Carbon Sequestration

- Research indicates soils beneath grasslands will significantly increase their carbon-storing capability as atmospheric CO₂ concentrations rise.

Carbon sequestration by grasslands is a less-investigated topic than carbon sequestration by forests. Nevertheless, several researchers have examined how grassland ecosystems might respond in this regard as the air's CO₂ concentration rises.

Fitter *et al.* (1997) transferred monoliths of two contrasting grasslands, a species-rich turf growing over limestone and a species-poor turf growing over a peaty soil, from Moor House National Nature Reserve in the United Kingdom to four “solardomes” at Lancaster University, where they maintained them for two years under natural daylight and air temperatures close to ambient. One set of two solardomes was exposed to ambient air and another set to air enriched with an extra 250 ppm CO₂. At various times throughout the experiment, the researchers made a number of measurements of above- and below-ground growth.

Shoot biomass was unaltered by the elevated level of atmospheric CO₂, but root biomass was enhanced by 40 to 50%. Furthermore, especially in the peat soil, root turnover was highly accelerated in the CO₂-enriched treatment—so much so, in fact, the authors conclude the increase in root biomass observed at the end of the experiment “was almost certainly a large underestimate of the amount of carbon transferred to the soil.” The authors further note the increased productivity the two grassland ecosystems exhibited under elevated atmospheric CO₂ concentrations, along with the consequent increases in soil organic matter, are “likely to persist.”

Cotrufo and Gorissen (1997) grew three grass species (*Lolium perenne* L. cv. Barlet, *Agrostis capillaris* L. cv. Bardot, and *Festuca ovina* L. cv. Barok) in 0.65-liter pots under two different levels of soil nitrogen in growth chambers maintained at 350 and 700 ppm CO₂ in continuously ¹⁴C-labeled atmospheres. They harvested half the plants after 32 days and the other half after 55 days. They analyzed the shoots, roots, and soils for total carbon (C) and ¹⁴C content.

They found elevated CO₂ increased the whole-plant dry weights of all three species by an average of 20% and, in general, increased root growth more than shoot growth. It also increased soil microbial biomass by slightly more than 15%. Of the ¹⁴C that was fixed, 90% remained in the plant and 10% was transferred to

the soil. There, 7% was found in the bulk soil and 3% was found in the rhizosphere soil close to the plant roots, split about equally between soil microbial biomass and soil residue.

The authors state what they observed “is consistent with the general finding that the soil microbial biomass is C-limited, and supports the hypothesis that a greater C input below-ground, as a result of increased size of the root system, at high CO₂ elicits an increase in soil microbial biomass.” They also state “elevated CO₂ will induce an increase in relative C allocation to below-ground sinks independent of nitrogen level.” Finally, they conclude their findings for all three grasses confirm “elevated CO₂ could result in greater soil C stores due to increased C-input into soils,” as well as “a higher residence time for C in soils, thus counteracting increased decomposition under higher temperatures.” Thus, they write, “we may well expect that this increased C input below-ground will be sustained in the longer term.” This phenomenon clearly would be expected to reduce the level to which atmospheric CO₂ concentrations would rise in its absence.

Casella and Soussana (1997) grew perennial ryegrass (*Lolium perenne* L. cv. Preference) swards in large containers at two different levels of soil nitrogen supply for two years at ambient and elevated (700 ppm) CO₂ concentrations, as well as at ambient and elevated (+3°C) temperature. The soils were maintained at field capacity via irrigation, but the water supply was reduced in summer to simulate characteristic summer water deficits. Throughout the experiment, they made a number of measurements on the plants and soils, including canopy gas exchanges, plant water soluble carbohydrates, and biomass production. The authors report “a relatively large part of the additional photosynthetic carbon is stored below-ground during the two first growing seasons after exposure to elevated CO₂, thereby increasing significantly the below-ground carbon pool.” At low and high soil nitrogen supply, for example, the elevated CO₂ increased soil carbon storage by 32 and 96%, respectively, “with no significant increased temperature effect.” The elevated temperature actually helped to increase soil carbon storage, because the enhanced soil desiccation at +3°C helped restrict below-ground respiration. Casella and Soussana conclude “this stimulation of the below-ground carbon sequestration in temperate grassland soils could exert a negative feed-back on the current rise of the atmospheric CO₂ concentration.”

Lutze and Gifford (1998) grew microcosms of the C₃ grass *Danthonia richardsonii* for four years in

glasshouses with atmospheric CO₂ concentrations of 360 or 720 ppm and three levels of soil nitrogen to determine the effects of elevated CO₂ and soil nutrition on microcosm carbon gain and water use. They conducted destructive harvests of plant material at six-month intervals throughout the project. Results indicated carbon accumulation in the microcosms was strongly correlated with soil nitrogen: Nitrogen was limiting productivity, even in the highest fertilization treatment. Nevertheless, when averaged across all harvests and nitrogen regimes, elevated CO₂ significantly increased total microcosm carbon gains by 15–34%, in spite of a 9% reduction in leaf area index. In addition, elevated CO₂ increased senesced leaf material per unit ground area at all harvests and nitrogen treatments by an average of 31%. Consequently, these phenomena led to final soil carbon contents in CO₂-enriched microcosms 4, 9, and 17% greater than in ambient microcosms at low, medium, and high soil nitrogen treatments, respectively. Elevated CO₂ also reduced microcosm water use by 25% across all nitrogen treatments, thereby allowing greater soil volumetric water contents to exist in CO₂-enriched microcosms.

Nitschelm *et al.* (1997) report white clover exposed to an atmospheric CO₂ concentration of 600 ppm for one growing season channeled 50% more newly fixed carbon compounds into the soil than similar plants exposed to ambient air. In addition, the clover’s roots decomposed at a rate 24% slower than roots of control plants, as also has been reported for white clover by David *et al.* (2001). These observations suggest rising CO₂ content will greatly enhance soil carbon sequestration under white clover ecosystems.

Van Ginkel *et al.* (1996) exposed mini-ecosystems comprised entirely of perennial ryegrass species to an atmospheric CO₂ concentration of 700 ppm for two months, finding a 92% increase in root growth and 19% and 14% decreases in root decomposition rates one and two years, respectively, after incubating ground roots in soils. Van Ginkel and Gorissen (1998) followed up this work, showing a 13% reduction in the decomposition rates of CO₂-enriched perennial ryegrass roots in both disturbed and undisturbed root profiles. This and other work led the authors to calculate CO₂-induced reductions in the decomposition of perennial ryegrass litter, which enhances soil carbon sequestration, could be large enough to remove over half of the anthropogenic CO₂ emissions that may be released in the next century (Van Ginkel *et al.*, 1999).

Van Ginkel *et al.* (2000) found elevated CO₂

decreased root decomposition rates of perennial ryegrass grown at 700 ppm CO₂ by 14% after 230 days of incubation in elevated CO₂. In addition, the scientists determined raising the incubation temperature by 2 °C had little effect on the CO₂-induced reductions in decomposition rate, for they were still 12% lower than those measured at 350 ppm CO₂. In a shorter-term experiment the researchers found even a 6 °C increase in air temperature could not counterbalance the CO₂-induced reductions in decomposition rate.

These results suggest future increases in the air's CO₂ content likely will cause slight reductions in rates of plant litter decomposition, thus allowing more carbon to remain sequestered from the atmosphere for longer periods of time, and this will be the case even if Earth's air temperature rises.

In some cases, however, atmospheric CO₂ enrichment has been reported to have little or no significant effect on litter quality and subsequent rates of litter decomposition. Hirschel *et al.* (1997) took fallen leaves from species common to alpine and calcareous grasslands and incubated them in mesh nylon bags placed on the soil surfaces of their respective mesocosms, subjecting them to ambient and twice-ambient concentrations of atmospheric CO₂. After one year of incubation, the decomposition rates of the litter produced under the ambient and elevated CO₂ conditions did not differ significantly from each other, except in the case of one alpine sedge, which exhibited reduced rates of decomposition under atmospheric CO₂ enrichment. Dukes and Field (2000) reported similar results after incubating litter derived from various combinations of grassland species common to California, USA, for an eight-month period at atmospheric CO₂ concentrations of 350 and 700 ppm and finding minimal effects of elevated CO₂ on decomposition rates.

In a five-year study of a grassland growing on a moderately fertile soil at Stanford University's Jasper Ridge Biological Preserve in central California—which utilized 20 open-top chambers (ten each at 360 and 720 ppm CO₂)—Hu *et al.* (2001) found a doubling of the air's CO₂ content increased both soil microbial biomass and plant nitrogen uptake. With less nitrogen left in the soil to be used by a larger number of microbes, microbial respiration per unit of soil microbe biomass significantly declined in the elevated CO₂ environments; with this decrease in microbial decomposition, there was an increase in carbon accumulation in the soil.

Hu *et al.* conclude this CO₂-induced chain of

events could readily cause terrestrial grassland ecosystems to become significantly stronger net carbon (C) sinks than they are currently, especially if their plants become more efficient at acquiring nitrogen (N) from soils of low C:N organic matter ratio. They also suggest such CO₂-enhanced grassland N acquisition might be prompted by increased root colonization by symbiotic mycorrhizal fungi, which has been found to be a rather common consequence of atmospheric CO₂ enrichment (Rillig *et al.*, 1998, 2000). Hence, the scientists conclude, as have many others, the carbon sequestered by these means “could partially offset the effects of anthropogenic CO₂ emissions on atmospheric CO₂ [concentration].”

How much extra carbon can be sequestered in the planet's grassland soils as a result of a doubling of the air's CO₂ content? A good first approximation at an answer is provided by Williams *et al.* (2000), who studied this phenomenon for eight years in a Kansas (USA) tallgrass prairie, utilizing open-top chambers enclosing mixtures of C₃ and C₄ grasses continually fumigated with air of either ambient or twice-ambient atmospheric CO₂ concentration. Williams *et al.* found the average soil water content in the first 15 cm of the soil profile was approximately 15% greater beneath the chambers receiving the extra supply of CO₂, due, presumably, to CO₂-induced reductions in plant stomatal conductance that blunted transpirational water loss. The saved moisture, in turn, enabled plants to be more productive during the growing season, and with a significant portion of that extra productivity directed belowground into roots, there was a nearly equivalent increase in soil microbial activity across the final five years of the study. The authors report there was an 8% increase in total soil carbon content over the course of the study.

Extrapolating this value to all of Earth's temperate grasslands, which make up about 10% of the land area of the globe, Williams *et al.* calculate the CO₂-induced increase in soil carbon sequestration could amount to an additional 1.3 Pg of carbon being sequestered in just the top 15 cm of the world's grassland soils over the next century.

Riedo *et al.* (2000) used a mechanistic pasture simulation model (PaSim) to predict changes in net primary productivity and carbon stocks in differently managed grasslands in response to increased atmospheric CO₂ concentration and climate change. Results indicated elevated CO₂ alone, or in combination with increased air temperature, enhanced net primary productivity at all simulated sites by 30 to 40%. In addition, the effects of elevated CO₂ and elevated air temperature were generally positive with

respect to grassland carbon stocks. Such simulations suggest the increasing CO₂ content of the air likely will stimulate primary productivity in managed grasslands, thus leading to greater biomass production and enhanced carbon storage in their associated soils. Grasslands cover nearly 20% of the land surface of the globe and store at least 10% of the soil organic matter of the planet.

Cardon *et al.* (2001) erected open-top chambers on two Mediterranean grassland communities in California, USA. They fumigated them for two years with air containing either ambient or twice-ambient atmospheric CO₂ concentrations. In addition, plants were grown with either low or high soil nutrient availability. The main thrust of this research was to use isotopic labeling to study the effects of elevated atmospheric CO₂ and soil nutrient availability on the decomposition of old and new organic carbon in the two grassland soils. Results indicated when soil nutrient availability was high, elevated CO₂ reduced the decomposition of older soil organic carbon by approximately 30% throughout the study. Thus, the turnover time and stabilization of this soil carbon pool was increased by elevated CO₂ exposure. However, the movement of newly fixed carbon into the older stabilized pools was decreased with atmospheric CO₂ enrichment, due to its preferential utilization by soil microbes. Thus, soil microbes switched from using older to newer soil organic carbon under CO₂-enriched conditions.

Thus, as the atmosphere's CO₂ content rises, carbon sequestration in the soils of Mediterranean grasslands likely will increase for two reasons. First, it should rise as a consequence of the greater retention times conferred upon the carbon in older soil organic carbon pools, which represent the largest reservoir of terrestrial carbon on Earth. Second, even though soil microbes exhibit a preference for newer carbon under CO₂-enriched conditions, it should rise because of the great increase in the amount of carbon going into newer soil carbon pools due to CO₂-enhanced root exudation, root turnover, and other types of litter production.

Higgins *et al.* (2002) constructed open-top chambers in portions of an annual grassland located in a Mediterranean-type climate in California, USA. They fumigated them with air of either 360 or 720 ppm CO₂ to study the effects of elevated CO₂ on root production and turnover. By the end of the growing season, the plants in the elevated-CO₂ chambers had increased their production of new root length by nearly 60%, but their root turnover rates were no different from those of the plants in the

ambient-treatment chambers. There was also an 18% increase in soil moisture content in the CO₂-enriched chambers. Thus, as the CO₂ content of the air increases, belowground biomass production should increase in this particular type of annual grassland, either directly from CO₂-induced increases in photosynthesis or indirectly from CO₂-induced reductions in water use, which tend to increase soil moisture content.

Hartwig *et al.* (2002) grew swards of perennial ryegrass (*Lolium perenne* L.) and the N₂-fixing white clover (*Trifolium repens* L.) in boxes placed in FACE plots receiving atmospheric CO₂ concentrations of 350 and 600 ppm in combination with low and high soil nitrogen fertilization for four years, to study the interactive effects of these variables on biomass production and nitrogen retention in these two contrasting ecosystems. They found elevated CO₂ increased average aboveground biomass in the white clover ecosystem by 80% but had no effect on aboveground biomass production in the perennial ryegrass ecosystem. Below the surface of the soil, however, just the opposite occurred: the extra CO₂ increased root biomass in the perennial ryegrass ecosystem by 94% while having no effect on the root biomass of white clover.

The total amount of nitrogen taken into the white clover ecosystem was significantly greater than that taken into the perennial ryegrass ecosystem. Elevated CO₂ exposure could explain much of this increase, as it roughly doubled the amount of nitrogen input through symbiotic N₂-fixation in the white clover. Nonetheless, all combinations of variables led to ecosystem nitrogen gains after four years of growth, with greater gains under higher, rather than lower, nitrogen fertilization. In addition, elevated CO₂ increased ecosystem nitrogen gains in all cases except in perennial ryegrass under low nitrogen fertilization.

These findings suggest as the air's CO₂ concentration increases, swards of perennial ryegrass and white clover likely will display increased rates of photosynthesis and greater biomass production. CO₂-induced increases in biomass most likely will be manifested aboveground in white clover and belowground in perennial ryegrass. In addition, both ecosystems should exhibit increased gains in nitrogen (except, perhaps, in the case of perennial ryegrass growing on low-nitrogen soils), with greater nitrogen gains occurring in white clover, as a result of CO₂-induced increases in symbiotic N₂-fixation.

Pendall *et al.* (2004) explain rhizodeposition is "the addition of C [carbon] from roots to soil C pools," and they note "because up to 80% of the

biomass and at least 50% of net primary production can occur below-ground in grasslands, changes in rhizodeposition will have a large impact on C cycling in these ecosystems (Milchunas and Lauenroth, 2001),” which may significantly impact the amount of carbon sequestered in grassland soils. Against this backdrop, Pendall *et al.* used open-top chambers to study various responses of a native C₃-C₄ grassland ecosystem in the shortgrass steppe region of northeastern Colorado, USA, to a doubling of the air’s CO₂ concentration (from 360 to 720 ppm) in an experiment that lasted five years. Total aboveground biomass was increased by an average of 33% over the course of the study in the CO₂-enriched chambers, and belowground biomass increased by an average of 23%. In addition, over the last four years of the experiment, rhizodeposition increased by 137% in the chambers exposed to elevated CO₂. However, Pendall *et al.* report “decomposition increased nearly as much as rhizodeposition,” leading to little net increase in soil C storage in the CO₂-enriched chambers relative to that found in the ambient-air chambers.

Although there was little increase in soil carbon sequestration in the CO₂-enriched chambers of this particular study, more biomass was produced in them each year, both above- and below-ground, than in the ambient-air chambers; and much more biomass made its way into the soil of the CO₂-enriched chambers. Hence it is likely that over the course of several decades the small yearly differences in soil C storage would eventually end up producing a substantially larger stash of carbon in the soil of the CO₂-enriched chambers.

Over the course of an eight-year open-top-chamber CO₂-enrichment (to twice ambient concentrations) study of a pristine (annually burned) tallgrass prairie north of Manhattan, Kansas, USA, composed of a mixture of C₃ and C₄ species, Williams *et al.* (2004) measured changes in the active, slow, and passive pools of carbon (C) and nitrogen (N), to determine how they were affected by the doubled atmospheric CO₂ concentration of their reasonably long-term experiment. They report, “on average, elevated CO₂ induced a 60% increase in root growth,” citing Owensby *et al.* (1999). They also found potentially mineralizable C was enhanced by 19% and 24%, respectively, in the 0–5 cm and 5–15 cm soil horizons, which they suggest implies “increases in plant inputs have outpaced increases in decomposition rates” in those layers. Likewise, they report potentially mineralizable N was enhanced by 14% in the 0–5 cm layer, and CO₂ enrichment resulted in greater recalcitrant N in the 5–15 cm soil

layer. Regarding these latter findings, they hypothesize “greater N translocated to aboveground biomass from deeper soil depths could ultimately be stored in roots and rhizomes near the soil surface, and would eventually turnover and become a part of the surface soil N pool.”

Williams *et al.* conclude “the 60% increase in root growth during the 8-year study was the likely catalyst for the greater potentially mineralizable soil C pools in the enriched CO₂ treatment,” and this finding “confirms that C can accrue in soils under elevated CO₂.” Specifically, they determined the total amount of extra new carbon sequestered in the soil due to their doubling of the air’s CO₂ concentration was 4 Mg C ha⁻¹ over the eight-year period, for an annual rate of extra (CO₂-induced) carbon sequestration of 0.5 Mg ha⁻¹ year⁻¹.

Working with a temperate grassland on the North Island of New Zealand under permanent grazing by sheep, cattle, and goats since at least 1940, Allard *et al.* (2005) measured above- and below-ground plant growth and litter production, along with root turnover and soil particulate organic matter quantity and quality, after almost four years of exposure to an extra ~105 ppm of atmospheric CO₂ (a target concentration of 475 ppm) in a moderate-term FACE experiment. The researchers report the elevated CO₂ did not alter aboveground herbage biomass and leaf litter production, but root growth rate and turnover “were strongly stimulated by CO₂ particularly at low soil moisture contents during summer.” As a result of the root responses, they also found “significantly more plant material was returned to the soil under elevated CO₂ leading to an accumulation of coarse (>1 mm) particulate organic matter (POM),” with a similar but not-yet-significant trend in fine POM. In addition, they state there was a CO₂-induced lowering of POM carbon/nitrogen ratio, which they “attributed to the higher proportion of legumes in the pasture under elevated CO₂.”

The six New Zealand and French researchers say their results “show that in grazed pastures with high plant species diversity we might expect extra carbon sequestration in soil organic matter mainly through an increase in carbon input rather than a decreasing quality of accumulating organic matter.” That they could detect the changes they did over so short a time interval, and with so small an increase in the atmosphere’s CO₂ concentration, is impressive, but it is just one among many similar findings of Jastrow *et al.* (2005) and the many studies the latter scientists reviewed in their meta-analysis of the subject. In addition, Allard *et al.* found indications of increased

soil nitrogen in their CO₂-enriched treatment, just as Jastrow *et al.* did, reinforcing the latter group's conclusions about this subject as well.

Edwards *et al.* (2005) grew well-watered mixtures of two plants—the legume white clover (*Trifolium repens* L.) and C₄ buffalo grass (*Stenotaphrum secundatum* (Walt.) Kuntze)—which were initially equal in plantlet size, number, and spatial distribution, for 15 months in sand placed in large plastic containers in greenhouses maintained at different atmospheric CO₂ concentrations (360 and 700 ppm) under three sand nutrient conditions (zero-N/low-P, zero-N/high-P, plus-N/high-P). They made ten harvests of all plant biomass over a height of 5 cm above the sand surface, after which the total carbon contents of the whole plants and their respective soils were determined. The slightly less than a doubling of the air's CO₂ concentration employed in this study led to increases of 22%, 41%, and 374% in the amounts of new carbon found in the soils in the zero-N/low-P, zero-N/high-P, and plus-N/high-P soil treatments, respectively. In addition, corresponding increases of 22%, 53%, and 53% in total new mesocosm carbon contents (comprised of soil plus plant carbon) were reported in each respective treatment. Thus, soil P deficiency in this study severely limited the ability of elevated CO₂ to stimulate total mesocosm carbon capture, and lack of N was most harmful to soil carbon capture. Consequently, in grasslands managed for animal production, Edwards *et al.* say “it may be possible to increase their potential to sequester C as atmospheric CO₂ increases by altering land management,” especially in ways that relieve these nutrient deficiencies, as also has been suggested by Jones and Donnelly (2004).

Pendall and King (2007) conducted a series of long-term (170–330 days) laboratory incubation experiments to examine changes in soil organic matter pool sizes and turnover rates in soil collected from an open-top chamber (OTC) atmospheric CO₂ enrichment study in the shortgrass steppe of northeastern Colorado, USA, where the air in the ambient CO₂ chambers (ACs) and elevated CO₂ chambers (ECs) had atmospheric CO₂ concentrations of 360 and 720 ppm, respectively. This degree of CO₂ enrichment enhanced both above- and below-ground plant growth by 15–35%. The authors found the “active pool carbon increased in EC relative to AC treatments systematically over the first 3 years of exposure to elevated CO₂ in topsoils and to a lesser degree in subsoils,” noting “these results are consistent with independent results from the same OTC study showing that rhizodeposition rates

doubled (Pendall *et al.*, 2004) and root production increased under elevated CO₂ (Milchunas *et al.*, 2005).” In addition, they report “new carbon turnover was not enhanced by elevated CO₂,” indicating “new carbon inputs under elevated CO₂ are not simply lost to mineralization” and “pool sizes may continue to increase under elevated CO₂.” Such findings, in the words of the two researchers, “suggest that soil carbon storage may increase in semi-arid grasslands under elevated CO₂.”

Adair *et al.* (2009) employed mass balance calculations to quantify the effects of biodiversity, atmospheric CO₂ concentration, and soil nitrogen (N) content on the total amount of C allocated belowground by plants (total belowground C allocation or TBCA), as well as ecosystem C storage, in an eight-year experiment that was part of the BioCON study of a periodically burned Minnesota grassland. The authors report annual TBCA increased in response to all three treatment variables—“elevated CO₂, enriched N, and increasing diversity”—and it was also “positively related to standing root biomass.” Upon removing the influence of root biomass, however, they state the effects of N and diversity became neutral or even negative (depending on the year), but “the effect of elevated CO₂ remained positive.” In years with fire, “greater litter production in high diversity, elevated CO₂, and enhanced N treatments increased annual ecosystem C loss.” Thus, under normal non-fire conditions, elevated CO₂, N, and biodiversity generally tend to increase ecosystem carbon gain, but if grasslands are frequently burned, they could remain neutral in this regard.

Belay-Tedla *et al.* (2009) note “the stability of carbon (C) and nitrogen (N) in soil organic matter (SOM) to perturbations such as global warming is critically important,” because “on a global scale, the soil contains 1500 Pg (1 Pg = 10¹⁵ g) of organic carbon and 300 Pg of total nitrogen” in its uppermost meter, so “relatively small changes in the amounts of soil C and N may therefore bring about substantial effects on atmospheric concentrations,” which in the case of the carbon contained in CO₂ may feed back either positively or negatively to enhance or reduce the original global warming.

In a study designed to explore these interactions in a specific biome, Belay-Tedla *et al.* “used sulfuric acid hydrolysis to quantify changes in labile and recalcitrant C and N fractions of soil in a tallgrass prairie ecosystem that had been continuously warmed with or without clipping for about 2.5 years,” conducting their work in “an old-field tallgrass prairie abandoned from agriculture 30 years ago and without

grazing during the past 20 years” in the Great Plains Apiaries of McClain County, Oklahoma, USA. Infrared heaters suspended 1.5 m above the ground warmed half the plots 24 hours a day, 365 days a year, for the 2.5-year period, increasing the daily mean air temperature at 25 cm above the ground by 1.1°C and soil temperature at 2.5 cm depth by 2.0°C.

The five researchers found “significant increases in both labile C and N (including microbial biomass) pools in response to experimental warming,” which “largely resulted from increased above- and below-ground biomass.” They also observed “a possible shift to a fungi-dominated microbial community,” noting “such a shift could favor soil C storage” as well. In addition, they report evidence suggesting “warming increased the percentage of total N for microbial biomass N,” and this enhanced N use efficiency “may be conducive for a continued supply of organic inputs.” Belay-Tedla *et al.* conclude their combined findings favor “long-term N retention and C accumulation in soils, leading to negative feedbacks of terrestrial ecosystems to climate warming.”

Ayres *et al.* (2008) investigated various responses of atmospheric CO₂ enrichment to approximately 350 ppm above ambient in experiments conducted on three grassland ecosystems in Colorado and California (USA) and Montpellier, France. The authors state “soil moisture increased in response to elevated CO₂ in the California, Colorado, and French stud[ies] (Hungate *et al.*, 1997; Nijs *et al.*, 2000; Morgan *et al.*, 2004).” As to the plants, the authors state “elevated CO₂ increased root biomass by approximately 3–32% in the first 5 years of the Coloradoan study (Pendall *et al.*, 2004), by 23% after 6 years in the Californian study (Rillig *et al.*, 1999), and by 31% after 6 months in the French study (Dhillion *et al.*, 1996).” Regarding nematodes, the researchers write, “CO₂ enrichment did not significantly affect the family richness, diversity, or PPI [plant parasitic nematode index] of herbivorous nematodes in the Colorado, California, or French study,” noting “in each experiment, neutral effects were the most frequent response to CO₂ enrichment.” Commenting on these findings, the seven researchers state “one consequence of increased root production, without changes in belowground herbivore populations, might be greater plant inputs to soil,” which “may lead to greater soil organic matter pools in grassland ecosystems, potentially enhancing soil carbon sequestration.”

The research findings discussed above suggest grasslands will become increasingly productive and

provide an ever-increasing brake on the upward trend in the air’s CO₂ concentration.

References

- Adair, E.C., Reich, P.B., Hobbie, S.E., and Knops, J.M.H. 2009. Interactive effects of time, CO₂, N, and diversity on total belowground carbon allocation and ecosystem carbon storage in a grassland community. *Ecosystems* **12**: 1037–1052.
- Allard, V., Newton, P.C.D., Lieffering, M., Soussana, J.-F., Carran, R.A., and Matthew, C. 2005. Increased quantity and quality of coarse soil organic matter fraction at elevated CO₂ in a grazed grassland are a consequence of enhanced root growth rate and turnover. *Plant and Soil* **276**: 49–60.
- Ayres, E., Wall, D.H., Simmons, B.L., Field, C.B., Milchunas, D.G., Morgan, J.A., and Roy, J. 2008. Belowground nematode herbivores are resistant to elevated atmospheric CO₂ concentrations in grassland ecosystems. *Soil Biology & Biochemistry* **40**: 978–985.
- Belay-Tedla, A., Zhou, X., Su, B., Wan, S., and Luo, Y. 2009. Labile, recalcitrant, and microbial carbon and nitrogen pools of a tallgrass prairie soil in the US Great Plains subjected to experimental warming and clipping. *Soil Biology & Biochemistry* **41**: 110–116.
- Cardon, Z.G., Hungate, B.A., Cambardella, C.A., Chapin, F.S., Field, C.B., Holland, E.A., and Mooney, H.A. 2001. *Soil Biology & Biochemistry* **33**: 365–373.
- Casella, E. and Soussana, J.-F. 1997. Long-term effects of CO₂ enrichment and temperature increase on the carbon balance of a temperate grass sward. *Journal of Experimental Botany* **48**: 1309–1321.
- Cotrufo, M.F. and Gorissen, A. 1997. Elevated CO₂ enhances below-ground C allocation in three perennial grass species at different levels of N availability. *New Phytologist* **137**: 421–431.
- David, J.-F., Malet, N., Couteaux, M.-M., and Roy, J. 2001. Feeding rates of the woodlouse *Armadillidium vulgare* on herb litters produced at two levels of atmospheric CO₂. *Oecologia* **127**: 343–349.
- Dhillion, S.D., Roy, J., and Abrams, M. 1996. Assessing the impact of elevated CO₂ on soil microbial activity in a Mediterranean model ecosystem. *Plant & Soil* **187**: 333–342.
- Dukes, J.S. and Field, C.B. 2000. Diverse mechanisms for CO₂ effects on grassland litter decomposition. *Global Change Biology* **6**: 145–154.
- Edwards, E.J., McCaffery, S., and Evans, J.R. 2005. Phosphorus status determines biomass response to elevated

- CO₂ in a legume:C₄ grass community. *Global Change Biology* **11**: 1968–1981.
- Fitter, A.H., Graves, J.D., Wolfenden, J., Self, G.K., Brown, T.K., Bogie, D., and Mansfield, T.A. 1997. Root production and turnover and carbon budgets of two contrasting grasslands under ambient and elevated atmospheric carbon dioxide concentrations. *New Phytologist* **137**: 247–255.
- Hartwig, U.A., Lüscher, A., Nosberger, J., and van Kessel, C. 2002. Nitrogen-15 budget in model ecosystems of white clover and perennial ryegrass exposed for four years at elevated atmospheric pCO₂. *Global Change Biology* **8**: 194–202.
- Higgins, P.A.T., Jackson, R.B., Des Rosiers, J.M., and Field, C.B. 2002. Root production and demography in a California annual grassland under elevated atmospheric carbon dioxide. *Global Change Biology* **8**: 841–850.
- Hirschel, G., Körner, C., and Arnone III, J.A. 1997. Will rising atmospheric CO₂ affect leaf litter quality and in situ decomposition rates in native plant communities? *Oecologia* **110**: 387–392.
- Hu, S., Chapin III, F.S., Firestone, M.K., Field, C.B., and Chiariello, N.R. 2001. Nitrogen limitation of microbial decomposition in a grassland under elevated CO₂. *Nature* **409**: 188–191.
- Hungate, B.A., Holland, E.A., Jackson, R.B., Chapin, F.S., Mooney, H.A., and Field, C.B. 1997. The fate of carbon in grasslands under carbon dioxide enrichment. *Nature* **388**: 576–579.
- Jastrow, J.D., Miller, R.M., Matamala, R., Norby, R.J., Boutton, T.W., Rice, C.W., and Owensby, C.E. 2005. Elevated atmospheric carbon dioxide increases soil carbon. *Global Change Biology* **11**: 2057–2064.
- Jones, M.B. and Donnelly, A. 2004. Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO₂. *New Phytologist* **164**: 423–439.
- Lutze, J.L. and Gifford, R.M. 1998. Carbon accumulation, distribution and water use of *Danthonia richardsonii* swards in response to CO₂ and nitrogen supply over four years of growth. *Global Change Biology* **4**: 851–861.
- Milchunas, D. and Lauenroth, W. 2001. Belowground primary production by carbon isotope decay and long-term root biomass dynamics. *Ecosystems* **4**: 139–150.
- Milchunas, D.G., Mosier, A.R., Morgan, J.A., LeCain, D.R., King, J.Y., and Nelson, J.A. 2005. Root production and tissue quality in a shortgrass steppe exposed to elevated CO₂: using a new ingrowth method. *Plant and Soil* **268**: 111–122.
- Morgan, J.A., Mosier, A.R., Milchunas, D.G., LeCain, D.R., Nelson, J.A., and Parton, W.J. 2004. CO₂ enhances productivity, alters species composition, and reduces digestibility of shortgrass steppe vegetation. *Ecological Applications* **14**: 208–219.
- Nijs, I., Roy, J., Salager, J.-L., and Fabreguettes, J. 2000. Elevated CO₂ alters carbon fluxes in early successional Mediterranean ecosystems. *Global Change Biology* **6**: 981–994.
- Nitschelm, J.J., Lüscher, A., Hartwig, U.A., and van Kessel, C. 1997. Using stable isotopes to determine soil carbon input differences under ambient and elevated atmospheric CO₂ conditions. *Global Change Biology* **3**: 411–416.
- Owensby, C.E., Ham, J.M., Knapp, A.K., and Auen, L.M. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO₂. *Global Change Biology* **5**: 497–506.
- Pendall, E. and King, J.Y. 2007. Soil organic matter dynamics in grassland soils under elevated CO₂: Insights from long-term incubations and stable isotopes. *Soil Biology & Biochemistry* **39**: 2628–2639.
- Pendall, E., Mosier, A.R., and Morgan, J.A. 2004. Rhizodeposition stimulated by elevated CO₂ in a semiarid grassland. *New Phytologist* **162**: 447–458.
- Riedo, M., Gyalistras, D., and Fuhrer, J. 2000. Net primary production and carbon stocks in differently managed grasslands: simulation of site-specific sensitivity to an increase in atmospheric CO₂ and to climate change. *Ecological Modelling* **134**: 207–227.
- Rillig, M.C., Allen, M.F., Klironomos, J.N., and Field, C.B. 1998. Arbuscular mycorrhizal percent root infection and infection intensity of *Bromus hordeaceus* grown in elevated atmospheric CO₂. *Mycologia* **90**: 199–205.
- Rillig, M.C., Field, C.B., and Allen, M.F. 1999. Soil biota responses to long-term atmospheric CO₂ enrichment in two California annual grasslands. *Oecologia* **119**: 572–577.
- Rillig, M.C., Hernandez, G.Y., and Newton, P.C.D. 2000. Arbuscular mycorrhizae respond to elevated atmospheric CO₂ after long-term exposure: evidence from a CO₂ spring in New Zealand supports the resource balance model. *Ecology Letters* **3**: 475–478.
- Van Ginkel, J.H. and Gorissen, A. 1998. In situ decomposition of grass roots as affected by elevated atmospheric carbon dioxide. *Soil Science Society of America Journal* **62**: 951–958.
- Van Ginkel, J.H., Gorissen, A., and Polci, D. 2000. Elevated atmospheric carbon dioxide concentration: effects of increased carbon input in a *Lolium perenne* soil on microorganisms and decomposition. *Soil Biology & Biochemistry* **32**: 449–456.

Van Ginkel, J.H., Gorissen, A., and van Veen, J.A. 1996. Long-term decomposition of grass roots as affected by elevated atmospheric carbon dioxide. *Journal of Environmental Quality* **25**: 1122–1128.

Van Ginkel, J.H., Whitmore, A.P., and Gorissen, A. 1999. *Lolium perenne* grasslands may function as a sink for atmospheric carbon dioxide. *Journal of Environmental Quality* **28**: 1580–1584.

Williams, M.A., Rice, C.W., Omay, A., and Owensby, C. 2004. Carbon and nitrogen pools in a tallgrass prairie soil under elevated carbon dioxide. *Soil Science Society of America Journal* **68**: 148–153.

Williams, M.A., Rice, C.W., and Owensby, C.E. 2000. Carbon dynamics and microbial activity in tall grass prairie exposed to elevated CO₂ for 8 years. *Plant and Soil* **227**: 127–137.

1.2.3 Peatlands

- In contrast to IPCC projections, the thawing of permafrost caused by increases in air temperature and CO₂ will not likely transform peatlands from carbon-sink to carbon-source ecosystems. Instead, as permafrost thaws, plants and trees can begin to grow again on these lands and in so doing, they sequester carbon.

Peatlands contain a vast amount of sequestered carbon—about as much, in fact, as is contained in the entire atmosphere. As a result, they are vital elements of the planet’s carbon cycle and can significantly impact its climate. This section reviews the findings of several papers that bear upon this topic.

IPCC predicts global warming will release long-sequestered carbon in Earth’s peatlands to the atmosphere, possibly freeing enough of it at a sufficiently rapid rate to rival CO₂ emissions from anthropogenic sources. The end result of this scenario would be a strong positive feedback to the ongoing rise in the air’s CO₂ content, which IPCC contends will lead to further warming of the planet. However, multiple studies have shown this scenario to be highly unlikely or altogether false.

One of the first cracks in this positive-feedback hypothesis was revealed by Oechel *et al.* (2000). They showed long-term measurements of net ecosystem CO₂ exchange rates in wet-sedge and moist-tussock tundra communities of the Alaskan Arctic indicated these ecosystems were changing gradually from carbon sources to carbon sinks. The transition occurred between 1992 and 1996, at the

apex of a regional warming trend that culminated with the highest summer temperature and surface water deficit of the previous four decades.

The scientists who documented this dramatic and unexpected biological transformation describe it as “a previously undemonstrated capacity for ecosystems to metabolically adjust to long-term changes in climate.” This ecological acclimation process is only one of several recognized phenomena that have caused scientists to radically revise their thinking about global change in Arctic regions.

Camill *et al.* (2001) investigated changes in peat accumulation across a regional gradient of mean annual temperature in Manitoba, Canada; net above-ground primary production and decomposition for major functional plant groups of the region; and soil cores from several frozen and thawed bog sites used to determine long-term changes in organic matter accumulation following the thawing of boreal peatlands. In direct contradiction of earlier thinking on the subject, but in confirmation of the more recent findings of Camill (1999a,b), the researchers report aboveground biomass and decomposition “were more strongly controlled by local succession than regional climate.” In other words, over a period of several years, natural changes in plant community composition generally “have stronger effects on carbon sequestration than do simple increases in temperature and aridity.” Their core-derived assessments of peat accumulation over the past two centuries demonstrated rates of biological carbon sequestration can almost double following the thawing of permafrost, in harmony with the findings of Robinson and Moore (2000) and Turetsky *et al.* (2000), who found rates of organic matter accumulation in other recently thawed peatlands to have risen by 60–72 percent.

Griffis and Rouse (2001) drew on the findings of experiments conducted over the past quarter-century at a subarctic sedge fen near Churchill, Manitoba, Canada, to develop an empirical model of net ecosystem CO₂ exchange there. The fundamental finding of this endeavor was “carbon acquisition is greatest during wet and warm conditions,” as is generally predicted for the world as a whole by today’s most advanced climate models. However, regional climate change predictions are not very dependable, so the two scientists investigated the consequences of a 4°C increase in temperature accompanied by both a 30 percent increase and decrease in precipitation. “In all cases,” they observe, “the equilibrium response showed substantial increases in carbon acquisition.” One of the reasons

for this finding, Griffis and Rouse explain, is “arctic ecosystems photosynthesize below their temperature optimum over the majority of the growing season,” so increasing temperatures enhance plant growth rates considerably more than they increase plant decay rates.

In summing up their findings, Griffis and Rouse state “warm surface temperatures combined with wet soil conditions in the early growing season increase above-ground biomass and carbon acquisition throughout the summer season.” They note, “wet spring conditions can lead to greater CO₂ acquisition through much of the growing period even when drier conditions persist.” They thus conclude if climate change plays out as described by current climate models—if the world becomes warmer and wetter—“northern wetlands should therefore become larger sinks for atmospheric CO₂.”

Mauquoy *et al.* (2002) analyzed three cores obtained from a raised peat bog in the UK (Walton Moss) and a single core obtained from a similar bog in Denmark (Lille Vildmose) for macro- and micro-fossils (pollen), bulk density, loss on ignition, carbon/nitrogen ratios, and humification, which they ¹⁴C dated by accelerator mass spectrometry. Among a variety of findings, they determined “the lowest carbon accumulation values for the Walton Moss monoliths between ca. cal AD 1300 and 1800 and between ca. cal AD 1490 and 1580 for Lille Vildmose occurred during the course of Little Ice Age deteriorations.” They describe this finding as being much the same as the observation “made by Oldfield *et al.* (1997) for a Swedish ‘aapa’ mire between ca. cal AD 1400 and 1800.” They also report carbon accumulation before this, in the Medieval Warm Period, was higher, as was also the case after the Little Ice Age, as Earth transitioned to the Modern Warm Period. Consequently, whereas IPCC predicts warming will hasten the release of carbon from ancient peat bogs, real-world data demonstrate just the opposite is more likely.

In a similar study, but one that concentrated more on the role of nitrogen than of temperature, Turunen *et al.* (2004) derived recent (0–150 years) and long-term (2,000–10,000 years) apparent carbon accumulation rates for several ombrotrophic peatlands in eastern Canada with the help of ²¹⁰Pb- and ¹⁴C-dating of soil-core materials. This work revealed the average long-term apparent rate of C accumulation at 15 sites was $19 \pm 8 \text{ g C m}^{-2} \text{ yr}^{-1}$, comparable to long-term rates observed in Finnish bogs by Tolonen and Turunen (1996) and Turunen *et al.* (2002). Recent C accumulation rates at 23 sites, however, were much

higher, averaging $73 \pm 17 \text{ g C m}^{-2} \text{ yr}^{-1}$. These results, the scientists write, are “similar to results from Finland (Tolonen and Turunen, 1996; Pitkanen *et al.*, 1999) and for boreal *Sphagnum* dominated peat deposits in North America (Tolonen *et al.*, 1988; Wieder *et al.*, 1994; Turetsky *et al.*, 2000).” Noting recent rates of C accumulation are “strikingly higher” than long-term rates, Turunen *et al.* suggest increased N deposition “leads to larger rates of C and N accumulation in the bogs, as has been found in European forests (Kauppi *et al.*, 1992; Berg and Matzner, 1997), and could account for some of the missing C sink in the global C budget.”

Payette *et al.* (2004) quantified the main patterns of change in a subarctic peatland on the eastern coast of Canada’s Hudson Bay, which were caused by permafrost decay between 1957 and 2003, based on detailed surveys conducted in 1973, 1983, 1993, and 2003. They found there was continuous permafrost thawing throughout the period of observation, so “about 18 percent of the initial frozen peatland surface was melted in 1957,” and thereafter “accelerated thawing occurred with only 38 percent, 28 percent and 13 percent of the original frozen surface still remaining in 1983, 1993 and 2003, respectively.” This process, in their words, was one of “terrestrialization” via the establishment of fen/bog vegetation, which nearly always results in either no net loss of carbon or actual carbon sequestration. Thus Payette *et al.* conclude, “contrary to current expectations, the melting of permafrost caused by recent climate change does not transform the peatland to a carbon-source ecosystem.” Instead, they write, “rapid terrestrialization exacerbates carbon-sink conditions and tends to balance the local carbon budget.”

In a study of experimental warming of Icelandic plant communities designed to see whether the warming of high-latitude tundra ecosystems would result in significant losses of species and reduced biodiversity, Jonsdottir *et al.* (2005) conducted a field experiment to learn how vegetation might respond to moderate warming at the low end of what is predicted by most climate models for a doubling of the air’s CO₂ content. They studied the effects of three to five years of modest surface warming (1°–2°C) on two widespread but contrasting tundra plant communities; one was a nutrient-deficient and species-poor moss heath, the other a species-rich dwarf shrub heath. At the end of the study, no changes in community structure were detected in the moss heath. In the dwarf shrub heath, the number of deciduous and evergreen dwarf shrubs increased more than 50%,

bryophytes decreased by 18%, and canopy height increased by 100%, but the researchers report they “detected no changes in species richness or other diversity measures in either community and the abundance of lichens did not change.” Although Jonsdottir *et al.*’s study was a relatively short-term experiment as far as ecosystem studies go, its results indicate a rise in temperature need not diminish the species diversity of high-latitude tundra ecosystems and may have a positive influence on plant growth.

In a study with an entirely new element of complexity, Cole *et al.* (2002) constructed 48 small microcosms from soil and litter they collected near the summit of Great Dun Fell, Cumbria, England. Subsequent to “defaunating” this material by reducing its temperature to -80°C for 24 hours, they thawed and inoculated it with native soil microbes. Half of the microcosms were incubated in the dark at 12°C and half at 18°C for two weeks, to establish near-identical communities of the soils’ natural complement of microflora in each microcosm. The first temperature was chosen to represent mean August soil temperature at a depth of 10 cm at the site of soil collection, and the latter was picked to be “close to model predictions for soil warming that might result from a doubling of CO_2 in blanket peat environments.”

Next, ten seedlings of *Festuca ovina*, an indigenous grass of blanket peat, were planted in each of the microcosms, and 100 enchytraeid worms were added to each of half of the mini-ecosystems, producing four experimental treatments: ambient temperature, ambient temperature plus enchytraeid worms, elevated temperature, and elevated temperature plus enchytraeid worms. Then, the 48 microcosms—sufficient to destructively harvest three replicates of each treatment four times throughout the course of the 64-day experiment—were arranged in a fully randomized design and maintained at either 12° or 18°C with alternating 12-hour light and dark periods, given distilled water every two days to maintain their original weights.

The researchers report finding elevated temperature reduced the ability of the enchytraeid worms to enhance the loss of carbon from the microcosms. At the normal ambient temperature, the presence of the worms enhanced dissolved organic carbon (DOC) loss by 16 percent, while at the elevated temperature expected for a doubling of the air’s CO_2 content they had no effect on DOC. In addition, Cole *et al.* note, “warming may cause drying at the soil surface, forcing enchytraeids to burrow to deeper subsurface horizons,” and since the worms are

known to have little influence on soil carbon dynamics below a depth of about 4 cm (Cole *et al.*, 2000), the researchers conclude this additional consequence of warming will further reduce the ability of enchytraeids to enhance carbon loss from blanket peatlands. In summing up their findings, Cole *et al.* conclude “the soil biotic response to warming in this study was negative,” because it resulted in a reduced loss of carbon to the atmosphere.

As to the effects of elevated CO_2 itself on the loss of DOC from soils, Freeman *et al.* (2004) note riverine transport of DOC has increased markedly in many places throughout the world over the past few decades (Schindler *et al.*, 1997; Freeman *et al.*, 2001; Worrall *et al.*, 2003), and they suggest this phenomenon may be related to the historical increase in the air’s CO_2 content.

The researchers’ first piece of evidence for this conclusion came from a three-year study of monoliths (11cm diameter x 20cm deep cores) taken from three Welsh peatlands—a bog that received nutrients solely from rainfall, a fen that gained more nutrients from surrounding soils and groundwater, and a riparian peatland that gained even more nutrients from nutrient-laden water transported from other terrestrial ecosystems via drainage streams—which they exposed to either ambient air or air enriched with an extra 235 ppm of CO_2 in a solardome facility. This study revealed the DOC released by monoliths from the three peatlands was significantly enhanced—by 14% in the bog, 49% in the fen, and 61% in the riparian peatland—by the additional CO_2 to which they were exposed. That is the order of response expected from what is known about the stimulation of net primary productivity due to atmospheric CO_2 enrichment—it is low in the face of low soil nutrients, intermediate when soil nutrient concentrations are intermediate, and high when soil nutrients are present in abundance. Consequently, Freeman *et al.* conclude the DOC increases they observed “were induced by increased primary production and DOC exudation from plants.”

To further test their hypothesis, they followed the translocation of labeled ^{13}C through the plant-soil systems of the different peat monoliths for about two weeks after exposing them to ~99 percent-pure $^{13}\text{CO}_2$ for five hours. This exercise revealed the plants in the ambient-air and CO_2 -enriched treatments assimilated 22.9 and 35.8 mg of ^{13}C from the air, respectively; the amount of DOC recovered from the leachate of the CO_2 -enriched monoliths was 0.6% of that assimilated, or 0.215 mg ($35.8 \text{ mg} \times 0.006 = 0.215 \text{ mg}$); and the proportion of DOC in the soil solution of the CO_2 -

enriched monoliths derived from recently assimilated CO₂ (the ¹³C labeled CO₂) was 10 times higher than the control.

This latter observation suggests the amount of DOC recovered from the leachate of the ambient-air monoliths was only about a tenth as much as that recovered from the leachate of the CO₂-enriched monoliths, which puts the former amount at about 0.022 mg. Hence, what really counts—the net sequestration of ¹³C experienced by the peat monoliths over the two-week period (which equals the amount that went into them minus the amount that went out), comes to 22.9 mg minus 0.022 mg = 22.878 mg for the ambient-air monoliths and 35.8 mg minus 0.215 mg = 35.585 mg for the CO₂-enriched monoliths. In the end, therefore, even though the CO₂-enriched monoliths lost 10 times more ¹³C via root exudation than did the ambient-air monoliths, they still sequestered about 55% more ¹³C overall, primarily in living-plant tissues.

Cai and Yu (2011) employed multiproxy data derived from a sediment core they extracted from Tannersville Bog near the edge of the Pocono Mountains in Monroe County, Pennsylvania (USA) to document the bog's historical peat accumulation pattern and rate, as well as climate variations experienced by this “temperate tree-covered poor fen” located at “the extreme warm end of climate space for northern peatlands.”

The two authors report, “carbon accumulation rates increased from 13.4 to 101.2 g C/m²/year during the last 8,000 years,” with a long-term average value of 27.3 g C/m²/year. This mean rate significantly exceeds the 18.6 g C/m²/year obtained for boreal, subarctic, and arctic peatlands based on measurements made at 33 sites in the Northern Hemisphere (Yu *et al.*, 2009). This fact led the authors to conclude their relatively high accumulation rate “was likely caused by high primary production associated with a warmer and wetter temperate climate.” Cai and Yu say their study implies “northern peatlands can continue to serve as carbon sinks under a warmer and wetter climate, providing a negative feedback to climate warming.”

Beilman *et al.* (2009) undertook further illumination of the relationship between climate and carbon accumulation in peatlands. They used “a network of cores from 77 peatland sites to determine controls on peat carbon content and peat carbon accumulation over the last 2000 years across Russia's West Siberian Lowland,” the world's largest wetland region. They found carbon accumulation over the past two millennia varied significantly with mean annual

air temperature, growing ever-greater as air temperature rose from -9 to 0°C, with maximum carbon accumulation occurring between -1 and 0°C, which is “where air-soil temperature differences optimize net primary production relative to soil respiration, e.g., near 0°C (Swanson *et al.*, 2000).” On average, the researchers report “cores from non-permafrost sites have accumulated four times more peat by depth and twice as much carbon than cores from permafrost sites.”

In light of these findings, Beilman *et al.* write, the “relationship between temperature and peat carbon sequestration, and the current spatial distribution of peatland ecosystems, should be an important consideration in future attempts to anticipate the impact of climate warming on the carbon sink potential of the West Siberian Lowland region.” With respect to that impact, they opine, “permafrost thaw may promote a boost in peat carbon sequestration in affected sites,” and, therefore, “future warming could result in a shift northward in long-term West Siberian Lowland carbon sequestration.”

Bao *et al.* (2010) also counter the claim peatland ecosystems will release great quantities of previously sequestered carbon to the atmosphere in the form of CO₂ and methane as temperatures warm. Working in the Changbai mountain region that runs along the boundary between China and North Korea, this group of researchers extracted eight peat cores, which they analyzed for numerous parameters, including those required to calculate the recent rate of carbon accumulation (RERCA) in the peatlands of that region over the past two centuries.

The four researchers report “obvious increasing trends in RERCA were observed in all peat cores,” as “organic carbon content declined from the top to the substrate.” In addition, they state the temporal increase in RERCA in the upper regions of the cores—which likely corresponded to the warmest segment of their two-century study period—“changed to a much greater extent in recent decades than in the earlier period of peat formation.”

Flanagan and Syed (2011) write, “northern peatland ecosystems are consistent net carbon (C) sinks that account for between one-quarter to one-third of the global soil carbon pool (Gorham, 1991; Turunen *et al.*, 2002),” noting their sequestration of carbon “results from moderate rates of ecosystem photosynthesis that exceed decomposition and autotrophic plant respiration (Gorham, 1991).” The scientists set out to conduct a long-term experiment to explore IPCC's contention that “exposure to warmer temperatures and drier conditions associated with

climate change will shift the balance between ecosystem photosynthesis and respiration providing a positive feedback to atmospheric CO₂ concentration.” They used the eddy covariance technique “to determine the sensitivity of ecosystem photosynthesis, respiration and net CO₂ exchange to variations in temperature and water table depth associated with inter-annual shifts in weather over a six-year period.”

Their work was conducted in “a moderately rich treed fen”—which they described as “the most abundant peatland type in western Canada”—at a peatland flux station northeast of Athabasca, Alberta, which was established in 2003 as part of the Fluxnet-Canada Research Network (Margolis *et al.*, 2006), and which during 2007–2009 was part of the follow-on Canadian Carbon Program. The researchers report, “contrary to previous predictions, both ecosystem photosynthesis and respiration showed similar increases in response to warmer and drier conditions,” such that “the ecosystem remained a strong net sink for CO₂ with an average net ecosystem production of 189 ± 47 gC/m²/year.” These “current net CO₂ uptake rates were much higher than carbon accumulation in peat determined from analyses of the relationship between peat age and cumulative carbon stock.” Flanagan and Syed conclude, “in the absence of fire or other major disturbance, significant net carbon sequestration could continue for decades at this site and help to reduce the positive feedback of climate change on increasing atmospheric CO₂ concentration.”

Also working in Canada, Turetsky *et al.* (2007) explored “the influence of differing permafrost regimes (bogs with no surface permafrost, localized permafrost features with surface permafrost, and internal lawns representing areas of permafrost degradation) on rates of peat accumulation at the southernmost limit of permafrost in continental Canada.” The five American researchers say the work revealed “surface permafrost inhibits peat accumulation and that degradation of surface permafrost stimulates net carbon storage in peatlands.” In fact, they report, “unfrozen bogs and internal lawns had net organic matter accumulation rates two-times faster than rates of accumulation in localized permafrost features over the most recent 25-year horizon.”

Turetsky *et al.* say their data suggest “permafrost degradation within peatland environments, likely triggered by climate change, could serve as a negative feedback to net radiative forcing via enhanced carbon accumulation as peat.” They note, however, “increased methane emissions to the atmosphere will

partially or even completely offset this enhanced peatland carbon sink for at least 70 years following permafrost degradation.” Nevertheless, they write, because “internal lawns succeed relatively quickly (within 70 years) to more bog-like conditions and [since] bogs in continental Canada are associated with low methane emissions, the degradation of localized permafrost in peatlands is likely over the long-term to serve as a negative feedback to radiative forcing.”

Daimaru *et al.* (2002) dug 27 soil pits at various locations in and around the central location of a snowpatch grassland on the southeastern slope of Japan’s Mt. Zarumori (~39.8°N, 140.8°E), examining the peat content of the soil and determining its age based on ¹⁴C dating and tephrochronology. They report “peaty topsoils were recognized at seven soil pits in the dense grassland” where the snow melts earlier in the season and the period for plant growth is the longest. In contrast, soils located in areas where the snowmelt occurs later in the season “lacked peaty topsoil.” Beneath these carbon-poor topsoils, Daimaru *et al.* found a carbon-rich layer they were able to date back to the Medieval Warm Period, suggesting the buried peat layers in the poor vegetation area accumulated in consequence of the warmer temperatures of that period. Consequently, as has been found in each of the other peatland studies referenced above, real-world observations show IPCC-based predictions—in terms of the influence of Earth’s peatlands on the planet’s temperature—do not match observational data. In stark contrast, these land types provide a negative feedback to global warming: When peatlands warm, they extract more, not less, CO₂ from the atmosphere, effectively applying a brake on rising temperatures, as opposed to pushing the planet past a tipping point toward a state of catastrophic runaway global warming.

At least one model-based study has reached the same conclusion. Noting “throughout the Holocene, northern peatlands have both accumulated carbon and emitted methane,” so “their impact on climate radiative forcing has been the net of cooling (persistent CO₂ uptake) and warming (persistent CH₄ emission),” Frolking and Roulet (2007) developed Holocene peatland carbon flux trajectories based on estimates of contemporary CH₄ flux, total accumulated peat C, and peatland initiation dates, which they used as inputs to a simple atmospheric perturbation model to calculate the net radiative impetus for surface air temperature change. The two researchers determined the impact on the current atmosphere of northern peatland development and carbon cycling through the Holocene is a net deficit

of 40–80 Pg CO₂-C (~20–40 ppm of atmospheric CO₂) and a net excess of ~200–400 Tg CH₄ (~75–150 ppb of atmospheric CH₄).

Frolking and Roulet note early in the Holocene the capture of CO₂ and emission of CH₄ by Earth's northern peatlands is likely to have produced a net warming impetus of up to +0.1 W m⁻². Over the following 8,000 to 11,000 years, however, they say Earth's peatlands have been doing just the opposite, and the current radiative forcing due to these atmospheric CO₂ and CH₄ perturbations represents a net cooling force on the order of -0.22 to -0.56 W m⁻², further establishing that the impetus for global cooling due to carbon sequestration by Earth's peatlands historically has been—and currently is—significantly greater than the global warming potential produced by their emissions of methane.

Finally, in an experimental as opposed to historical study, Fenner *et al.* (2007) collected intact peat monoliths—comprised predominantly of *Sphagnum* (*S. subnitens* Russ. and Warnst.) and *Festuca ovina* L., with small amounts of *Juncus effusus* L. and *Polytrichum commune* Hedw.—in perfusion systems that allowed for fine control of the water table and lateral water movements, which they maintained for approximately three years in solardomes with atmospheric CO₂ concentrations of ambient or ambient plus 235 ppm, while daily supplying the mini-ecosystems with synthetic rainwater comparable in volume and nutrient content to that received at the site from which the monoliths were extracted.

At the end of their three-year experiment, the seven UK researchers write, “species composition showed a shift from a *Sphagnum*-dominated community to one in which vascular monocotyledonous species dominated,” as *S. subnitens* cover declined by 39% under elevated CO₂, whereas *J. effusus* cover increased from less than 1% in the control perfusion systems to 40% in the systems exposed to elevated CO₂. Also, “aboveground plant biomass showed a substantial increase under elevated CO₂ (115%, *P* < 0.01) as did belowground biomass (96%, *P* < 0.01).” In addition, they report “*J. effusus* roots were observed to be particularly thick, deep, and extensive under elevated CO₂.”

The research summarized above suggests as the air's CO₂ content rises, the carbon content of the planet's peatlands most likely also will continue to rise, and dramatically so, notwithstanding model-based projections to the contrary.

References

- Bao, K., Yu, X., Jia, L., and Wang, G. 2010. Recent carbon accumulation in Changbai Mountain peatlands, northeast China. *Mountain Research and Development* 30: 33–41.
- Beilman, D.W., MacDonald, G.M., Smith, L.C., and Reimer, P.J. 2009. Carbon accumulation in peatlands of West Siberia over the last 2000 years. *Global Biogeochemical Cycles* 23: 10.1029/2007GB003112.
- Berg, B. and Matzner, E. 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. *Environmental Reviews* 5: 1–25.
- Cai, S. and Yu, Z. 2011. Response of a warm temperate peatland to Holocene climate change in northeastern Pennsylvania. *Quaternary Research* 75: 531–540.
- Camill, P. 1999a. Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. *Canadian Journal of Botany* 77: 721–733.
- Camill, P. 1999b. Peat accumulation and succession following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Ecoscience* 6: 592–602.
- Camill, P., Lynch, J.A., Clark, J.S., Adams, J.B., and Jordan, B. 2001. Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Ecosystems* 4: 461–478.
- Cole, L., Bardgett, R.D., and Ineson, P. 2000. Enchytraeid worms (Oligochaeta) enhance mineralization of carbon in organic upland soils. *European Journal of Soil Science* 51: 185–192.
- Cole, L., Bardgett, R.D., Ineson, P., and Hobbs, P.J. 2002. Enchytraeid worm (Oligochaeta) influences on microbial community structure, nutrient dynamics and plant growth in blanket peat subjected to warming. *Soil Biology & Biochemistry* 34: 83–92.
- Daimaru, H., Ohtani, Y., Ikeda, S., Okamoto, T., and Kajimoto, T. 2002. Paleoclimatic implication of buried peat layers in a subalpine snowpatch grassland on Mt. Zarumori, northern Japan. *Catena* 48: 53–65.
- Fenner, N., Ostle, N.J., McNamara, N., Sparks, T., Harmens, H., Reynolds, B., and Freeman, C. 2007. Elevated CO₂ effects on peatland plant community carbon dynamics and DOC production. *Ecosystems* 10: 635–647.
- Flanagan, L.B. and Syed, K.H. 2011. Stimulation of both photosynthesis and respiration in response to warmer and drier conditions in a boreal peatland ecosystem. *Global Change Biology* 17: 2271–2287.
- Freeman, C., Evans, C.D., Monteith, D.T., Reynolds, B., and Fenner, N. 2002. Export of organic carbon from peat soils. *Nature* 412: 785.

Climate Change Reconsidered II: Biological Impacts

- Freeman, C., Fenner, N., Ostle, N.J., Kang, H., Dowrick, D.J., Reynolds, B., Lock, M.A., Sleep, D., Hughes, S., and Hudson, J. 2004. Export of dissolved organic carbon from peatlands under elevated carbon dioxide levels. *Nature* **430**: 195–198.
- Frolking, S. and Roulet, N.T. 2007. Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. *Global Change Biology* **13**: 1079–1088.
- Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* **1**: 185–192.
- Griffis, T.J. and Rouse, W.R. 2001. Modelling the interannual variability of net ecosystem CO₂ exchange at a subarctic sedge fen. *Global Change Biology* **7**: 511–530.
- Jonsdottir, I.S., Magnusson, B., Gudmundsson, J., Elmarsdottir, A., and Hjartarson, H. 2005. Variable sensitivity of plant communities in Iceland to experimental warming. *Global Change Biology* **11**: 553–563.
- Kauppi, P.E., Mielikainen, K., and Kuusela, K. 1992. Biomass and carbon budget of European forests. *Science* **256**: 70–74.
- Margolis, H.A., Flanagan, L.B., and Amiro, B.D. 2006. The Fluxnet-Canada research network: influence of climate and disturbance on carbon cycling in forests and peatlands. *Agricultural and Forest Meteorology* **140**: 1–5.
- Mauquoy, D., Engelkes, T., Groot, M.H.M., Markesteijn, F., Oudejans, M.G., van der Plicht, J., and van Geel, B. 2002. High-resolution records of late-Holocene climate change and carbon accumulation in two north-west European ombrotrophic peat bogs. *Palaeogeography, Palaeoclimatology, Palaeoecology* **186**: 275–310.
- Oechel, W.C., Vourlitis, G.L., Hastings, S.J., Zulueta, R.C., Hinzman, L., and Kane, D. 2000. Acclimation of ecosystem CO₂ exchange in the Alaskan Arctic in response to decadal climate warming. *Nature* **406**: 978–981.
- Payette, S., Delwaide, A., Caccianiga, M., and Beauchemin, M. 2004. Accelerated thawing of subarctic peatland permafrost over the last 50 years. *Geophysical Research Letters* **31**: 10.1029/2004GL020358.
- Pitkanen, A., Turunen, J., and Tolonen, K. 1999. The role of fire in the carbon dynamics of a mire, Eastern Finland. *The Holocene* **9**: 453–462.
- Robinson, S.D. and Moore, T.R. 2000. The influence of permafrost and fire upon carbon accumulation in high boreal peatlands, Northwest Territories, Canada. *Arctic, Antarctic and Alpine Research* **32**: 155–166.
- Schindler, D.W., Curtis, P.J., Bayley, S.E., Parker, B.R., Beaty, K.G., and Stainton, M.P. 1997. Climate-induced changes in the dissolved organic carbon budgets of boreal lakes. *Biogeochemistry* **36**: 9–28.
- Swanson, D.K., Lacelle, B., and Tarnocai, C. 2000. Temperature and the boreal-subarctic maximum in soil organic carbon. *Geog. Phys. Quat.* **54**: 157–167.
- Tolonen, K., Davis, R.B., and Widoff, L. 1988. Peat accumulation rates in selected Maine peat deposits. *Maine Geological Survey, Department of Conservation Bulletin* **33**: 1–99.
- Tolonen, K. and Turunen, J. 1996. Accumulation rates of carbon in mires in Finland and implications for climate change. *The Holocene* **6**: 171–178.
- Turetsky, M.R., Wieder, R.K., Vitt, D.H., Evans, R.J., and Scott, K.D. 2007. The disappearance of relict permafrost in boreal North America: Effects on peatland carbon storage and fluxes. *Global Change Biology* **13**: 1922–1934.
- Turetsky, M.R., Wieder, R.K., Williams, C.J., and Vitt, D.H. 2000. Organic matter accumulation, peat chemistry, and permafrost melting in peatlands of boreal Alberta. *Ecoscience* **7**: 379–392.
- Turunen, J., Roulet, N.T., Moore, T.R., and Richard, P.J.H. 2004. Nitrogen deposition and increased carbon accumulation in ombrotrophic peatlands in eastern Canada. *Global Biogeochemical Cycles* **18**: 10.1029/2003GB002154.
- Turunen, J., Tomppo, E., Tolonen, K., and Reinikainen, A. 2002. Estimating carbon accumulation rates of undrained mires in Finland: Application to boreal and subarctic regions. *The Holocene* **12**: 69–80.
- Wieder, R.K., Novak, M., Schell, W.R., and Rhodes, T. 1994. Rates of peat accumulation over the past 200 years in five Sphagnum-dominated peatlands in the United States. *Journal of Paleolimnology* **12**: 35–47.
- Worrall, F., Burt, T., and Shedden, R. 2003. Long term records of riverine dissolved organic matter. *Biogeochemistry* **64**: 165–178.
- Yu, Z.C., Beilman, D.W., and Jones, M.C. 2009. Sensitivity of northern peatland carbon dynamics to Holocene climate change. In: Baird, A.J., Belyea, L.R., Comax, X., Reeve, A., and Slater, I. (Eds.) *Carbon Cycling in Northern Peatlands*. American Geophysical Union, Washington, DC, USA, pp. 55–69.

1.2.4 Wetlands

- Rising atmospheric CO₂ likely will enhance the productivity and carbon sequestering ability of wetlands. In addition, elevated CO₂ may assist some coastal wetlands in counterbalancing the negative impacts of rising seas.

The early works of Jacob *et al.* (1995) and Drake *et*

al. (1996a) were among the first to demonstrate atmospheric CO₂ enrichment enhances vegetative productivity in wetland ecosystems. Drake *et al.* (1996b) also showed elevated levels of atmospheric CO₂ reduce insect and fungal damage to wetland plants (Drake *et al.*, 1996b). Since that time, many other studies have reinforced these initial findings and revealed still other positive wetland impacts of the ongoing rise in the air's CO₂ content.

Rasse *et al.* (2003) developed a model for calculating net ecosystem exchange (NEE) of CO₂ between C₃ wetland sedge (*Scirpus olneyi* Gray) communities and the atmosphere, based on published ecophysiological data and measurements of various photosynthetic parameters made at the Chesapeake Bay CO₂-enrichment study described by Curtis *et al.* (1989a,b). This model indicated the *S. olneyi* community responded favorably to a near-doubled atmospheric CO₂ concentration by increasing its NEE by 35–40%, which Rasse *et al.* compare to the mean net photosynthetic increase of 60% reported by Norby *et al.* (1999) in an extensive review that included several tree species and ecosystems. Rasse *et al.* write, “because *Scirpus*-dominated ecosystems are extremely productive (Drake and Leadley, 1991), a 35–40% productivity increase might represent a larger additional amount of carbon fixed as compared to a 60% increase in less productive forest ecosystems.” In addition, because there are about six million square kilometers of wetlands worldwide, with approximately 15% of that area located in temperate regions (Mitsch *et al.*, 1994), Rasse *et al.* conclude “temperate C₃ wetlands have a huge potential for increased plant productivity [and, therefore, carbon sequestration] during the 21st century.”

Dakora and Drake (2000) exposed plant communities of *Scirpus olneyi* and the C₄ grass *Spartina patens* to atmospheric CO₂ concentrations of 360 and 660 ppm in open-top chambers to study the effects of elevated CO₂ on nitrogenase activity and nitrogen fixation in these plants and in the non-symbiotic nitrogen-fixing microbes that inhabit the sediments in which the plants grow. They report the extra CO₂ increased nitrogenase activity by 35 and 13% in *S. olneyi* and *S. patens*, respectively, and these stimulations led to increases in nitrogen incorporation of 73 and 23%, respectively, in the same plants. These responses, they add, are “in rough proportion to the relative effect of elevated CO₂ on canopy photosynthesis measured throughout the day.” They also report the elevated CO₂ significantly stimulated nitrogenase activity in the non-symbiotic nitrogen-

fixing microbes living in the soil sediments, suggesting increases in the air's CO₂ content produce “an increase in the N₂-fixing activity of free-living [microbes] in the marsh ecosystem.”

Hussein *et al.* (2004) measured carbon sequestration along two transects across submerging coastal landscapes (Hell Hook and Cedar Creek) of the Chesapeake Bay in Dorchester County, Maryland, USA, and used this data to develop a model of carbon sequestration by coastal marshes. They found “coastal marsh soils are accreting vertically and migrating laterally over the [adjacent] low-lying forest soils to keep pace with sea-level rise,” and during the past 150 years, the rate of carbon sequestration by the marsh soils averaged $83.5 \pm 23 \text{ g m}^{-2} \text{ yr}^{-1}$, whereas prior to that period it had averaged $29.2 \pm 5.35 \text{ g m}^{-2} \text{ yr}^{-1}$.

These sequestration rates are much greater than those of either local forest or agricultural soils. In addition, the three scientists report, “carbon sequestration in mineral soils of agro- and upland-forest ecosystems is generally of limited capacity and tends to reach steady-state condition within relatively short time,” but “in coastal marsh soils, carbon sequestration will continue to occur with time by accumulation in the organic horizons, and with increasing storage capacity.” Based on a model they developed from their data, for example, Hussein *et al.* project sea-level rise will cause carbon sequestration by coastal marsh ecosystems over the next 100 years to average $400 \pm 162 \text{ g m}^{-2} \text{ yr}^{-1}$. Thus they conclude, “coastal marsh ecosystems tend to sequester carbon continuously with increasing storage capacity as marsh age progresses,” and “carbon sequestration in coastal marsh ecosystems under positive accretionary balance acts as a negative feedback mechanism to global warming.”

Returning to the Chesapeake Bay wetland study at the 17-year point of its progression, Rasse *et al.* (2005) evaluated the long-term effects of atmospheric CO₂ enrichment on the net CO₂ exchange, shoot density, and shoot biomass of the wetland sedge, *Scirpus olneyi*, as well as how these effects have been influenced by salinity, one of the main environmental stressors of the wetland. In every year of the past 17 years, they found the net CO₂ exchange rate and shoot biomass and density of the plants growing in the CO₂-enriched (ambient +340 ppm) air were greater than those of the plants growing in ambient air. The extra CO₂ also boosted the net CO₂ exchange rate by 80% in the first year of the study, but the enhancement declined to about 35% by the end of the third year and remained relatively constant at that value over the

following 15 years. Shoot biomass and density also increased, but whereas the CO₂-induced stimulation of the net CO₂ exchange rate remained essentially constant over the last 15 years, the CO₂-induced stimulations of shoot biomass and density increased over time. After five years of a nearly constant stimulation of 16%, for example, shoot density increased in near linear fashion to a value 128% above the ambient-air value at the end of year 17. The response of shoot biomass to CO₂ enrichment was also nearly linear, reaching a value approximately 70% above ambient at year 17. In addition, the trends in shoot density and biomass do not appear to be leveling off, leading one to wonder just how high the CO₂-induced stimulations ultimately will rise.

Salinity was closely correlated with net CO₂ exchange, shoot density, and shoot biomass, such that the higher the salinity, the more detrimental were its effects on these variables. Nevertheless, even at the highest levels of salinity reported, atmospheric CO₂ enrichment was able to produce a positive, albeit reduced, stimulatory effect on net CO₂ exchange. For shoot biomass and density, the responses were better still. Not only did atmospheric CO₂ enrichment essentially eradicate the detrimental effects of salinity, there was, in the words of Rasse *et al.*, “circumstantial evidence suggesting that salinity stress increased the stimulation of shoot density by elevated atmospheric CO₂ concentration.”

This experiment demonstrates several important things. First, as the researchers state, their results “leave no doubt as to the sustained response of the salt marsh sedge to elevated atmospheric CO₂ concentration.” Second, given that the initial responses of the three growth variables declined or remained low during the first few years of the study, but leveled out or increased thereafter, it is clear much more long-term research needs to be carried out if we are to ascertain the full and correct impacts of atmospheric CO₂ enrichment on plants. In the case of the wetland sedge of this study, for example, it took about ten growing seasons before an increasing trend in the shoot density could be recognized. Finally, there is the researchers’ “most important finding”—“that a species response to elevated atmospheric CO₂ concentration can continually increase when [it] is under stress and declining in its natural environment.”

Erickson *et al.* (2007) present data “on 18 years of measurement of above and belowground biomass, tissue N concentration and total standing crop of N for a *Scirpus olneyi*-dominated (C₃ sedge) community, a *Spartina patens*-dominated (C₄ grass) community and a C₃-C₄-mixed species community exposed to

ambient and elevated (ambient + 340 ppm) atmospheric CO₂ concentration [via open-top chamber technology] in natural salinity and sea level conditions of a Chesapeake Bay wetland.” This report shows “elevated atmospheric CO₂ enhancement of C₃ biomass was sustained through time in the *S. olneyi*-dominated community, averaging about 40% for shoots and 26% for roots, whereas elevated CO₂ had no significant overall effect on biomass production in the C₄ grass community.” In addition, the authors state, “the greatest amount of carbon was added to the *S. olneyi*-dominated community during years when shoot N concentration was reduced the most, suggesting that the availability of N was not the most or even the main limitation to elevated CO₂ stimulation of carbon accumulation in this ecosystem.” These findings, the four researchers conclude, “demonstrate that elevated CO₂ effects on biomass production can be sustained through time,” even when N availability is at the lowest of levels typically encountered in the wetland. They note similar CO₂-induced “sustained enhancement of growth has been found in a scrub oak ecosystem (Dijkstra *et al.*, 2002; Hymus *et al.*, 2002), a tallgrass prairie (Owensby *et al.*, 1999) and several forested ecosystems (Norby *et al.*, 2005), indicating that increased productivity of many ecosystems will follow global increases in atmospheric CO₂ concentration.”

Working with *Phragmites australis*—a wetland plant found in every U.S. state and numerous other places around the world—in a study with very different implications, Scholefield *et al.* (2004) measured isoprene emissions from plants growing at different distances from a natural CO₂ spring located in central Italy, where atmospheric CO₂ concentrations of approximately 350, 400, 550, and 800 ppm likely had prevailed for the entire lifetimes of the plants. They found as long-term atmospheric CO₂ concentrations rose, plant isoprene emissions dropped: Over the first 50 ppm increase in the air’s CO₂ concentration, they were reduced to approximately 65% of what they were at ambient CO₂, and for CO₂ increases of 200 and 450 ppm, they were respectively reduced to only about 30% and 7% of what they were in ambient-CO₂ air, as best we can determine from the bar graph of the authors’ data.

These CO₂-induced reductions in plant isoprene emissions are significant because isoprene, a highly reactive non-methane hydrocarbon (NMHC) emitted by vegetation in copious quantities at current atmospheric CO₂ concentrations, is responsible for the production of vast amounts of plant- and animal-harming ozone (Chameides *et al.*, 1988; Harley *et al.*,

1999). Poisson *et al.* (2000), for example, calculated current concentrations of NMHC emissions (the vast majority of which are isoprene) increase surface ozone concentrations by 50–60% over land and by as much as 40% over the world's oceans. In addition, biogenic NMHCs (with isoprene being the most important) play a major role in the global tropospheric chemistry of methane, one of the atmosphere's most powerful greenhouse gases, boosting methane's atmospheric lifetime by approximately 14% above what it would be without isoprene (Poisson *et al.*, 2000). This being the case, if other plants behave similarly—and much evidence suggests they do (Monson and Fall, 1989; Loreto and Sharkey, 1990; Sharkey *et al.*, 1991; Loreto *et al.*, 2001; Rosenstiel *et al.*, 2003)—the ongoing rise in the air's CO₂ content can be expected to enhance plant productivity, mitigate the deleterious consequences of one of Earth's worst air pollutants (ozone), and reduce the atmospheric lifetime of one of the planet's most powerful greenhouse gases (methane).

As background for their work, Langley *et al.* (2009) note “tidal wetlands experiencing increased rates of sea-level rise (SLR) must increase rates of soil elevation gain to avoid permanent conversion to open water.” As for how that might happen, they note “root zone expansion by accumulation of plant material is essential to maintaining a constant surface elevation relative to rising sea level.” Against this backdrop, in Kirkpatrick Marsh—a microtidal sub-estuary of Chesapeake Bay, where each of several 200-m² plots was outfitted with a surface elevation table (SET) to measure soil elevation change—Langley *et al.* exposed half of the plots to an extra 340 ppm of CO₂ for two years. Data “from a greenhouse mesocosm experiment (Cherry *et al.*, 2009) were used to examine how elevated CO₂ might affect elevation response under simulated SLR scenarios.”

The five researchers report the extra CO₂ of their marsh experiment increased fine root productivity by an average of 36% over the two-year study, and aboveground biomass production was increased by as much as 30%, “consistent with a 20-year record of elevated CO₂ treatment in a previous CO₂ study on the same marsh (Erickson *et al.*, 2007).” In addition, they say the elevated CO₂ caused an increase in root zone thickness of 4.9 mm/year compared with only 0.7 mm/year in the ambient CO₂ treatment, so there was “a slight loss of elevation in ambient CO₂ (–0.9 mm/year) compared with an elevation gain (3.0 mm/year) in the elevated CO₂ treatment.” Furthermore, they report the greenhouse mesocosm

experiment of Cherry *et al.* (2009) “revealed that the CO₂ effect was enhanced under salinity and flooding conditions likely to accompany future SLR.”

Langley *et al.* conclude, “by stimulating biogenic contributions to marsh elevation, increases in the greenhouse gas, CO₂, may paradoxically aid some coastal wetlands in counterbalancing rising seas.” They say their findings “bear particular importance given the threat of accelerating SLR to coastal wetlands worldwide,” citing the recent EPA report of Reed *et al.* (2008) which suggests “a 2-mm increase in the rate of SLR will threaten or eliminate a large portion of mid-Atlantic marshes.” Once again, however, the proven and positive growth-promoting effect of atmospheric CO₂ enrichment more than compensates for its hypothetical and negative global-warming effect.

Kirwan *et al.* (2009) write, “when subjected to future [projected] rates of sea level rise, numerical models and statistical projections predict that marshland worldwide will decline on the order of 10–50% during the next 50–100 years,” and “such a decline could represent a catastrophic loss of ecosystem services by one of Earth's most valuable coastal environments.” To explore this subject further, Kirwan *et al.* “compiled 56 measurements of aboveground annual productivity for *Spartina alterniflora*, the dominant macrophyte in North American coastal wetlands,” along the Gulf Coast and Eastern Seaboard of the United States, as well as the east coast of Canada.

The researchers report, “despite local and temporal variability, a significant ($r = 0.83$; $P < 0.000001$) latitudinal gradient of 25 g m²/year per degree of latitude exists across the entire geographic range of the compilation.” In addition, “the latitudinal gradient in productivity appears to be driven by temperature,” noting “annual productivity most significantly correlates with mean annual temperature and the annual number of growing degree days.” Consequently, Kirwan *et al.* estimate the response of *S. alterniflora* productivity to future increases in global temperature, noting their results suggest “an increase in global temperature of 2–4°C by 2100 (IPCC, 2007) would cause productivity to increase by about 50–100 g m²/year.” For mid-Atlantic and northern marshes with current productivities ranging from 450 to 250 g m²/year, they say the result they obtained “represents approximately a 10–40% increase in annual productivity,” which they describe as being of “a magnitude similar to that of marsh lost due to sea level change (10–50%),” as calculated by numerical models for the same time period. They

therefore conclude, “increased growth under a warming climate may compensate for the amount of productivity lost by eroding marshland.”

The increase in atmospheric CO₂ concentration expected for the current century likely will boost marsh productivity even more, further strengthening this conclusion. In addition, it is widely recognized, as Kirwan *et al.* state, “increased vegetation growth will tend to promote higher marsh accretion rates, stabilize channel expansion, and decrease the ability for waves to erode the marsh platform.” As a result, they conclude, “the combined impacts of future global change (e.g. sea level, temperature, CO₂) could actually increase the total productivity of marshland.”

Mateos-Naranjo *et al.* (2010) obtained 15 cm-diameter clumps of *S. maritima* from a low-marsh site along the southwest coast of Spain in April 2007, which they transplanted into individual plastic pots filled with perlite that rested on shallow trays filled with Hoagland’s solution of three different salinities (0, 170, or 510 mM NaCl). The research team maintained the plants in controlled environment chambers having atmospheric CO₂ concentrations of either 380 ppm or 700 ppm (an increase of 84%) for periods of 30 days, during which time they measured a number of plant properties and processes. The four researchers report the 84% increase in the atmosphere’s CO₂ concentration stimulated the growth of *S. maritima* by about 65% in all three salinity treatments; the graphical representation of the halophyte’s water use efficiency indicates this important property of the plant was enhanced by approximately 10%, 100%, and 160% in the 0, 170, and 510 mM salinity treatments, respectively, because “increasing CO₂ concentration has a positive effect on the photochemical apparatus, helping to counteract salt stress experienced by plants at current CO₂ concentrations.” The UK and Spanish scientists say their results suggest the productivity of *S. maritima* “might increase in a future scenario of rising atmospheric CO₂ concentration in environments with salinities as high as that of seawater,” good news for what they describe as “an important pioneer and ecosystem engineer in salt marshes.”

Kathilankal *et al.* (2011) made a series of physiological measurements on smooth cordgrass, which is believed to possess C₄ physiology, at two locations in the Virginia Coast Reserve’s Long Term Ecological Research area—Fowling Point Marsh (a lagoon salt marsh) and Oyster Marsh (a mainland fringing marsh)—to investigate how light, temperature, and intercellular CO₂ concentration affected the marsh plant’s rate of photosynthesis. They used

the functional relationships between these environmental variables and *S. alterniflora*’s physiological responses to improve C₄-leaf photosynthesis models ultimately employed to determine the net impact of potential increases in air temperature and atmospheric CO₂ concentration on the productivity of smooth cordgrass in a CO₂-enriched and warmer world.

Instead of acting like a C₄ plant, the modeling studies and field measurements indicate “*S. alterniflora* exhibited physiological traits similar to C₃-C₄ intermediate plants,” so one could expect “atmospheric warming in conjunction with an increase in atmospheric CO₂ would enhance photosynthesis in *S. alterniflora*,” the six scientists discovered. In further support of this conclusion, they note “McKee and Rooth (2008) reported a significant stimulation in *S. alterniflora* biomass in plants grown under elevated CO₂,” and “warming experiments in New England (Charles and Dukes, 2009) demonstrated that *S. alterniflora* increased productivity with increasing temperature,” while the plant’s optimum temperature for photosynthesis also will “likely increase in response to enriched CO₂ conditions,” citing Simon *et al.* (1984).

In the concluding paragraph of their report, Kathilankal *et al.* declare “in a scenario of atmospheric warming and increased atmospheric CO₂ levels, *S. alterniflora* will likely respond positively to both changes,” and they suggest these responses “will result in increased *S. alterniflora* productivity,” which should be beneficial for western Atlantic intertidal marshes and the many beneficial services that smooth cordgrass provides to those ecosystems.

References

- Chameides, W.L., Lindsay, R.W., Richardson, J., and Kiang, C.S. 1988. The role of biogenic hydrocarbons in urban photochemical smog: Atlanta as a case study. *Science* **241**: 1473–1475.
- Charles, H. and Dukes, J.S. 2009. Effects of warming and altered precipitation on plant and nutrient dynamics of a New England salt marsh. *Ecological Applications* **19**: 1758–1773.
- Cherry, J.A., McKee, K., and Grace, J.B. 2009. Elevated CO₂ enhances biological contributions to elevation change in coastal wetlands by offsetting stressors associated with sea-level rise. *Journal of Ecology* **97**: 67–77.
- Curtis, P.S., Drake, B.G., Leadly, P.W., Arp, W.J., and Whigham, D.F. 1989a. Growth and senescence in plant communities exposed to elevated CO₂ concentrations on an estuarine marsh. *Oecologia* **78**: 20–26.

- Curtis, P.S., Drake, B.G., and Whigham, D.F. 1989b. Nitrogen and carbon dynamics in C₃ and C₄ estuarine marsh plants grown under elevated CO₂ *in situ*. *Oecologia* **78**: 297–301.
- Dakora, F.D. and Drake, B.G. 2000. Elevated CO₂ stimulates associative N₂ fixation in a C₃ plant of the Chesapeake Bay wetland. *Plant, Cell and Environment* **23**: 943–953.
- Dijkstra, P., Hymus, G.J., and Colavito, D., *et al.* 2002. Elevated atmospheric CO₂ stimulates shoot growth in a Florida scrub oak ecosystem. *Global Change Biology* **8**: 90–103.
- Drake, B.G. and Leadley, P.W. 1991. Canopy photosynthesis of crops and native plant communities exposed to long-term elevated CO₂. *Plant, Cell and Environment* **14**: 853–860.
- Drake, B.G., Muehe, M.S., Peresta, G., Gonzalez-Meler, M.A., and Matamala, R. 1996a. Acclimation of photosynthesis, respiration and ecosystem carbon flux of a wetland on Chesapeake Bay, Maryland to elevated atmospheric CO₂ concentration. *Plant and Soil* **187**: 111–118.
- Drake, B.G., Peresta, G., Beugeling, E., and Matamala, R. 1996b. Long-term elevated CO₂ exposure in a Chesapeake Bay wetland: Ecosystem gas exchange, primary production, and tissue nitrogen. In: Koch, G.W. and Mooney, H.A. (Eds.) *Carbon Dioxide and Terrestrial Ecosystems*. Academic Press, San Diego, CA, pp. 197–213.
- Erickson, J.E., Megonigal, J.P., Peresta, G., and Drake, B.G. 2007. Salinity and sea level mediate elevated CO₂ effects on C₃-C₄ plant interactions and tissue nitrogen in a Chesapeake Bay tidal wetland. *Global Change Biology* **13**: 202–215.
- Harley, P.C., Monson, R.K., and Lerda, M.T. 1999. Ecological and evolutionary aspects of isoprene emission from plants. *Oecologia* **118**: 109–123.
- Hussein, A.H., Rabenhorst, M.C., and Tucker, M.L. 2004. Modeling of carbon sequestration in coastal marsh soils. *Soil Science Society of America Journal* **68**: 1786–1795.
- Hymus, G.J., Pontai, J.Y., and Li, J., *et al.* 2002. Seasonal variability in the effect of elevated CO₂ on ecosystem leaf area index in a scrub-oak ecosystem. *Global Change Biology* **8**: 931–940.
- Jacob, J., Greitner, C., and Drake, B.G. 1995. Acclimation of photosynthesis in relation to Rubisco and nonstructural carbohydrate content and *in situ* carboxylase activity in *Scirpus olneyi* grown at elevated CO₂ in the field. *Plant, Cell and Environment* **18**: 875–884.
- Kathilankal, J.C., Mozdzer, T.J., Fuentes, J.D., McGlathery, K.J., D’Odorico, P., and Ziemann, J.C. 2011. Physiological responses of *Spartina alterniflora* to varying environmental conditions in Virginia marshes. *Hydrobiologia* **669**: 167–181.
- Kirwan, M.L., Guntenspergen, G.R., and Morris, J.T. 2009. Latitudinal trends in *Spartina alterniflora* productivity and the response of coastal marshes to global change. *Global Change Biology* **15**: 1982–1989.
- Langley, J.A., McKee, K.L., Cahoon, D.R., Cherry, J.A., and Megonigal, J.P. 2009. Elevated CO₂ stimulates marsh elevation gain, counterbalancing sea-level rise. *Proceedings of the National Academy of Sciences, USA* **106**: 6182–6186.
- Loreto, F., Fischbach, R.J., Schnitzler, J.-P., Ciccioli, P., Brancaleoni, E., Calfapietra, C., and Seufert, G. 2001. Monoterpene emission and monoterpene synthase activities in the Mediterranean evergreen oak *Quercus ilex* L. grown at elevated CO₂ concentrations. *Global Change Biology* **7**: 709–717.
- Loreto F. and Sharkey, T.D. 1990. A gas exchange study of photosynthesis and isoprene emission in red oak (*Quercus rubra* L.). *Planta* **182**: 523–531.
- Mateos-Naranjo, E., Redondo-Gomez, S., Andrades-Moreno, L., and Davy, A.J. 2010. Growth and photosynthetic responses of the cordgrass *Spartina maritima* to CO₂ enrichment and salinity. *Chemosphere* **81**: 725–731.
- McKee, K.L. and Rooth, J.E. 2008. Where temperate meets tropical: Multi-factorial effects of elevated CO₂, nitrogen enrichment, and competition on a mangrove-salt marsh community. *Global Change Biology* **14**: 971–984.
- Monson, R.K. and Fall, R. 1989. Isoprene emission from aspen leaves. *Plant Physiology* **90**: 267–274.
- Mitsch, W.J., Mitsch, R.H., and Turner, R.E. 1994. Wetlands of the Old and New Worlds: ecology and management. In: Mitsch, W.J. (Ed.) *Global Wetlands Old World and New*. Elsevier, Amsterdam, The Netherlands.
- Norby, R.J., DeLucia, E.H., and Gielen, B., *et al.* 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proceedings of the National Academy of Science* **102**: 18,052–18,056.
- Norby, R.J., Wullschlegel, S.D., Gunderson, C.A., Johnson, D.W., and Ceulemans, R. 1999. Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant, Cell and Environment* **22**: 683–714.
- Owensby, C.E., Ham, J.M., and Knapp, A.K., *et al.* 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO₂. *Global Change Biology* **5**: 497–506.
- Poisson, N., Kanakidou, M., and Crutzen, P.J. 2000.

Impact of non-methane hydrocarbons on tropospheric chemistry and the oxidizing power of the global troposphere: 3-dimensional modeling results. *Journal of Atmospheric Chemistry et al.*: 157–230.

Rasse, D.P., Li, J.-H., and Drake, B.G. 2003. Carbon dioxide assimilation by a wetland sedge canopy exposed to ambient and elevated CO₂: measurements and model analysis. *Functional Ecology* **17**: 222–230.

Rasse, D.P., Peresta, G., and Drake, B.G. 2005. Seventeen years of elevated CO₂ exposure in a Chesapeake Bay Wetland: sustained but contrasting responses of plant growth and CO₂ uptake. *Global Change Biology* **11**: 369–377.

Reed, D.J., *et al.* 2008. Site-Specific Scenarios for Wetlands Accretion as Sea Level Rises in the Mid-Atlantic Region. Section 2.1. Background Documents Supporting Climate Change Science Program Synthesis and Assessment Product. Titus, J.G. and Strange, E.M. (Eds.). EPA 430R07004, U.S. Environmental Protection Agency, Washington, DC.

Rosentiel, T.N., Potosnak, M.J., Griffin, K.L., Fall, R., and Monson, R.K. 2003. Increased CO₂ uncouples growth from isoprene emission in an agriforest ecosystem. *Nature* **421**: 256–259.

Scholefield, P.A., Doick, K.J., Herbert, B.M.J., Hewitt, C.N.S., Schnitzler, J.-P., Pinelli, P., and Loreto, F. 2004. Impact of rising CO₂ on emissions of volatile organic compounds: isoprene emission from *Phragmites australis* growing at elevated CO₂ in a natural carbon dioxide spring. *Plant, Cell and Environment* **27**: 393–401.

Sharkey, T.D., Loreto, F., and Delwiche, C.F. 1991. High carbon dioxide and Sun/shade effect on isoprene emissions from oak and aspen tree leaves. *Plant, Cell and Environment* **14**: 333–338.

1.2.5 Soils

1.2.5.1 Bacteria

- Rising atmospheric CO₂ concentrations likely will allow greater numbers of beneficial bacteria (those that help sequester carbon and nitrogen) to exist in soils and anaerobic water environments. This two-pronged phenomenon would be a great boon to terrestrial and aquatic ecosystems.

Nearly all of Earth's plant life responds favorably to increases in the air's CO₂ content by exhibiting enhanced rates of photosynthesis and biomass production. Consequently, these phenomena tend to increase soil carbon contents by increasing root

exudation of organic compounds and the amount of plant litter returned to the soil. Thus, it can be expected that CO₂-mediated increases in soil carbon content will affect soil bacterial communities. This section explores the findings of several scientists who have studied the effects of elevated CO₂ on bacteria.

Regarding beneficial terrestrial bacteria, Ronn *et al.* (2003) grew wheat (*Triticum aestivum* L. cv. Minaret) in open-top chambers fumigated with either ambient air or air enriched with an extra 320 ppm of CO₂; on two occasions during the growing season they assessed various plant and soil characteristics, total protozoan numbers, and numbers of culturable bacteria. They found “higher numbers of bacterivorous protozoa in soil under plants grown at elevated CO₂ and larger amounts of root-derived substrates in the soil at plant maturity.” Ronn *et al.* note “protozoan grazing generally enhances carbon and nitrogen mineralization in soil,” which typically results in more nitrogen being made available to plants. This phenomenon, in turn, enables plants to increase their biomass (as was observed in the CO₂-enriched plants in this experiment) without suffering reductions in tissue nitrogen concentration (as also was observed in the CO₂-enriched plants in this experiment). The end result of these linked phenomena was thus more high-quality wheat production in response to atmospheric CO₂ enrichment.

Montealegre *et al.* (2002) obtained similar results by growing white clover (*Trifolium repens* L.) and perennial ryegrass (*Lolium perenne* L.) in free-air CO₂ enrichment (FACE) plots maintained at atmospheric CO₂ concentrations of 350 and 600 ppm for three years and then sampling the soil to determine the effects of elevated CO₂ on its bacterial populations. Although elevated CO₂ increased the total number of bacteria and respiring bacteria in the bulk soil beneath white clover by 40 and 70%, respectively, it had no significant impact on bulk-soil bacterial numbers beneath perennial ryegrass. When the total bacterial numbers in the *rhizosphere* soil—which lies within about 1.5 mm of plant roots and is characterized by heightened biological activity and chemical weathering of minerals—were expressed on a per unit land area basis, the scientists found elevated CO₂ increased the total number of bacteria and respiring bacteria beneath white clover by about 100 and 250%, respectively, and it increased the total number of bacteria and respiring bacteria beneath perennial ryegrass by approximately 85 and 125%, respectively.

In a related study from the same FACE clover

and ryegrass plots, Marilley *et al.* (1999) report atmospheric CO₂ enrichment also altered the profile of bacterial communities in a plant species-dependent manner. In ryegrass, for example, elevated CO₂ increased the dominance of *Pseudomonas* species, which enhance plant growth by many different mechanisms. In white clover, it increased the dominance of *Rhizobium* species, which enhance plant growth by making atmospheric nitrogen available for utilization. After three years of differential CO₂ treatment in the same FACE experiment, Montealegre *et al.* (2000) determined the genetic structure of 120 isolates of the symbiotic bacterium *Rhizobium leguminosarum* associated with roots of white clover, finding atmospheric CO₂ enrichment favored some of the isolates over others. When these isolates were mixed with isolates favored in ambient air and the resulting combination was exposed to CO₂-enriched air, the isolates favored by elevated CO₂ produced 17% more nodules on roots than the isolates favored in ambient air.

Zak *et al.* (2000) grew six genotypically different aspen (*Populus tremuloides*) cuttings in open-top chambers for 2.5 growing seasons in Michigan, USA, at atmospheric CO₂ concentrations of 350 and 700 ppm under adequate and inadequate supplies of soil nitrogen, reporting the effects of elevated CO₂ and soil nitrogen on soil microbial composition, biomass, and functioning. Although atmospheric CO₂ enrichment had no effect on soil microbial biomass, even after 2.5 years of treatment, high soil nitrogen supply increased it fivefold over that observed in low soil nitrogen plots. Similarly, elevated CO₂ did not significantly impact microbial community composition, whereas high soil nitrogen supply did. Atmospheric CO₂ did not influence microbial rates of nitrogen mineralization, nor did it alter the microbial demand for inorganic nitrogen.

The several observations of Zak *et al.* suggest the increased fine root biomass and turnover, which led to greater carbon inputs to the soils of the CO₂-enriched plots, were not significant enough to elicit any responses in microbial community composition, biomass, and functioning, likely due to the enormous amount of background organic carbon present in the experimental soils, which was approximately 1,000-fold greater than that contributed by the aspen roots. Notwithstanding this observation, the authors conducted an eloquent review of the scientific literature pertaining to this topic, and they conclude when root-associated soil carbon inputs are sufficiently large, relative to native soil organic carbon contents, they can influence microbial community composition,

biomass, and functioning.

Therefore, as atmospheric CO₂ concentrations rise, it is likely aspen trees will exhibit significant increases in growth, regardless of soil nitrogen availability. These growth increases will occur both above- and below-ground, stimulating greater carbon inputs to soils. Because most forest soils are already relatively rich in organic carbon, however, it is likely the extra carbon inputs resulting from the increasing CO₂ content of the air will have little impact on soil microbial composition, biomass, and functioning.

Fu *et al.* (2008) employed semi-continuous culturing methods that used filtered, microwave-sterilized surface Sargasso seawater enriched with phosphate and trace nutrients to examine the physiological responses of steady-state iron (Fe)-replete and Fe-limited cultures of the biogeochemically critical marine unicellular diazotrophic cyanobacterium *Crocospaera watsonii* at 380 ppm and 750 ppm CO₂ levels. When the seawater was replete with iron, they found daily primary production at 750 ppm CO₂ was 21% greater than it was at 380 ppm, but when the seawater was iron-limited, daily primary production at 750 ppm CO₂ was 150% greater than it was at 380 ppm. With respect to N₂ fixation, rates varied little between the two CO₂ treatments when the seawater was iron-limited, but when the seawater was replete with iron, N₂ fixation at 750 ppm CO₂ was 60% greater than it was at 380 ppm.

In discussing their findings, Fu *et al.* write “several studies examining the marine diazotrophic cyanobacterium *Trichodesmium* have shown significant increases in N₂ fixation and photosynthesis in response to elevated CO₂ concentration (Hutchins *et al.*, 2007; Levitan *et al.*, 2007; Ramos *et al.*, 2007),” and they say their data “extend these findings to encompass the marine unicellular N₂-fixing cyanobacterium *Crocospaera*.” This group, they add, “is now recognized as being perhaps equally as important as *Trichodesmium* to the ocean nitrogen cycle (Montoya *et al.*, 2004).” Consequently, they conclude, “anthropogenic CO₂ enrichment could substantially increase global oceanic N₂ and CO₂ fixation,” which would be a boon to the marine biosphere.

Feng *et al.* (2009) measured a number of characteristics of purple phototrophic bacteria (PPB) within the rhizosphere and bulk soils of a rice/wheat rotation system at the Nianyu Experimental Station in Jiangsu Province, China, under two CO₂ treatments. Rice fields, in their words, “represent the most important agricultural ecosystems in Asia, since rice

and wheat are the main source for food supply, and more than 90% of rice fields around the world are located in Asia,” and “purple phototrophic bacteria (PPB) are thought to be crucial in the nutrient cycling of rice fields.” The Chinese researchers say PPB “thrive in the anaerobic portions of all kinds of aquatic environments, and have long been recognized as one of the key players in global carbon and nitrogen cycles.” The researchers grew rice plants (*Oryza sativa* L.) under standard paddy culture at two levels of soil nitrogen (N) fertility (low and high) and two levels of atmospheric CO₂ concentrations (ambient and ambient +200 ppm).

Throughout this period they measured a number of PPB characteristics. Feng *et al.* report, “based on denaturant gradient gel electrophoresis (DGGE) analysis of *pufM* gene encoding the M subunit of anoxygenic PPB light reaction center, elevated CO₂ appeared to enhance the biodiversity of PPB in flooded paddy soils.” They continue, “this was further supported by canonical correspondence analysis (CCA) of DGGE fingerprinting pattern of *pufM* genes in paddy soils as well as Shannon diversity indices.” They also note “real-time quantitative PCR analysis of *pufM* gene further indicated that PPB abundance was stimulated by elevated CO₂ in bulk soil,” and “N fertilization enhanced the biodiversity of PPB under elevated atmospheric CO₂.” Feng *et al.* state the significance of these findings by noting “PPB inoculation into the flood water [in rice paddy culture] could lead to grain yield increase by 29% (Elbadry *et al.*, 1999; Harada *et al.*, 2005),” and “PPB are thought to be capable of fixing nitrogen.” Feng *et al.* (2011) expressed similar sentiments in discussing the results of the same experiment, acknowledging the importance of elevated CO₂ concentrations on PPB to “enhance the microbial food chain and promote the growth and yield of crops.”

The above observations suggest rising atmospheric CO₂ levels likely will allow similar or greater numbers of bacteria to exist in terrestrial environments, enhancing carbon and nitrogen sequestration, which in turn will stimulate the growth and productivity of the surrounding environments.

References

- Elbadry, M., Gamal-Eldin, H., and Elbanna, K. 1999. Effects of *Rhodobacter capsulatus* inoculation in combination with graded levels of nitrogen fertilizer on growth and yield of rice in pots and lysimeter experiments. *World Journal of Microbiology and Biotechnology* **15**: 393–395.
- Feng, Y., Lin, X., Wang, Y., Zhang, J., Mao, T., Yin, R., and Zhu, J. 2009. Free-air CO₂ enrichment (FACE) enhances the biodiversity of purple phototrophic bacteria in flooded paddy soil. *Plant and Soil* **324**: 317–328.
- Feng, Y., Lin, X., Zhang, J., Mao, T., and Zhu, J. 2011. Soil purple phototrophic bacterial diversity under double cropping (rice-wheat) with free-air CO₂ enrichment (FACE). *European Journal of Soil Science* **62**: 533–540.
- Fu, F.-X., Mulholland, M.R., Garcia, N.S., Beck, A., Bernhardt, P.W., Warner, M.E., Sanudo-Wilhelmy, S.A., and Hutchins, D.A. 2008. Interactions between changing pCO₂, N₂ fixation, and Fe limitation in the marine unicellular cyanobacterium *Crocospaera*. *Limnology and Oceanography* **53**: 2472–2484.
- Harada, N., Nishiyama, M., Otsuka, S., and Matsumoto, S. 2005. Effects of inoculation of phototrophic bacteria on grain yield of rice and nitrogenase activity of paddy soil in a pot experiment. *Soil Science and Plant Nutrition* **51**: 361–367.
- Hutchins, D.A., Fu, F.-X., Zhang, Y., Warner, M.E., Feng, Y., Portune, K., Bernhardt, P.W., and Mulholland, M.R. 2007. CO₂ control of *Trichodesmium* N₂ fixation, photosynthesis, growth rates, and elemental ratios: Implications for past, present, and future ocean biogeochemistry. *Limnology and Oceanography* **52**: 1293–1304.
- Levitan, O., Rosenberg, G., Setlik, I., Setlikova, E., Grigel, J., Klepetar, J., Prasil, O., and Berman-Frank, I. 2007. Elevated CO₂ enhances nitrogen fixation and growth in the marine cyanobacterium *Trichodesmium*. *Global Change Biology* **13**: 531–538.
- Marilley, L., Hartwig, U.A., and Aragno, M. 1999. Influence of an elevated atmospheric CO₂ content on soil and rhizosphere bacterial communities beneath *Lolium perenne* and *Trifolium repens* under field conditions. *Microbial Ecology* **38**: 39–49.
- Montealegre, C.M., van Kessel, C., Blumenthal, J.M., Hur, H.G., Hartwig, U.A., and Sadowsky, M.J. 2000. Elevated atmospheric CO₂ alters microbial population structure in a pasture ecosystem. *Global Change Biology* **6**: 475–482.
- Montealegre, C.M., van Kessel, C., Russelle, M.P., and Sadowsky, M.J. 2002. Changes in microbial activity and composition in a pasture ecosystem exposed to elevated atmospheric carbon dioxide. *Plant and Soil* **243**: 197–207.
- Montoya, J.P., Holl, C.M., Zehr, J.P., Hansen, A., Villareal, T.A., and Capone, D.G. 2004. High rates of N₂ fixation by unicellular diazotrophs in the oligotrophic Pacific Ocean. *Nature* **430**: 1027–1031.
- Ramos, J.B.E., Biswas, H., Schulz, K.G., Laroche, J., and Riebesell, U. 2007. Effect of rising atmospheric carbon dioxide on the marine nitrogen fixer *Trichodesmium*.

Global Biogeochemical Cycles **21**: 10.1029/2006GB002898.

Ronn, R., Ekelund, F., and Christensen, S. 2003. Effects of elevated atmospheric CO₂ on protozoan abundance in soil planted with wheat and on decomposition of wheat roots. *Plant and Soil* **251**: 13–21.

Zak, D.R., Pregitzer, K.S., Curtis, P.S., and Holmes, W.E. 2000. Atmospheric CO₂ and the composition and function of soil microbial communities. *Ecological Applications* **10**: 47–59.

1.2.5.2 Carbon Sequestration

- The aerial fertilization effect of atmospheric CO₂ enrichment likely will result in greater soil carbon stores due to increased carbon-input into soils, even in nutrient-poor soils and in spite of predicted increases in temperature. In addition, the soil-carbon-sequestering capability of Earth's vegetation likely will act as a significant brake on the rate of rise of the air's CO₂ content and thereby help to mute any CO₂-induced impetus for global warming.

As the CO₂ content of the air increases, nearly all plants respond favorably by increasing their photosynthetic rates and producing greater amounts of biomass. Invariably, this phenomenon leads to greater inputs of carbon to the soil in the form of roots, root exudates, and senesced plant material. Much research has been conducted to determine whether these biological inputs will increase the carbon sequestering abilities of soils, particularly if air temperatures rise, which some scientists have predicted will enhance plant litter decomposition rates to the point they will exacerbate global warming. This section summarizes research that has addressed this subject.

Atmospheric CO₂ enrichment typically has but a small effect on the decomposition rates of senesced plant materials present in soils. Nonetheless, CO₂ enrichment often leads to significantly greater soil carbon sequestration, as demonstrated by De Angelis *et al.* (2000), who report a 4% reduction in the decomposition rate of leaf litter beneath stands of 30-year-old Mediterranean forest species enriched with air of 710 ppm CO₂, concluding, “if this effect is coupled to an increase in primary production [which nearly always occurs in response to elevated CO₂] there will be a net rise of C-storage in the soils of forest ecosystems.” Similarly, in a study of soybean

and sorghum plant residues grown at 705 ppm CO₂, where decomposition rates were not affected by elevated CO₂, Henning *et al.* (1996) concluded “the possibility exists for increased soil C storage under field crops in an elevated CO₂ world,” due to the greater residue production resulting from CO₂-enhanced plant growth.

In a study that revealed how these phenomena once manifested themselves in a field of clover (*Trifolium repens* L.) at the Swiss Federal Institute of Technology near Zurich, a 71% increase in atmospheric CO₂ concentration increased above-ground growth by 146%, and it increased the pumping of newly fixed carbon into the soil of the CO₂-enriched plots by approximately 50% (Nitschelm *et al.* 1997). In addition, root decomposition in the CO₂-enriched plots was found to be 24% less than in the ambient-treatment plots. The researchers conclude, “the occurrence at elevated CO₂ of both greater plant material input, through higher yields, and reduced residue decomposition rates would be expected to impact soil carbon storage significantly.” In a similar study of the effects of a doubling of the air's CO₂ concentration on three grass species, Cotrufo and Gorissen (1997) conclude “elevated CO₂ could result in greater soil carbon stores due to increased carbon-input into soils.”

One year later, Verburg *et al.* (1998) grew one-year-old heather plants (*Calluna vulgaris* L.) for two months in greenhouses maintained at atmospheric CO₂ concentrations of 380 and 580 ppm in combination with low and high levels of soil nitrogen before exposing them to ¹⁴CO₂ for one day, to study the fate of recently fixed carbon in their experimental plant-soil system. They found the extra CO₂ increased net ¹⁴C uptake in heather by approximately 43%, irrespective of soil nitrogen content. In addition, soil ¹⁴C increased in elevated CO₂ plots by 17% and 25% at low and high soil nitrogen levels, respectively. Also, although total soil respiration initially was higher in the CO₂-enriched plots (for two days post ¹⁴CO₂ labeling), it declined and became significantly lower than the soil respiration rate displayed by plots exposed to ambient air within two weeks. That trend persisted throughout the remaining four weeks of the study. Thus it would appear soil carbon sequestration beneath heather communities likely will increase in the future with further increases in the air's CO₂ concentration.

Similar results have been reported for other shrubs and trees that possess the ability to store more carbon in their associated soils than do grasses, as noted by Gill and Burke (1999). Pregitzer *et al.*

(2000), for example, grew aspen seedlings for 2.5 years at 700 ppm CO₂ and observed fine root biomass was 65 and 17% greater than that produced by seedlings growing at ambient CO₂ concentration on nitrogen-rich and nitrogen-poor soils, respectively. The researchers state such increases in soil carbon inputs “can be substantial,” even under low soil nitrogen conditions. Rouhier and Reed (1999) also note soil carbon was significantly greater beneath seedlings of birch grown at 700 ppm CO₂ than it was beneath seedlings grown at 350 ppm CO₂. Leavitt *et al.* (1994) found 10% of the organic carbon present in soils beneath CO₂-enriched cotton plants grown for only three years at 550 ppm CO₂ came from the extra CO₂, which was stable-isotope labeled to trace its path through this woody agricultural species and into the soil.

In a study that included air temperature as a variable, Casella and Soussana (1997) grew perennial ryegrass (*Lolium perenne* L.) in ambient and elevated (700 ppm) CO₂ at two different levels of soil nitrogen and at ambient and elevated (+3°C) temperature for two years. They found “a relatively large part of the additional photosynthetic carbon is stored below-ground during the two first growing seasons after exposure to elevated CO₂, thereby increasing significantly the below-ground carbon pool.” At the low and high levels of soil nitrogen supply, for example, the elevated CO₂ increased soil carbon storage by 32 and 96%, respectively, “with no significant increased temperature effect,” which led the two scientists to conclude, in spite of predicted increases in temperature, “this stimulation of the below-ground carbon sequestration in temperate grassland soils could exert a negative feed-back on the current rise of the atmospheric CO₂ concentration.” Along these same lines, van Ginkel and Gorissen (1998) and van Ginkel *et al.* (1999)—who performed similar experiments using *Lolium perenne*—conclude the effects of atmospheric CO₂ enrichment on increasing plant growth and decreasing decomposition rates of plant litter are “more than sufficient to counteract the positive feedback [on decomposition rates] caused by [an] increase in air temperature.”

Fitter *et al.* (1999) heated upland grass ecosystem soils by nearly 3°C and found root production and root death were increased by equivalent amounts. Hence, they conclude elevated temperatures “will have no direct effect on the soil carbon store [in upland grass communities].” Similarly, Johnson *et al.* (2000) warmed Arctic tundra ecosystems by nearly 6°C for eight years, reporting warming had no

significant effect on ecosystem respiration. In addition, Liski *et al.* (1999) showed carbon storage in soils of both high- and low-productivity boreal forests increased with temperature along a temperature gradient in Finland. Thus it is clear any warming likely will have little or no impact on soil carbon sequestration rates, and if there is an impact, it may be positive.

Increased soil carbon storage occurring from the ongoing rise in the air’s CO₂ content should have wide-ranging positive influences on agriculture. In considering soil carbon storage in the context of global climate change, Rosenzweig and Hillel (2000) state “our management of the soil should be aimed at enhancing soil organic matter for the multiple complementary purposes of improving soil fertility and soil structure, reducing erosion, and helping to mitigate the greenhouse effect.” In an experiment where soybeans were grown at an atmospheric CO₂ concentration of 500 ppm, Islam *et al.* (1999) report soil particulate organic carbon content was significantly increased, as were the amounts of dissolved carbon, humic, and fulvic acids. These findings led them to conclude “one of the main benefits arising from the greater supply of organic residues to soils under CO₂ enrichment is an improvement of soil structure.” In a similar study, Insam *et al.* (1999) note fumigation of artificial tropical ecosystems with 610 ppm CO₂ for about 1.5 years increased humic substances in their soils by nearly 30%.

Ross *et al.* (2000) collected soil samples from around a natural CO₂ vent in New Zealand to determine the effects of elevated CO₂ (510–900 ppm vs. 440–460 ppm) on soil carbon and nitrogen contents. The soil at the site was considered to be a gley, and the overlying vegetation was typical of native grasslands in the area, consisting of both C₃ and C₄ species. They found several decades of exposure to elevated atmospheric CO₂ significantly increased the soil’s organic carbon and total nitrogen contents by 24%, and it increased microbial carbon and nitrogen contents by 116%. These results led Ross *et al.* to conclude storage of C and N in gley soils “can increase under prolonged exposure to elevated CO₂” and “increased storage of soil organic matter at such springs can occur, even when soil C concentrations are already high.” Thus, as the air’s CO₂ content rises, vegetated gley soils will sequester increasingly greater amounts of both carbon and nitrogen, and they will exhibit enhanced biological activity both above- and below-ground.

Hu *et al.* (2001) studied carbon and nitrogen

relations in the plants and moderately fertile soil of a sandstone grassland at Stanford University's Jasper Ridge Biological Preserve in central California near the conclusion of a five-year study conducted between 1992 and 1997, where two CO₂ treatments (360 and 720 ppm) were maintained in 20 open-top chambers (ten replicates per treatment). This effort revealed the rise in atmospheric CO₂ increased both soil microbial biomass and plant nitrogen uptake, the net effect being less nitrogen was left in the soil for microbes to use, which resulted in decreased microbial respiration per unit biomass and, hence, decreased microbial decomposition and increased ecosystem carbon accumulation.

King *et al.* (2001) grew O₃-sensitive and O₃-tolerant aspen (*Populus tremuloides* Michx.) clones alone and in mixed stands of paper birch (*Betula papyrifera* Marsh.) for two years in 30m-diameter free-air CO₂ enrichment (FACE) plots in Rhinelander, Wisconsin, which they maintained at CO₂ concentrations of 360 and 560 ppm with and without exposure to elevated O₃ (1.5 times ambient concentrations), to study the interactive effects of these parameters on fine-root production and belowground carbon cycling in the soils associated with these stands. They found the elevated CO₂ significantly enhanced the production of fine root biomass by 133 and 83% for aspen and aspen-birch mixed stands, respectively. In contrast, elevated O₃ had no effect on fine-root biomass, but simultaneous exposure to elevated O₃ and CO₂ increased fine-root biomass by approximately 66% for both types of stands. And when averaged across both stands, elevated CO₂ also increased dead root biomass by 140%, but another example of elevated CO₂ increasing carbon inputs to soils.

In August 1996, Andrews and Schlesinger (2001) and a number of other researchers established circular FACE plots (30 meters in diameter) that they exposed to air of either 360 or 560 ppm CO₂. This modest increase in the air's CO₂ content increased the weathering rate of parent rock material, as indicated by a 271% increase in soil mineral cation concentration and a 162% increase in soil alkalinity after the second year of CO₂ enrichment. In addition, the elevated CO₂ increased the flux of dissolved inorganic carbon compounds to the groundwater by 33%. Extrapolating this phenomenon to the global land area covered by forests, the two researchers remark the observed increase in the efflux of dissolved inorganic carbon compounds to groundwater "may act to buffer the rate of CO₂ increase in the atmosphere over geologic time periods."

Working in the same plots at the same time, Pritchard *et al.* (2001) studied the effects of elevated CO₂ on belowground root dynamics as assessed by mini-rhizotrons inserted into the low-nutrient (nitrogen and phosphorus) soils of the experimental plots. After one year of treatment, they report total standing root length and root numbers per minirhizotron were 16 and 34% greater, respectively, in the CO₂-enriched plots than in the ambient-air plots. In addition, the elevated CO₂ increased the diameter of living and dead roots by 8 and 6%, respectively, and annual root production and root mortality were 26 and 46% greater in the CO₂-enriched plots than in the control plots. All of these phenomena would be expected to result in enhanced carbon sequestration in the soils in which the trees were rooted.

In another contemporaneous paper, Cardon *et al.* (2001) write, "soil organic carbon (SOC) is the largest reservoir of organic carbon in the terrestrial biosphere." They affirm this in introducing their experimental study of the potential effects of the ongoing rise in the air's CO₂ content on this vast store of material, which was once the "C" in the CO₂ of much of Earth's atmosphere, where it was freely wafted about prior to being assimilated by plants and sequestered in the soil.

Occupying such a pivotal position as it does in the planetary carbon cycle, SOC is of great interest to scientists who worry about its stability. Among other things, Cardon *et al.* wanted to know whether allowing more CO₂ to be emitted to the atmosphere would lead to even more carbon being sequestered in the soil (a logical hypothesis), or if it would somehow cause a reduction in what was already there (a less logical hypothesis but one that cannot be ignored).

Cardon *et al.* studied soil carbon income and outgo in a number of small microcosms of two annual C₃ grassland communities (sandstone and serpentine) of contrived high and low soil-nutrient availability maintained out-of-doors in open-top chambers at the Jasper Ridge Biological Preserve in Stanford, California, from October 1994 through August 1996. Key to their study was the utilization of isotopic tracer techniques to determine the sizes of the various SOC pools through time. They grew the C₃ plants in a soil obtained from a C₄ grassland in Colorado, which ensured that the original organic carbon of their experimental soil would have a different isotopic signature from the organic carbon that would be injected into it by the C₃ plants that grew upon it. In addition, the carbon of the fossil fuel-derived CO₂ supplied to the CO₂-enriched chambers

had yet a third unique isotopic signature.

They found the extra CO₂ supplied to half of the mini-ecosystems increased the total root biomass in the serpentine grassland microcosms by a factor of three in both high and low soil-nutrient availability treatments, and it increased total root biomass in the sandstone grassland microcosms by a factor of four in both the high and low soil-nutrient availability treatments. Thus there was a tremendous CO₂-induced increase in the amount of organic material that eventually would become available for incorporation into the soils of both grassland microcosms.

With so much new organic matter being added to the soils of the CO₂-enriched microcosms, Cardon *et al.* hypothesized previously carbon-limited microbes in these soils would alter their survival strategy and turn from breaking down older, more recalcitrant soil organic matter to attack the more abundant and labile rhizodeposits being laid down in the newly carbon-rich soils of the CO₂-enriched microcosms. This rhizodeposition, as they christened it, consists of “all deposition of organic carbon from living root systems to soils, including compounds lost through root exudation, sloughing of dead cells during root growth, and fine root turnover,” which, as noted above, was dramatically enhanced by atmospheric CO₂ enrichment.

The upshot of this scenario—which seems thoroughly vindicated in light of the observations about to be described—is that the experimentally imposed increase in atmospheric CO₂ concentration actually retarded the decomposition of the older SOC of the imported soil. Also, this phenomenon effectively increased the turnover time of the original SOC, significantly increasing its stability.

“If this reduction in breakdown of older SOC is sustained,” write Cardon *et al.*, “an increased retention of carbon in older SOC pools might be expected under elevated relative to ambient CO₂.” Therefore, not only does atmospheric CO₂ enrichment lead to higher rates of carbon input to soils, it likely also leads to slower rates of carbon withdrawal from them. That allows ever-more carbon to be locked away in Earth’s soil bank as the air’s CO₂ content rises. And that phenomenon appears to keep the air’s rate of CO₂ rise from accelerating too greatly, even in the face of yearly increases in anthropogenic CO₂ emissions.

Since biological activity generally increases with rising temperatures—especially when the initial temperature is below the freezing point of water—it might be reasoned global warming would enhance

rates of soil microbial respiration, leading to increases in the soil-to-air flux of CO₂. However, as Neilsen *et al.* (2001) noted, “over-winter processes account for a significant portion (20–70%) of annual ecosystem carbon and nitrogen cycling and soil-atmosphere trace gas fluxes.” Therefore, it was not immediately apparent what the ultimate consequences of warming-induced reductions in the frequency and severity of freezing would be.

To find the answer, Neilsen *et al.* collected samples of soil from a northern hardwood-dominated forest in New Hampshire, USA. These samples, from nearly pure stands of sugar maple (*Acer saccharum* Marshall) and yellow birch (*Betula alleghaniensis* Britton), were placed in small vessels and either maintained at the normal laboratory temperature of 20–25°C or subjected to mild and severe freezes of -3 and -13°C, respectively, for ten days, after which all samples were kept at the normal laboratory temperature for 23 additional days. Neilsen *et al.* measured the evolution of CO₂ from the soils at the beginning and end of the full 33-day period, as well as at three other times during the course of the experiment.

They found freezing had a significant effect on CO₂ evolution from the soils. Cumulative 33-day totals of respiration (in units of mg carbon per kg of soil) for the soil samples taken from the maple stand were 1,497, 2,120, and 3,882 for the control and -3 and -13°C temperature treatments, respectively, which represent carbon loss enhancements (relative to the control) of 42 and 159% for the -3 and -13°C treatments, respectively, an increased carbon loss of $13 \pm 1\%$ for each degree C below freezing. For the soil samples taken from the birch stand, the corresponding respiration numbers were 1,734, 2,866, and 5,063, representing carbon loss enhancements of 65 and 192% for the -3 and -13°C treatments, respectively, or an increased carbon loss of $18 \pm 3\%$ for each degree C below freezing.

It can be readily appreciated how these research results relate to the subject of global warming effects on soil carbon sequestration. As temperatures gradually warm over the course of many years and climate zones move poleward in latitude and upward in elevation, regions that experienced many hard freezes in the past will experience fewer of them in the future, and other regions will undergo a shift from hard freezes to mild freezes. Still other regions that experienced mild freezes in the past will experience fewer—or none—in the future. And in all of these situations, together with every permutation that falls somewhere between them, there will be a tendency

for less carbon to be released to the atmosphere, which means more will remain sequestered in the soil.

The great deserts of Africa and Asia have a huge potential for sequestering carbon, because they are currently so barren their soil carbon contents have essentially nowhere to go but up. The problem with this scenario, however, is that their soils blow away with every wisp of wind that disturbs their surfaces. The ongoing rise in the air's CO₂ content could do much to reverse this trend. At higher atmospheric CO₂ concentrations, nearly all plants are more efficient at utilizing water (Morison, 1985). Hence, as the air's CO₂ content rises, the vegetation that rings Earth's deserts should be able to encroach upon them and more effectively protect their surfaces from the ravages of wind, thereby reducing soil and carbon losses due to erosion. Also, rising atmospheric CO₂ concentrations should increase the stability of surface soil crusts held together by lichens and/or algae (Tuba *et al.*, 1998; Brostoff *et al.*, 2002), which also should help to reduce the deleterious effects of wind erosion (Evans and Johansen, 1999). In addition, many of the algal components of desert soil crusts are nitrogen-fixers (Evans and Belnap, 1999), and their CO₂-enhanced presence should lead to more nitrogen being made available to other plants, which should accelerate the development of soil-protecting ecosystems even more.

The end result of all these phenomena working together is greater carbon storage, both above- and below-ground, in what was previously little more than a source of dust for the rest of the world. And therein lies one of the great unanticipated benefits of the CO₂-induced greening of the globe's deserts: less airborne dust to spread havoc across Earth.

To better understand this phenomenon, it is helpful to refer to an article in the *American Scientist* magazine titled "The Global Transport of Dust." Griffin *et al.* (2002) began their essay with a description of the magnitude of soil materials wafted about by the wind. "By some estimates," they write, "as much as two billion metric tons of dust are lifted into the Earth's atmosphere every year." Riding along on those particles are "pollutants such as herbicides and pesticides and a significant number of microorganisms—bacteria, viruses and fungi." The four scientists calculate there are easily enough bacteria thus moved about the planet each year "to form a microbial bridge between Earth and Jupiter."

And although it does not traverse interplanetary space, dust from Africa and Asia does cross both the Atlantic and Pacific Oceans. Griffin *et al.* report, for example, dust storms originating in North Africa

"routinely affect the air quality in Europe and the Middle East" and millions of tons of African sediment "fall on the North Amazon Basin of South America every year." Likewise, Prospero (2001) notes everyone in the United States living east of the Mississippi River is affected by dust of African origin. And in April 2001, Griffin *et al.* report, a large dust cloud originating over the Gobi Desert of China "moved eastward across the globe, crossing Korea, Japan, the Pacific (in five days), North America (causing sporadic reports of poor air quality in the United States), the Atlantic Ocean and then Europe."

Many of the biological entities associated with the dust particles that are thus dispersed about the planet have serious consequences for plants, animals, and humans. Airborne fungi from Africa that frequently make their way to the Americas, for example, cause sugar cane rust, coffee rust, and banana leaf spot. Griffin *et al.* also describe how the scourge of Caribbean sea fans—*Aspergillus sydowii*—"is also found in the Caribbean atmosphere during African dust events," noting the region's "sea fans and other coral reef organisms have experienced a steady decline since the late 1970s," when worsening drought in Africa predisposed increasing amounts of soil there to wind erosion (Prospero, 2001). They also state they expect "future research will show that many other coral diseases are spread by dust from both Africa and Asia."

As to human health effects, Griffin *et al.* note "African dust is reported to be a vector for the meningococcal meningitis pathogen *Neisseria meningitis* in sub-Saharan Africa," and outbreaks of the disease often followed localized or regional dust events that resulted in many fatalities. They also report a 17-fold increase in the incidence of asthma on the island of Barbados since 1973, "which corresponds to the period when the quantities of African dust in the region started to increase."

Because the dust clouds that reach the Americas from Africa and Asia have traveled such long distances, most of the larger particles they originally contained generally fall out along the way. The particles that remain, therefore, are typically very small—so small, in fact, that Griffin *et al.* report, "once they are inhaled into the lungs they cannot be exhaled." What makes this situation especially serious is the tiny dust particles typically are heavily coated with iron, and a substantial fraction of that iron is released to the lung tissue when the particles are deposited there. And iron, as Prospero notes, is "particularly efficient in producing an inflammatory response in the lungs."

In light of these observations, it is clear the slow but steady acceleration of carbon sequestration in the deserts of Africa and Asia, which is being provided by the ongoing rise in the air's CO₂ content, is producing more than just local benefits. Plants and animals far and wide, on land and in the sea, together with people everywhere, will ultimately benefit, if they are not already doing so, from the reduced airborne-dispersal of pathogens responsible for many debilitating diseases, as source-region soils become better protected against the erosive power of the wind. And if natural carbon sequestration tendencies can bring about these ancillary benefits, so too can those of man. Consequently, citizens involved in local carbon sequestration projects can take satisfaction their efforts are having a positive impact on the global environment in more ways than one. Even if rising concentrations of atmospheric CO₂ have no substantial impact on the world's climate, there are many other reasons to be involved in projects designed to enhance the productivity of the planet's managed and natural ecosystems, not the least of which is the reduction of airborne dust caused by wind-induced soil erosion.

Moving from desert to tropical isle, Dilustro *et al.* (2002) note soils store approximately three times more carbon than plants do, but almost all of that carbon is transferred to the soil through plants. They also note plant root responses to elevated CO₂ have been largely overlooked in this regard, and they thus conclude some of the carbon missing from current global carbon cycle models may be sequestered belowground. Intrigued by the possibility that enhanced carbon transfer to soils via plants responding to the aerial fertilization effect of atmospheric CO₂ enrichment may account for much of the carbon that exits the atmosphere each year, the four researchers designed an experiment to provide some potential answers to this important question.

On a small barrier island in the northern part of the Kennedy Space Center, Florida, USA, the group of scientists erected 16 open-top chambers around clumps of evergreen scrub oaks and associated saw palmetto shrubs that comprised a fire-adapted ecosystem that historically had been maintained by natural fire cycles of 10- to 15-year intervals, which had last been burned in February 1996, just prior to the start of their experiment. They maintained half of the chambers at the CO₂ concentration of the ambient air, and the other half—starting on 15 May 1996—at CO₂ concentrations approximately 350 ppm above ambient. In addition, in the soils of each of the 16 chambers, the scientists inserted two mini-rhizotron

tubes to a depth of 101 cm, through which they viewed the growth and development of the ecosystem's fine-roots at three-month intervals, from March 1996 to December 1997, via tiny video camera systems.

Dilustro *et al.* write “our hypothesis that elevated atmospheric CO₂ would increase fine-root density, productivity, mortality and turnover was demonstrated.” By the end of the 21-month study period, the fine-root length density of the re-sprouting trees and shrubs in the ambient-air chambers had attained a mean of 7.53 mm cm⁻² in the top 101 cm of soil, and the re-sprouting plants in the CO₂-enriched chambers had attained a mean of 21.36 mm cm⁻², indicating a CO₂-induced increase of 184% in this important root property. Concomitantly, there was also a 55% increase in ecosystem aboveground biomass, and all this happened, the scientists note, “despite water and nutrient limited conditions.”

Dilustro *et al.* state “the increased rates of fine root growth coupled with no change in decomposition rate suggest a potential increased rate of carbon input into the soil.” Furthermore, their detailed fine-root data for June 1997 indicate a mean CO₂-induced increase in fine-root length density of approximately 75% in the top three-fourths of the soil profile, and an increase on the order of 125% in the bottom quarter. Hence, there are strong indications the bottom layer of soil was being supplied with a greater proportion of extra carbon than were the upper soil layers.

Ritchie and McCarty (2003) write, “recent studies indicate that soil erosion and redeposition may establish an ecosystem disequilibrium that will promote carbon sequestration in the biosphere (Stallard, 1998; Harden *et al.*, 1999).” In this scenario, they continue, “soil erosion on the uplands moves soil carbon to deposition sites on the landscape and promotes soil carbon replacement at the eroded sites from the production of vegetative biomass.” Often, these deposition sites are riparian systems with high net primary productivity, which also leads to increased onsite storage of carbon. As to the validity of these concepts, Ritchie and McCarty note “the capacity of riparian and flood plain systems to capture sediments has been documented (Ritchie *et al.*, 1975; Walling *et al.*, 1999) as well as the ability of these systems to store carbon has been documented (Lal *et al.*, 1998).”

The two researchers collected and analyzed for carbon content profiles of soils obtained from an upland area and adjacent riparian system into which the upland area drained. Results indicated the riparian

system acted as a filter, removing eroded soil materials from the overland flow before they reached the stream that drained the area, so that soil carbon content was significantly greater in the riparian soils than in the upland soils. Ritchie and McCarty report carbon storage in the riparian soils was 3.8 times greater than in the upland soils in the upper 20 cm of the soil profile and 4.7 times greater in the upper 30 cm, and they report the earlier work of Ritchie and McCarty (2001) suggests “there may be as much as 10–15 times more carbon in the total profile (0–200 cm) of the riparian soils.” These results put a bright new face on what was long believed to be a phenomenon of no virtue whatsoever—precipitation-driven soil erosion. In addition, they provide a new reason for protecting Earth’s wetlands: preserving an important sink for atmospheric CO₂.

Working concurrently, Jongmans *et al.* (2003) carried out a micro-morphological study of structural development and organic matter distribution in two calcareous marine loam soils on which pear trees had been grown for the prior 45 years. The soil of one of these Dutch orchards exhibited little or no earthworm activity, and the soil of the other orchard exhibited high earthworm activity, a difference resulting from different levels of heavy metal contamination of the soils of the two orchards due to the prior use of different amounts of fungicides.

The absence of earthworms in the first orchard led to topsoil compaction, restricted litter incorporation into the mineral portion of the soil, less fragmentation of particulate organic matter, and restricted mixing of organic matter with the mineral soil’s clay fraction. Furthermore, without earthworms there were no earthworm casts, and the five researchers point out “the rate of organic matter decomposition can be decreased in worm casts compared to bulk soil aggregates,” citing Martin (1991) and Haynes and Fraser (1998).

Thus, based on their own findings and others, Jongmans *et al.* conclude “earthworms play an important role in the intimate mixing of organic residues and fine mineral soil particles and the formation of organic matter-rich micro-aggregates and can, therefore, contribute to physical protection of organic matter, thereby slowing down organic matter turnover and increasing the soil’s potential for carbon sequestration.” These points take on added significance when we consider elevated levels of atmospheric CO₂ tend to increase earthworm populations and activities, as has been demonstrated by Zaller and Arnone (1997, 1999). Thus, the ongoing rise in the air’s CO₂ content likely will help more of

the extra organic matter that is produced under CO₂-enriched conditions to remain in the soil even longer than it otherwise would remain due to the organic-matter-conserving nature of the increased activities of the increased earthworm populations shown to occur as a consequence of increases in the atmosphere’s CO₂ concentration.

Prior *et al.* (2004) speculate “enhanced aboveground crop growth under elevated CO₂, leading to more soil surface residue and greater percent ground cover (Prior *et al.*, 1997) coupled with positive shifts in crop root systems (Prior *et al.*, 2003), may have the potential to alter soil structural characteristics.” To see whether this inference was correct, and if it was, to see whether elevated atmospheric CO₂ concentrations tend to enhance or degrade soil physical properties, Prior *et al.* grew soybean (*Glycine max* (L.) Merr. cv. Stonewall) and sorghum (*Sorghum bicolor* (L.) Moench cv. Savanna 5) plants from seed to maturity for five consecutive growing seasons in open-top chambers maintained at atmospheric CO₂ concentrations of either 360 or 720 ppm. The soil in which the plants grew had been fallow for more than 25 years prior to the start of the study and was located in a huge outdoor bin, where at the end of each growing season aboveground non-yield residues (stalks, soybean pod hulls, and sorghum chaff), including 10% (by weight) of the grain yield, were allowed to remain on the surfaces of the plots to simulate no-tillage farming, after which measurements of soil properties made at the beginning of the experiment were compared with similar measurements made at its conclusion.

The elevated CO₂ had no effect on soil bulk density in the sorghum plot, but lowered it in the soybean plot by approximately 5%. The elevated CO₂ also had no effect on soil saturated hydraulic conductivity in the sorghum plot, but increased it in the soybean plot by about 42%. Soil aggregate stability was increased in both plots, but by a greater amount in the soybean plot, and total soil carbon content was increased by 16% in the sorghum plot and 29% in the soybean plot. Consequently, the soils of both plots experienced some improvements in response to the experimental doubling of the air’s CO₂ content, although there were more and greater improvements in the soybean plot than in the sorghum plot. Prior *et al.* conclude their findings indicate a significant “potential for improvements in soil carbon storage, water infiltration and soil water retention, and reduced erosion,” valuable positive consequences they describe as “CO₂-induced benefits.”

Krull *et al.* (2005) report “colonization of grasslands or savannas by trees over the last 50–100 years, often described as ‘thickening,’ has received attention due to the large potential for carbon sequestration in woody biomass.” It was a hot topic because many studies have attributed thickening to “the increase in atmospheric CO₂, causing CO₂ fertilization and resulting in increased water use efficiency in C₃ plants,” as discussed by Berry and Roderick (2002) and Grunzweig *et al.* (2003). In addition, they write, “much of the change in atmospheric CO₂ occurred over the last 50 years [1953–2003 = 64 ppm] with the most significant changes being in the last 20 years [1983–2003 = 33 ppm].”

Working at a site some 40 km northwest of Longreach, Queensland, Australia, Krull *et al.* measured vertical profiles of $\delta^{13}\text{C}$ and ^{14}C of bulk and size-separated soil organic matter to infer the time course of changes in these parameters along a transect spanning the dynamic transition zone between C₄-dominated grassland and C₃-dominated woodland, an ecotone that comprised different-age specimens of leguminous gidgee trees (*Acacia cambagei*) interspersed with occasional whitewood trees (*Atalaya hemiglauc*). Then, since the longtime landholder reported thickening by the *Acacia* trees occurred “at least since the 1950s,” they tested whether the observed changes in soil carbon stocks could be reproduced by the Roth-Carbon turnover model over a 50-year time period.

The eight researchers conclude “much of the vegetation change at this site occurred over the last 50 years.” In addition, they found approximately twice as much total organic carbon in the soil beneath the fully established woodland as in the soil beneath the pristine grassland. They conclude their findings “stress the importance of viewing soils as dynamic systems and indicating the potential for soil organic carbon sequestration in grazed semi-arid woodlands.” Such land use represents a form of agroforestry, the virtues of which were touted by Mutuo *et al.* (2005).

Also, the findings of Krull *et al.* suggest the operation of an important negative feedback that can slow the rate-of-rise of the air’s CO₂ content. The ongoing enrichment of the air with CO₂ from the burning of fossil fuels enables woody species to colonize less-productive grasslands more readily and thereby extract greater amounts of CO₂ from the atmosphere, meanwhile providing many benefits to the soil in which the trees are rooted.

Parenthetically, it is important to note papers published in journals such as *Science* and *Nature*

typically attract much attention, especially when they deal with high-profile subjects such as global warming, which some have described as a threat worse than nuclear warfare or global terrorism. When a study describes a phenomenon that could exacerbate that threat, it behooves its authors and the editors of the journal in which it is published to be especially careful in the way they describe what was found and what its implications may be.

A case in point is the report of Heath *et al.* (2005), who studied soil sequestration of root-derived carbon from seedlings of six European tree species and found it to decline in response to atmospheric CO₂ enrichment. This finding led them to write, “should similar processes operate in forest ecosystems, the size of the annual terrestrial carbon sink may be substantially reduced, resulting in a positive feedback on the rate of increase in atmospheric carbon dioxide concentration.” This outcome was parroted by the journal’s editors, who state the new findings “raise the possibility that the future rise in atmospheric CO₂ concentrations could be higher than expected.”

How reasonable are these speculations? To answer this question, it is important to know how closely—or not—the experimental setting of Heath *et al.*’s study reproduced real-world forests or orchards. Was their study a FACE experiment, such as that conducted in the Duke University Forest, where multiple 30m-diameter plots of initially 13-year-old loblolly pine trees had been exposed continuously to ambient and elevated concentrations of atmospheric CO₂ each growing season since August 1996? Or was it an out-of-doors open-top chamber study, such as the Phoenix, Arizona sour orange tree experiment, where trees were grown from the sapling stage to mature adults for 17 years of continuous CO₂ enrichment? It was in fact neither of these.

The Heath *et al.* experiment was only a 15-month study conducted in small greenhouses, where seedlings were grown in vertical sections of 16cm-diameter polyethylene tubes supplied with only 10 liters of soil, and their results are not consistent with more comprehensive experiments such as the Duke University FACE experiment. To their credit, Heath *et al.* readily acknowledge the many deficiencies of their study. They state, for example, “young trees, grown in mesocosms in a semi-controlled environment and protected from major herbivores, may respond differently from mature trees growing in a natural forest.” They also note their experiment “ran for only two growing seasons” and “the input of leaf

litter to the soil was excluded.” With respect to these latter two points, they also state “the possibility that longer term increased inputs of leaf litter under elevated CO₂ could counteract the effect on the sequestration of root-derived carbon cannot be ruled out.” And they admit, “although soil microbial respiration increased under elevated CO₂, the effect of this on the decomposition of native soil carbon is not known.”

That these deficiencies likely precluded the discovery of the truth sought by Heath *et al.* in their experiment is revealed by their acknowledgment, “in contrast to our experiment, CO₂ enrichment caused an increase in soil carbon sequestration beneath *Betula* seedlings over the course of one growing season (Ineson *et al.*, 1996),” and “free-air CO₂ enrichment (FACE) also caused an increase in the sequestration of new carbon in C₄ soil cores transplanted into former agricultural ground beneath 2- to 3-year-old *Populus* saplings (Hoosbeek *et al.*, 2004).” Consequently, and after reviewing the results of still other pertinent experiments, they ultimately conclude “there is insufficient evidence to predict with certainty whether plant responses to elevated CO₂ will result in increased or decreased sequestration of new carbon in the soils of forest ecosystems.”

In light of these observations, which were made in Heath *et al.*’s own paper and which suggest there is no compelling reason to conclude their results bear any resemblance to what will actually occur in the real world as the air’s CO₂ content climbs, one wonders why their paper was accepted for publication in so prestigious a journal as *Science*. It seems all too likely it was not for scientific reasons at all but more likely for the support the paper could be seen as providing for the political views of the journal’s editor, who strongly supported Kyoto-type regulations of anthropogenic CO₂ emissions.

In a contemporary study suffering from some of the same problems as Heath *et al.*, Bellamy *et al.* (2005) measured soil carbon contents at 2,179 locations across England and Wales between 1994 and 2003, adjacent to points where similar measurements had been made between 1978 and 1983, after which rates of change of soil carbon content were calculated for the quarter-century period 1978–2003. They report “carbon was lost from soils across England and Wales over the survey period at a mean rate of 0.6% yr⁻¹,” which they attribute to “climate change,” noting over the period of study “the mean temperature across England and Wales increased by about 0.5°C.”

Bellamy *et al.* thus conclude, “losses of soil

carbon in the UK, and by inference in other temperate regions, are likely to have been offsetting absorption by terrestrial sinks.” Associated Press writer Michael McDonough begins his review of the study (7 September 2005) by stating, “rising temperatures resulting from climate change are likely causing soil in England and Wales to lose large amounts of carbon, possibly further contributing to the greenhouse gas effect.” These conclusions are not as well supported as they were portrayed to be.

Bellamy *et al.* resampled only 38.5% of the original sites sampled between 1978 and 1983, so the vast majority of England and Wales, much less “other temperate regions” of the globe, was not assessed for changes in soil organic carbon (SOC) content. In addition, the five researchers claim “the relationship between rate of carbon loss and carbon content is irrespective of land use,” which was key to their being able to claim “a link to climate change.” However, in an accompanying article that raised several other concerns, Schulze and Freibauer (2005) write, in “re-inspecting the results, we think that the land-use factor has played a role—for example, only alteration in land use and gradual changes in land management can explain why croplands lost more carbon than other areas.” They also note studies conducted in China, Finland, and Flanders “attribute most of the SOC loss to changes in land use and management.” Even Bellamy *et al.* admit “various changes in land use will have contributed to carbon losses from soils across England and Wales over the survey period, both under agricultural uses (drainage schemes, post-war grassland conversion, increased stocking rates) and non-agricultural uses (afforestation on wet soils, increased erosion, increased burning of upland vegetation).” However, they state they did “not have sufficient data at the scale of the National Soil Inventory to explore these effects,” so they really did *not* know the role played by land use, which meant they really did not know the role played by climate change.

Schulze and Freibauer also note the SOC losses observed by Bellamy *et al.* “occurred independently of soil properties, challenging our knowledge about SOC stability,” as this observation was at odds with what had been learned about the subject over the years. They also point out the carbon losses were proportional to SOC concentration, which implies “a first-order decay of a homogeneous pool” which “contradicts the view that SOC in carbon-rich soils contains a higher fraction of stable carbon than does that in carbon-poor soils.”

Finally, Schulze and Freibauer note SOC contents

may have changed in deeper soil layers than the top 15 cm layer measured by Bellamy *et al.*, possibly in compensating ways, and they are firm in their opinion “increased temperature alone seems to be too weak a driver” to have caused the observed changes in SOC. Thus, Bellamy *et al.* merely scratched the surface of the controversial topic in a way that failed to reveal the truth.

Callesen *et al.* (2003) measured SOC contents of forest floors and mineral soils to a depth of 100 cm in 234 well-drained Danish, Finnish, Norwegian, and Swedish forests between latitudes 55° and 68°N and longitudes 6° and 28°E. They then performed a number of analyses with the data, the first of which they say revealed “soil organic carbon in forest floors and mineral soil + forest floors was positively correlated with temperature and precipitation in the study region.” They also report “a similar increase in SOC with temperature and precipitation was found in nine pine stands on sandy soils in the same latitude range but between 22° and 29°E (Vucetich *et al.*, 2000) representing the same temperature gradient but a lower precipitation range.” And they affirm the positive correlation with temperature was greatest for coarse-textured soils, less for medium-textured soils, and negligible for fine-textured soils.

The Nordic scientists write, “the increase in SOC with temperature and precipitation is interpreted as an indirect effect of higher net primary production,” further noting in Europe “increasing site productivity has been reported in both nemoral forests and in boreal forests at higher latitudes (Eriksson and Karlsson, 1996; Skovsgaard and Henriksen, 1996; Cannell *et al.*, 1998),” and this increase “could be attributed to increased atmospheric CO₂ concentrations along with the fertilizer effect of nitrogen deposition, and management regimes optimizing forest production.” These broad-based findings suggest just the opposite of what Bellamy *et al.* had claimed to be occurring in the top 15 cm of soils in England and Wales had actually been happening in the top 100 cm of soils throughout much of Europe, producing a negative feedback to both rising air temperatures and atmospheric CO₂ concentrations.

Lichter *et al.* (2005) reviewed what had been learned to that point in time about the effects of an atmospheric CO₂ enrichment of 200 ppm on the soil carbon dynamics of the Duke Forest (an aggrading loblolly pine stand near Chapel Hill, North Carolina, USA) during the first six years of the long-term FACE experiment being conducted there. Over this period, they report, organic C accumulated in the forest floor of the elevated CO₂ plots at a rate 52 ± 16

$\text{g C m}^{-2} \text{ yr}^{-1}$ greater than what would have been expected during reforestation under ambient CO₂ conditions, as represented by the rate of C accumulation in the forest floor of the ambient CO₂ plots.

This additional C sink, in their words, “resulted from increased C inputs of $50 \pm 30 \text{ g C m}^{-2} \text{ yr}^{-1}$ to the forest floor in response to CO₂ enhancement of primary production.” And since there was “no evidence that the overall rate of decomposition of the forest floor decreased under the elevated CO₂ treatment,” they conclude “the additional C sink in the forest floor of the elevated CO₂ treatment ... is wholly dependent on the net primary production enhancement and increased C inputs,” which after six years had increased the forest floor’s organic C content by approximately 27%, as best as could be determined from their plotted data. The data gave no indication this trend will decline anytime soon.

With respect to the underlying mineral soil, Lichter *et al.* report they detected no statistically significant treatment effects on the C content of the bulk mineral soil or the intra-aggregate particulate organic matter and mineral-associated organic matter fractions after six years of CO₂ enrichment. Nevertheless, there was a nearly statistically significant ($P = 0.11$) increase of 18.5% in the free light fraction of the organic matter in the top 15 cm of the soil profile, and a 3.9% increase in the total intra-aggregate particulate organic matter there. The sum of the organic C in these two categories plus the mineral-associated organic C was 11.5% greater in the CO₂-enriched plots than in the ambient treatment plots.

Although Lichter *et al.* expressed pessimism and a belief “forest soils are unlikely to sequester significant additional quantities of atmospheric C associated with CO₂ fertilization because of the low rates of C input to refractory and protected soil organic matter pools,” the CO₂-enriched trees of their study continued to demonstrate a large and unabated growth advantage over the ambient-CO₂ trees, and both the forest floor and the surface soil horizon beneath the CO₂-enriched trees continued to accumulate more organic C than the forest floor and surface soil horizon beneath the ambient-CO₂ trees. And, therefore, the un-stimulated refractory and protected soil organic matter pools of which Lichter *et al.* write could yet begin to show increased carbon accumulation.

In addition to the naturally occurring phenomena that tend to mute the rate of rise of the anthropogenic-driven increase in the atmosphere’s CO₂ con-

centration, there are others that owe their existence to human ingenuity. Prior *et al.* (2005) describe a multifaceted field management system developed to help farmers conserve resources and increase crop yields while simultaneously stimulating carbon sequestration in their fields.

Unlike a conventional cropping system, this conservation system employed little to no tillage and used special crop rotations. In the southern United States, where Prior *et al.* had been testing the two approaches for the prior five years, the conventional cropping system consisted of a rotation cycle where grain sorghum and soybean were rotated each year with spring tillage after winter fallow that produced only a light growth of weeds. In the conservation cropping system, grain sorghum and soybean were also rotated, but in the place of weeds were three cover crops: crimson clover, sunn hemp, and wheat, which were similarly rotated but without tillage.

To see how the two management systems compared in terms of crop production and soil carbon sequestration, and how well they might fare in the high-CO₂ world expected to prevail a half-century or so from now, the five U.S. Department of Agriculture scientists employed the systems for four years (two complete cropping cycles) in 7-meter-wide x 76-meter-long x 2-meter-deep bins filled with a silt loam soil, upon which they constructed a number of clear-plastic-wall open-top chambers they maintained at atmospheric CO₂ concentrations that averaged either 375 ppm (ambient) or 683 ppm (enriched) over the four years of their study.

In terms of the cumulative residue produced over the two cropping cycles, the scientists found little interaction between management practices and atmospheric CO₂ concentration, with conservation practices increasing this parameter by about 90% in both CO₂ treatments, elevated CO₂ increasing it by approximately 30% in both of the management treatments, and conservation practices and elevated CO₂ together increasing it by 150%. In terms of the carbon retained and incorporated into the first 5 cm of the soil at the end of the two cropping cycles, however, there were significant interactions. The elevated CO₂ increased this important soil property by about 10% in the conventional system, but by 45% in the conservation system, and the application of conservation practices increased 0–5 cm soil carbon storage by close to 45% in ambient-CO₂ air but by nearly 90% in elevated-CO₂ air. Together, the two treatments increased surface soil carbon storage by close to 110%.

Clearly, increasing atmospheric CO₂ concentra-

tions and best-management conservation practices work hand-in-hand to boost crop yields and residue production while increasing soil carbon storage, with each factor bringing out the best in the other. In addition, as Prior *et al.* note, “in an elevated CO₂ environment there will be larger amounts of crop residue and consequently more ground cover,” so “accumulation of additional surface litter may improve water infiltration (and storage) and help ameliorate water quality problems by reducing runoff and soil erosion.”

Jastrow *et al.* (2005) write many field-scale CO₂-enrichment studies “have failed to detect significant changes in soil C against the relatively large, spatially heterogeneous pool of existing soil organic matter, leading to the general conclusion that the potential for increased soil C is limited (Hungate *et al.*, 1997; Gill *et al.*, 2002; Hagedorn *et al.*, 2003; Lichter *et al.*, 2005).” And an additional long-held opinion, as they relate it, is, “if CO₂-stimulated increases in soil organic C do occur, they will be allocated to rapidly cycling, labile pools with little, if any, long-term stabilization,” citing Hungate *et al.* (1997) and Lichter *et al.* (2005). By the time of Jastrow *et al.*’s writing, however, after many long and arduous experiments had been conducted and their data properly analyzed, the truth was beginning to be seen to be quite different.

The long-awaited confirmation of the more optimistic view of the subject was firmly established by Jastrow *et al.* (2005). They describe and further analyze the findings of the first five years of the deciduous forest FACE study being conducted at Oak Ridge, Tennessee (Norby *et al.*, 2001); the entire eight years of the prairie grassland open-top chamber study at Manhattan, Kansas (Owensby *et al.*, 1993); and 35 other similar studies.

They found atmospheric CO₂ enrichment to approximately 200 ppm above ambient “increased C stocks in the forest soil at an average rate of 44 ± 9 g C m⁻² yr⁻¹,” and “in the prairie, the incremental increase in C stocks corresponded to an average accrual rate of 59 ± 19 g C m⁻² yr⁻¹.” This happened because “both systems responded to CO₂ enrichment with large increases in root production,” and “even though native C stocks were relatively large, over half of the accrued C at both sites was incorporated into micro-aggregates, which protect C and increase its longevity.” Likewise, their meta-analysis of the 35 independent experimental observations indicated CO₂ enrichment ranging from 200 to 350 ppm over periods ranging from two to nine years increased soil C over soil depths ranging from 5 to 20 cm by 5.6%

(95% CI = 2.8–8.4%), “supporting the generality of the accrual measured in the forest and prairie experiments.”

The seven scientists say their findings “clearly demonstrate that mineral soil C, including micro-aggregate protected pools, can increase measurably in response to a step-function increase in atmospheric CO₂ concentrations,” and “the C storage capacities of mineral soils—even those with large organic matter stocks—are not necessarily saturated at present and may be capable of serving as C sinks if inputs increase as a result of passive CO₂ fertilization.” In addition, they write “the meta-analysis, which included some multifactor studies and data collected over a wide range of climatic conditions, suggests that soil C accrual ... is likely to be a general response to CO₂ enrichment.”

This response, Jastrow *et al.* state, “is not insignificant.” They note, “if mineral soil C in the surface 20 cm of the world’s temperate forests, temperate grasslands, shrublands, and croplands (234 Pg C ... according to Jobbagy and Jackson, 2000) were to increase by 5.6% or at a rate of 19 g C m⁻² yr⁻¹, then 8–13 Pg of C might be accumulated within a 10-year period.” That suggests the amount of carbon found in the soils of these biomes could be doubled over a period of 180 years (234 Pg C divided by 1.3 Pg C per year = 180 years).

These several observations demonstrate the soil-carbon-sequestering capability of Earth’s vegetation can indeed act as a significant brake on the rate of rise of the air’s CO₂ content and thereby help mute any CO₂-induced impetus for global warming.

At the Sky Oaks CO₂ enrichment site of San Diego State University in California, located in chaparral vegetation dominated by chemise (*Adenostoma fasciculatum*) shrubs, researchers constructed 12 2-m by 2-m by 2-m closed chambers so as to contain a central individual *Adenostoma* shrub and its surrounding herbaceous plants. Beginning in December 1995, they maintained the chambers continuously at six atmospheric CO₂ concentrations ranging from 250 to 750 ppm in 100-ppm increments. At various times throughout 1999, they took measurements of net ecosystem exchange of CO₂ and collected soil samples for analyses of arbuscular mycorrhizal (AM) fungi and sequestered carbon found in both bulk soil and water-stable aggregates.

Treseder *et al.* (2003) report “plants and soils within the chambers took up more carbon under CO₂ enrichment.” Specifically, the chambers exposed to 250 to 550 ppm CO₂ released an average of 703 g C

m⁻² year⁻¹, and the chambers in the 650–750-ppm treatments absorbed an average of 160 g C m⁻² year⁻¹. Likely driven by these dramatic CO₂-induced differences in net ecosystem exchange of CO₂, it was not surprising, as they describe it, “pools of total carbon in bulk soil and in water-stable aggregates increased 1.5- and three-fold, respectively, between the 250- and 650-ppm treatments.” In addition, they found “the abundance of live AM hyphae and spores rose markedly over the same range of CO₂.” Thus Treseder *et al.* conclude the augmentation of the carbon pools found in their study, “if common in other ecosystems, appears substantial enough to influence sequestration of CO₂ originating from fossil fuel burning and deforestation.”

In another study from the same location utilizing the identical experimental chambers, Allen *et al.* (2005) assessed the various ways carbon entered the soil and was sequestered there. They found the “total allocation of carbon to soil increased significantly through the study period with elevated CO₂,” as did “new carbon inputs into macro-aggregates.” This latter observation is very important, as these aggregates, in their words, “have increasing concentrations of glomalin, a glycoprotein produced by arbuscular mycorrhizal fungi (Rillig *et al.*, 1999),” a substance that acts to create and stabilize soil aggregates and protect the carbon they contain. In addition, the scientists report CO₂ effects on soil bacteria “were not detectable.” They report microbial mass was “negatively affected by increasing CO₂,” noting, “under extended nitrogen limitation the plants ultimately garner the nitrogen,” and the plants “ultimately outcompete microbes for these scarce soil resources,” citing Hu *et al.* (2001).

In concluding the discussion of their findings, Allen *et al.* remark, “undisturbed arid shrublands may not fix comparatively large amounts of carbon, but they may sequester a large fraction of that carbon.” Noting “carbon allocated to arbuscular mycorrhizal fungi forms a large part of the macro-aggregate structure in the form of glomalin (Rillig *et al.*, 2002),” and those aggregates “may be protected from decomposition,” they conclude the enhanced formation of such aggregates in CO₂-enriched air forms “an important [carbon] sequestration pathway” in chaparral ecosystems.

Working in the Mojave Desert at the FACE facility located near Mercury, Nevada, USA, where various shrubs and perennial grasses grow, Billings and Schaeffer (2004) examined the effects of atmospheric CO₂ enrichment (to 550 ppm throughout each growing season since April 1997) on soil

nitrogen (N) dynamics via measurements of foliage C and N contents and isotope composition, and by measuring resin-available N and rates of soil respiration in the field in conjunction with assessments of potential C evolution and net N mineralization derived from long-term soil incubations. Their findings showed the “effects of elevated CO₂ on soil C and N dynamics are variable and complex, with many competing processes,” and “changes in soil microbial activity with elevated CO₂ ... could affect both mineralizing and immobilizing microbial processes.” Nevertheless, the bulk of their observations suggest “elevated CO₂ may increase root and/or soil microbial activity,” which more often than not “can result in periodic increases in resin-available N, particularly when soil moisture is available.” They say these several interrelated phenomena “may translate into more plant available N at these times.” The two researchers thus conclude “if increases in plant-available N are maintained, particularly when soil moisture is available, arid ecosystems may be able to sustain any increases in productivity induced by elevated CO₂.”

In studying the potential for the long-term storage of carbon in Earth's soils, Lagomarsino *et al.* (2006) note an increase of labile carbon below ground, such as is typically provided by atmospheric CO₂ enrichment, “could induce two mechanisms acting in opposite ways: (1) an enhanced soil organic matter decomposition due to the stimulation of microbial activity through the so-called *priming effect* (Kuzakov *et al.*, 2000); and (2) a retarded mineralization of native soil organic carbon due to the preference of microbes for easily decomposable substrates (Cardon *et al.*, 2001).”

In a study designed to determine which mechanism is likely the stronger of the two, Lagomarsino *et al.* conducted physical and chemical analyses of soils they sampled in June and October 2004 at the POPFACE experimental plantation in central Italy, where clones of *Populus alba*, *Populus nigra*, and *Populus x euramericana* had been grown since 1999 with nitrogen fertilization throughout the 2002–2004 growing seasons. Hoosbeek *et al.* (2004) observed a priming effect of the newly incorporated litter in the first rotation cycle of trees exposed to air containing an approximate 50% increase in atmospheric CO₂ concentration, but in the second rotation cycle Hoosbeek *et al.* (2006) observed an accumulation of carbon in the soil of that treatment. In harmony with this latter observation, Lagomarsino *et al.*'s 2004 data reveal no increase in carbon mineralization activity under elevated CO₂, but rather

a decrease of microbial basal respiration in the non-rhizospheric soil of the CO₂-enriched treatment. And noting “microbial carbon immobilization was the dominant process under elevated CO₂, limiting the carbon losses from soil,” Lagomarsino *et al.* conclude their results suggest “a possible positive trend for carbon storage on the long term, independent of soil nitrogen availability.”

Cheng *et al.* (2007) conducted a two-year FACE study of sorghum (*Sorghum bicolor* (L.) Moench) near Phoenix, Arizona (USA), where they studied the dynamics of soil organic carbon (SOC) pools comprised of labile and recalcitrant SOC of short and long mean residence time (MRT), respectively, under control conditions (360 ppm CO₂) and FACE conditions (560 ppm CO₂), together with water-adequate (wet) and water-deficient (dry) treatments. They note it is difficult to measure changes in total SOC content over periods of only a few years because soils typically contain large amounts of carbon compared to what they sequester annually. Their study proved no exception to this rule, as no significant differences in total SOC could be detected between the control and FACE treatments over the two years of the sorghum experiment.

Nevertheless, they learned much by other means, such as stable-carbon isotopic ($\delta^{13}\text{C}$) tracing, which revealed 53% of the final SOC in the FACE plot was in the recalcitrant or long MRT carbon pool and 47% in the labile or short MRT pool, whereas in the control plot 46% and 54% of the final SOC was in the recalcitrant and labile pools, respectively. This indicates “elevated CO₂ transferred more SOC into the slow-decay carbon pool,” the ten researchers write. In addition, they report “isotopic mixing models revealed that increased new sorghum residue input to the recalcitrant pool mainly accounts for this change, especially for the upper soil horizon (0–30 cm) where new carbon in recalcitrant soil pools of FACE wet and dry treatments was 1.7 and 2.8 times as large as that in respective Control recalcitrant pools.” In addition, Cheng *et al.* state “old C in the recalcitrant pool under elevated CO₂ was higher than that under ambient CO₂, indicating that elevated CO₂ reduces the decay of the old C in [the] recalcitrant pool.”

Therefore, because “higher recalcitrant C content and lower labile C content in the soils were detected under elevated CO₂ relative to ambient CO₂ treatments, suggesting that SOC under elevated CO₂ becomes more stable against chemical and biological degradation,” the ten scientists say their results imply terrestrial agro-ecosystems may play a critical role in

sequestering CO₂ under future atmospheric conditions.

Bockheim (2007) explains “cryoturbation is a dominant process in permafrost regions and refers collectively to all soil movements due to frost action,” and reports several prior studies suggested cryoturbation “was particularly active during mid-Holocene warming periods in the arctic.” Bockheim thus studied the effect sustained warming will have on redistribution of soil organic carbon, and whether this redistribution will exacerbate or mitigate the release of CO₂ to the atmosphere. The study focused on the amount of soil organic carbon (SOC) incorporated via cryoturbation into the active layer and near-surface permafrost of 21 sites in northern Alaska, 10 of which were located in the Arctic Coastal Plain and 11 of which were in the Arctic Foothills. Based on data acquired from the 21 sites, the University of Wisconsin researcher determined “55% of the SOC density of the active layer and near-surface permafrost could be attributed to redistribution from cryoturbation,” listing “five lines of evidence suggesting that increased cryoturbation from arctic warming will result in increased storage of SOC.”

First, Bockheim states “once cryoturbation has moved SOC to the cold, deeper soil layers, little or no biological decomposition will take place.” Second, “major organic horizons that are cryoturbated ... are 10 to 50% more dense than the equivalent uncryoturbated horizons,” and “low-density SOC may be more susceptible to decomposition than high-density SOC.” Third, “low-molecular-weight neutrally charged organic compounds are more biodegradable than high-molecular fractions.” Fourth, “Kaiser *et al.* (2007) reported lower decomposition rates of redistributed SOC in Siberian subsoils than in equivalent material collected from the surface.” And fifth, “mechanistic models (Waelbroeck *et al.*, 1997) predict that sustained arctic warming will result in permafrost thawing and a delayed long-lasting increase in SOC storage.”

Bockheim concludes, “these results suggest that continued warming of the arctic may accelerate cryoturbation,” and “this, in turn, will increase the incorporation of dense, high-molecular-weight SOC at depth, thereby enabling the soil to store more SOC than at present and reducing the loss of CO₂ to the atmosphere from soil respiration”—essentially just the opposite of what IPCC contends.

Pendall and King (2007) conducted a series of long-term (170–330 days) laboratory incubation experiments to examine changes in soil organic

matter pool sizes and turnover rates in soil collected from an open-top chamber (OTC) atmospheric CO₂ enrichment study in the shortgrass steppe of northeastern Colorado, USA, where the air in the ambient CO₂ chambers (ACs) and elevated CO₂ chambers (ECs) had atmospheric CO₂ concentrations of 360 and 720 ppm, respectively, and where this degree of CO₂ enrichment enhanced both above- and below-ground plant growth by 15–35%. They also discovered “active pool carbon increased in EC relative to AC treatments systematically over the first 3 years of exposure to elevated CO₂ in topsoils and to a lesser degree in subsoils,” and they remark, “these results are consistent with independent results from the same OTC study showing that rhizo-deposition rates doubled and root production increased under elevated CO₂.” In addition, they report “new carbon turnover was not enhanced by elevated CO₂,” confirming “new carbon inputs under elevated CO₂ are not simply lost to mineralization” and “pool sizes may continue to increase under elevated CO₂.” The two researchers conclude, “these results suggest that soil carbon storage may increase in semi-arid grasslands under elevated CO₂,” and they opine this phenomenon, in turn, would tend to mitigate the global warming thought by many to accompany increases in the air’s CO₂ content.

Marhan *et al.* (2008) studied undisturbed soil cores with and without visible wheat residues extracted at the conclusion of the third year of a mini-FACE experiment conducted in a field near Hohenheim, Germany planted annually to spring wheat (*Triticum aestivum* L.). The researchers examined the effect of elevated atmospheric CO₂ concentration (an extra 160 ppm) on the decomposition of the wheat residues present in the soil by measuring CO₂ evolution from the cores, as well as the leaching of inorganic and organic carbon from them, during 191 days of core incubations in the laboratory. They found cumulative residue decomposition was not affected by elevated CO₂ when no wheat residues were visible in the cores. When such residues were visible, however, decomposition was “significantly lower” (by 19%) in the elevated compared to the ambient CO₂ treatment, which for the more common 300 ppm degree of atmospheric CO₂ enrichment roughly translates to a decomposition reduction of 36%. In addition, they report more dissolved inorganic carbon (DIC) was leached from the elevated CO₂ treatment cores, both with and without visible plant residues, than from similar cores from the ambient CO₂ treatment (47.2% and 29.5%, respectively, for their degree of CO₂ enrichment,

which equates to about 88% and 55%, respectively, for a 300 ppm increase in atmospheric CO₂ concentration). These extra amounts of DIC represent “an additional possible mechanism for carbon sequestration in soils of arable cropping systems under future elevated CO₂ concentrations,” they note. They also report stubble and root biomass was higher by 12.0 and 9.44%, respectively, in soil cores taken from the elevated CO₂ plots at the end of the study, which equates to approximate stubble and root biomass enhancements of 22% and 18%, respectively, for a 300 ppm increase in atmospheric CO₂ concentration. With respect to the potential for enhanced carbon sequestration in wheat (and other cereal-crop) fields in a CO₂-enriched world of the future, therefore, the six scientists conclude, “increased input of plant residues and reduced decomposition of plant-derived carbon” are “possible mechanisms for enhanced carbon sequestration under elevated atmospheric CO₂ concentration.”

Hopkins *et al.* (2009) write there were “two sets of long-term experimental plots which have been under constant and known management for over a century and for which historical data exist that allow comparison over recent decades to determine what, if any, changes in SOC have occurred.” These unique plots were the Palace Leas Meadow Hay Plots in northeast England, established in 1897, and the plots of the Park Grass Continuous Hay Experiment established in 1856 at Rothamsted in southeast England. In studying them, Hopkins *et al.* say they determined “there were no significant differences between 1982 and 2006 for the Palace Leas plots or between 1959 and 2002 for the Park Grass plots,” leading them to conclude, “there has been no consistent decrease in SOC stocks in surface soils under old, permanent grassland in England in recent decades, even though meteorological records for both sites indicate significant warming of the soil and air between 1980 and 2000.” They theorize “the lack of a consistent decline in SOC content linked to increased soil temperature since 1980 may be due to a compensatory increase in primary production,” citing Jenkinson *et al.* (1991).

Martens *et al.* (2009) write, “the generally higher above and belowground productivity of C₃ plants under elevated CO₂ leads to the conclusion that more rhizo-depositions (roots and exudates) are transferred into soils, potentially increasing soil carbon content,” but they note most FACE and outdoor chamber studies have failed to detect significant changes in soil organic carbon (SOC) due to the typically large amount and spatially heterogeneous nature of

preexisting SOC. In an attempt to overcome these difficulties, Martens *et al.* cultivated well-watered and well-fertilized spring wheat (cv. Minaret) in stainless steel cylinders forced into the soil of control and free-air CO₂-enriched (to 180 ppm above ambient) plots at the experimental farm of the Federal Research Institute in Braunschweig, Germany, where between stem elongation and beginning of ripening the plants were repeatedly pulse-labeled with ¹⁴CO₂ and thereafter monitored daily for soil-borne total CO₂ and ¹⁴CO₂ until harvest, after which the distribution of ¹⁴C was analyzed in all plant parts, soil, soil mineral fractions, and soil microbial biomass.

The four researchers found “in comparison to ambient conditions, 28% more ¹⁴CO₂ and 12% more total CO₂ was evolved from soil under elevated CO₂,” and “in the root-free soil 27% more residual ¹⁴C was found in the free-air CO₂-enriched soil than in the soil from the ambient treatment.” In addition, they say, in soil samples from both treatments about 80% of residual ¹⁴C was “integrated into the stable, clay bound soil organic matter pool,” which suggests, “under FACE conditions a considerable contribution was made to the long-term storage of soil carbon in this soil.” Thus Martens *et al.* were able to “show for the first time,” as they describe it, “that a crop plant grown under FACE conditions deposited significantly more carbon to soil than those grown under ambient CO₂ in the field,” and “the additional carbon input under elevated CO₂ did not induce an accelerated degradation of pre-existing soil organic matter (no positive priming effect).” Those findings demonstrate “wheat plants grown under elevated CO₂ can contribute to an additional net carbon gain in soils,” which is especially beneficial to the biosphere.

Springsteen *et al.* (2010) write “woody plant expansion within grassland ecosystems is a worldwide phenomenon, and dramatic vegetation shifts from grassland to savanna/woodlands have occurred over the past 50–100 years in North America,” noting one of the chief factors contributing to this phenomenon is believed to be the concomitant historical increase in the air’s carbon dioxide concentration, as suggested by Archer *et al.* (1995), Polley (1997), Bond and Midgley (2000), and Bond *et al.* (2003). They also state once shrublands are established, they tend to persist for a number of possible reasons, one of which is a type of feedback phenomenon referred to as *islands of fertility*, which “occurs when resources accumulate in soils beneath woody plants due to litterfall, interception of wet and dry deposition, nitrogen fixation, and animal droppings,” as described by Schlesinger *et al.* (1990),

Archer *et al.* (1995), Reynolds *et al.* (1999), and Lopez-Pintor *et al.* (2006). They report, “changes in soil attributes under woody vegetation have been documented in the arid grasslands of the southern Great Plains, including increases in soil carbon and nitrogen,” citing Reynolds *et al.* (1999), Hibbard *et al.* (2001, 2003), McCulley *et al.* (2004), Schade and Hobbie (2005), and Liao *et al.* (2006).

In their work at the USDA-ARS Northern Great Plains Research Laboratory near Mandan, North Dakota (USA), Springsteen *et al.* examined near-surface (upper 15 cm) soil biogeochemistry along a 42-year (1963–2005) chrono-sequence, which encompassed grassland, woodland, and grassland-woodland transition zones in a northern Great Plains grassland, to determine the influence of woody plant expansion on soil carbon and nitrogen contents. The four researchers report total soil carbon content rose by 26% across the chrono-sequence from grassland to woodland within the 0–15 cm soil depth, and total soil nitrogen content rose by 31%. In addition, they report, the rate of woody shrub expansion from 1963 to 1988 (25 years) was ~1,800 m² per year at their study site, and from 1988 to 2005 (17 years) it was ~3,800 m² per year, or just a little more than doubled.

Yang *et al.* (2010) write, “soil stores more than twice as much carbon than does vegetation or the atmosphere,” citing Schlesinger (1997), and they note many people believe “climate warming is likely to accelerate the decomposition of soil organic carbon which could lead to increased carbon release from soils, providing a positive feedback to climate change (Davidson and Janssens, 2006).” To test that belief, Yang *et al.* “conducted five consecutive regional soil surveys in China’s grasslands during 2001–2005 and sampled 981 soil profiles from 327 sites across the northern part of the country,” comparing their results “with data of 275 soil profiles derived from China’s National Soil Inventory during the 1980s.” The seven scientists report the organic carbon stock in the upper 30 cm of soil in northern China’s grasslands “did not show significant association with mean annual temperature,” and “grassland soil organic carbon stock did not change significantly over the past two decades.”

Yang *et al.* conclude, “it has been often asserted that soil will act as a carbon source because of its sensitivity to global environmental change (e.g., Melillo *et al.*, 2002; Bellamy *et al.*, 2005; Schipper *et al.*, 2007),” but “in contrast to these previous reports, our results indicate that soil organic carbon stock in northern China’s grasslands has not experienced significant changes during the past two decades,

despite measureable climate change.”

Iversen *et al.* (2012) explored the fate of carbon (C) and nitrogen (N) in the soil of a sweetgum tree (*Liquidambar styraciflua* L.) plantation in Oak Ridge, Tennessee (USA) at the conclusion of a nearly 12-year FACE study. The four researchers report net primary productivity increased in response to atmospheric CO₂ enrichment “even though production in the sweetgum stand was limited by soil N availability.” In addition, they write, “the majority of the additional C fixed under elevated CO₂ was allocated belowground to the production of fine roots,” with the largest increases in root biomass production and mortality being “at relatively deep soil depths (i.e., below 30 cm),” with the end result “soil C and N contents were greater throughout the soil profile under elevated CO₂ at the conclusion of the experiment.” With respect to carbon, for example, “soil C content was ~19% greater throughout the soil profile after more than 11 years of CO₂ enrichment.”

Iversen *et al.* conclude, “the greater residence time of C in deeper soil indicates that inputs from deep roots under elevated CO₂ may increase the potential for long-term storage of C and N in forested ecosystems.” They add, “this finding suggests greater C accrual in elevated CO₂ compared with ambient CO₂ during the experiment, consistent with the conclusion of a meta-analysis that indicated increased ecosystem C storage under elevated CO₂ (Luo *et al.*, 2006).” These observations presage “the potential of future forests to store C and mitigate some portion of rising atmospheric CO₂,” as they state in the concluding sentence of their report.

Zhou *et al.* (2013) took advantage of a long-term field experiment with increased temperature and precipitation, established in late April 2005 in a semiarid temperate steppe in Duolun County, Inner Mongolia, China, “to investigate the effects of warming, increased precipitation and their interactions on SOC [soil organic carbon] fraction” by quantifying “labile SOC, recalcitrant SOC and stable SOC at 0–10 and 10–20 cm depths.” They found “neither warming nor increased precipitation affected total SOC and stable SOC at either depth,” but “increased precipitation significantly increased labile SOC at the 0–10 cm depth” and “warming decreased labile SOC and marginally but significantly increased recalcitrant SOC at the 10–20 cm depth.” They also found “significant interactive effects of warming and increased precipitation on labile SOC and recalcitrant SOC at the 0–10 cm depths.”

Zhou *et al.* conclude, “given that the absolute increase of SOC in the recalcitrant SOC pool was

much greater than the decrease in labile SOC, and that the mean residence time of recalcitrant SOC is much greater, our results suggest that soil C storage at 10–20 cm depth may increase with increasing temperature in this semiarid grassland,” which represents a net negative feedback on predicted global warming and a tremendous benefit for the terrestrial biosphere.

References

- Allen, M.F., Klironomos, J.N., Treseder, K.K., and Oechel, W.C. 2005. Responses of soil biota to elevated CO₂ in a chaparral ecosystem. *Ecological Applications* **15**: 1701–1711.
- Andrews, J.A. and Schlesinger, W.H. 2001. Soil CO₂ dynamics, acidification, and chemical weathering in a temperate forest with experimental CO₂ enrichment. *Global Biogeochemical Cycles* **15**: 149–162.
- Archer, S., Schimel, D.S., and Holland, E.A. 1995. Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change* **29**: 91–99.
- Bellamy, P.H., Loveland, P.J., Bradley, R.I., Lark, R.M., and Kirk, G.J.D. 2005. Carbon losses from all soils across England and Wales 1978–2003. *Nature* **437**: 245–248.
- Billings, S.A. and Schaeffer, S.M. 2004. Soil microbial activity and N availability with elevated CO₂ in Mojave Desert soils. *Global Biogeochemical Cycles* **18**: 10.1029/2003GB002137.
- Bockheim, J.G. 2007. Importance of cryoturbation in redistributing organic carbon in permafrost-affected soils. *Soil Science Society of America Journal* **71**: 1335–1342.
- Bond, W.J. and Midgley, G.F. 2000. A proposed CO₂-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* **6**: 865–869.
- Bond, W.J., Midgley, G.F., and Woodward, F.I. 2003. The importance of low atmospheric CO₂ and fire in promoting the spread of grasslands and savannas. *Global Change Biology* **9**: 973–982.
- Brostoff, W.N., Sharifi, M.R., and Rundel, P.W. 2002. Photosynthesis of cryptobiotic crusts in a seasonally inundated system of pans and dunes at Edwards Air Force Base, western Mojave Desert, California: laboratory studies. *Flora* **197**: 143–151.
- Callesen, I., Liski, J., Raulund-Rasmussen, K., Olsson, M.T., Tau-Strand, L., Vesterdal, L., and Westman, C.J. 2003. Soil carbon stores in Nordic well-drained forest soils—relationships with climate and texture class. *Global Change Biology* **9**: 358–370.
- Cannell, M.G.R., Thornley, J.H.M., Mobbs, D.C., and Friend, A.D. 1998. UK conifer forests may be growing faster in response to increased N deposition, atmospheric CO₂ and temperature. *Forestry* **71**: 277–296.
- Cardon, Z.G., Hungate, B.A., Cambardella, C.A., Chapin III, F.S., Field, C.B., Holland, E.A., and Mooney, H.A. 2001. Contrasting effects of elevated CO₂ on old and new soil carbon pools. *Soil Biology & Biochemistry* **33**: 365–373.
- Casella, E. and Soussana, J.-F. 1997. Long-term effects of CO₂ enrichment and temperature increase on the carbon balance of a temperate grass sward. *Journal of Experimental Botany* **48**: 1309–1321.
- Cheng, L., Leavitt, S.W., Kimball, B.A., Pinter Jr., P.J., Ottman, M.J., Matthias, A., Wall, G.W., Brooks, T., Williams, D.G., and Thompson, T.L. 2007. Dynamics of labile and recalcitrant soil carbon pools in a sorghum free-air CO₂ enrichment (FACE) agroecosystem. *Soil Biology & Biochemistry* **39**: 2250–2263.
- Cotrufo, M.F. and Gorissen, A. 1997. Elevated CO₂ enhances below-ground C allocation in three perennial grass species at different levels of N availability. *New Phytologist* **137**: 421–431.
- Davidson, E.A. and Janssens, I.A. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **440**: 165–173.
- De Angelis, P., Chigwerewe, K.S., and Mugnozza, G.E.S. 2000. Litter quality and decomposition in a CO₂-enriched Mediterranean forest ecosystem. *Plant and Soil* **224**: 31–41.
- Dilustro, J.J., Day, F.P., Drake, B.G., and Hinkle, C.R. 2002. Abundance, production and mortality of fine roots under elevated atmospheric CO₂ in an oak-scrub ecosystem. *Environmental and Experimental Botany* **48**: 149–159.
- Eriksson, H. and Karlsson, K. 1996. Long-term changes in site index in growth and yield experiments with Norway Spruce (*Picea abies* L.) (Karst) and Scots Pine (*Pinus sylvestris*) in Sweden. *European Forest Institute Research Report* **5**: 79–87.
- Evans, R.D. and Belnap, J. 1999. Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. *Ecology* **80**: 150–160.
- Evans, R.D. and Johansen, J.R. 1999. Microbiotic crusts and ecosystem processes. *Critical Reviews in Plant Sciences* **18**: 183–225.
- Fitter, A.H., Self, G.K., Brown, T.K., Bogie, D.S., Graves, J.D., Benham, D., and Ineson, P. 1999. Root production and turnover in an upland grassland subjected to artificial soil warming respond to radiation flux and nutrients, not temperature. *Oecologia* **120**: 575–581.

Climate Change Reconsidered II: Biological Impacts

- Gill, R.A. and Burke, I.C. 1999. Ecosystem consequences of plant life form changes at three sites in the semiarid United States. *Oecologia* **121**: 551–563.
- Gill, R.A., Polley, H.W., Johnson, H.B., Anderson, L.J., Maherali, H., and Jackson, R.B. 2002. Nonlinear grassland responses to past and future atmospheric CO₂. *Nature* **417**: 279–282.
- Griffin, D.W., Kellogg, C.A., Garrison, V.H., and Shinn, E.A. 2002. The global transport of dust. *American Scientist* **90**: 228–235.
- Hagedorn, F., Spinnler, D., Bundt, M., Blaser, P., and Siegwolf, R. The input and fate of new C in two forest soils under elevated CO₂. *Global Change Biology* **9**: 862–872.
- Harden, J.W., Sharpe, J.M., Parton, W.P., Ojima, D.S., Fries, T.L., Huntington, T.G., and Dabney, S.M. 1999. Dynamic replacement and loss of soil carbon on eroding cropland. *Global Biogeochemical Cycles* **14**: 855–901.
- Haynes, R.J. and Fraser, P.M. 1998. A comparison of aggregate stability and biological activity in earthworm casts and uningested soil as affected by amendment with wheat and lucerne straw. *European Journal of Soil Science* **49**: 629–636.
- Heath, J., Ayres, E., Possell, M., Bardgett, R.D., Black, H.I.J., Grant, H., Ineson, P., and Kerstiens, G. 2005. Rising atmospheric CO₂ reduces sequestration of root-derived soil carbon. *Science* **309**: 1711–1713.
- Henning, F.P., Wood, C.W., Rogers, H.H., Runion, G.B., and Prior, S.A. 1996. Composition and decomposition of soybean and sorghum tissues grown under elevated atmospheric carbon dioxide. *Journal of Environmental Quality* **25**: 822–827.
- Hibbard, K.A., Archer, S., Schimel, D.S., and Valentine, D.W. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* **82**: 1999–2011.
- Hibbard, K.A., Schimel, D.S., Archer, S., Ojima, D.S., and Parton, W. 2003. Grassland to woodland transitions: integrating changes in landscape structure and biogeochemistry. *Ecological Applications* **13**: 911–926.
- Hoosbeek, M.R., Li, Y., and Scarascia-Mugnozza, G. 2006. Free atmospheric CO₂ enrichment (FACE) increased labile and total carbon in the mineral soil of a short rotation Poplar plantation. *Plant and Soil* **281**: 247–254.
- Hoosbeek, M.R., Lukac, M., van Dam, D., Godbold, D.L., Velthorst, E.J., Biondi, F.A., Peressotti, A., Cotrufo, M.F., de Angelis, P., and Scarascia-Mugnozza, G. 2004. More new carbon in the mineral soil of a poplar plantation under Free Air Carbon Enrichment (POPFACE): Cause of increased priming effect? *Global Biogeochemical Cycles* **18**: GB1040.
- Hopkins, D.W., Waite, I.S., McNicol, J.W., Poulton, P.R., Macdonald, A.J., and O'Donnell, A.G. 2009. Soil organic carbon contents in long-term experimental grassland plots in the UK (Palace Leas and Park Grass) have *not* changed consistently in recent decades. *Global Change Biology* **15**: 1739–1754.
- Hu, S., Chapin III, F.S., Firestone, M.K., Field, C.B., and Chiariello, N.R. 2001. Nitrogen limitation of microbial decomposition in a grassland under elevated CO₂. *Nature* **409**: 188–191.
- Hungate, B.A., Holland E.A., Jackson, R.B., Chapin III, F.S., Mooney, H.A., and Field, C.B. 1997. The fate of carbon in grasslands under carbon dioxide enrichment. *Nature* **388**: 576–579.
- Ineson, P., Cotrufo, M.F., Bol, R., Harkness, D.D., and Blum, H. 1996. Quantification of soil carbon inputs under elevated CO₂: C₃ plants in a C₄ soil. *Plant and Soil* **187**: 345.
- Insam, H., Baath, E., Berreck, M., Frostegard, A., Gerzabek, M.H., Kraft, A., Schinner, F., Schweiger, P., and Tschuggnall, G. 1999. Responses of the soil microbiota to elevated CO₂ in an artificial tropical ecosystem. *Journal of Microbiological Methods* **36**: 45–54.
- Islam, K.R., Mulchi, C.L. and Ali, A.A. 1999. Tropospheric carbon dioxide or ozone enrichments and moisture effects on soil organic carbon quality. *Journal of Environmental Quality* **28**: 1629–1636.
- Jastrow, J.D., Miller, R.M., Matamala, R., Norby, R.J., Boutton, T.W., Rice, C.W., and Owensby, C.E. 2005. Elevated atmospheric carbon dioxide increases soil carbon. *Global Change Biology* **11**: 2057–2064.
- Jenkinson, D.S., Adams, D.E., and Wild, A. 1991. Model estimates of CO₂ emissions from soil in response to global warming. *Nature* **351**: 304–306.
- Jobbagy, E.G. and Jackson, R.B. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* **10**: 423–436.
- Johnson, L.C., Shaver, G.R., Cades, D.H., Rastetter, E., Nadelhoffer, K., Giblin, A., Laundre, J., and Stanley, A. 2000. Plant carbon-nutrient interactions control CO₂ exchange in Alaskan wet sedge tundra ecosystems. *Ecology* **81**: 453–469.
- Jongmans, A.G., Pulleman, M.M., Balabane, M., van Oort, F., and Marinissen, J.C.Y. 2003. Soil structure and characteristics of organic matter in two orchards differing in earthworm activity. *Applied Soil Ecology* **24**: 219–232.
- Kaiser, C., Meyer, H., Biasi, C., Rusalimova, O., Barsukov, P., and Richter, A. 2007. Conservation of soil organic matter through cryoturbation of arctic soils in Siberia.

Journal of Geophysical Research **112**: 10.1029/2006JG000258.

King, J.S., Pregitzer, K.S., Zak, D.R., Sober, J., Isebrands, J.G., Dickson, R.E., Hendrey, G.R., and Karnosky, D.F. 2001. Fine-root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO₂ and tropospheric O₃. *Oecologia* **128**: 237–250.

Krull, E.S., Skjemstad, J.O., Burrows, W.H., Bray, S.G., Wynn, J.G., Bol, R., Spouncer, L., and Harms, B. 2005. Recent vegetation changes in central Queensland, Australia: Evidence from $\delta^{13}\text{C}$ and ^{14}C analyses of soil organic matter. *Geoderma* **126**: 241–259.

Kuzyakov, Y., Friedel, J.K., and Stahr, K. 2000. Review of mechanisms and quantification of priming effects. *Soil Biology and Biochemistry* **32**: 1485–1498.

Lagomarsino, A., Moscatelli, M.C., De Angelis, P., and Grego, S. 2006. Labile substrates quality as the main driving force of microbial mineralization activity in a poplar plantation soil under elevated CO₂ and nitrogen fertilization. *Science of the Total Environment* **372**: 256–265.

Lal, R., Kimble, J.M., Follett, R.F., and Cole, C.V. 1998. *The Potential of US Cropland to Sequester Carbon and Mitigate the Greenhouse Effect*. Ann Arbor Press, Chelsea, Michigan, USA.

Leavitt, S.W., Paul, E.A., Kimball, B.A., Hendrey, G.R., Mauney, J.R., Rauschkolb, R., Rogers, H., Lewin, K.F., Nagy, J., Pinter Jr., P.J., and Johnson, H.B. 1994. Carbon isotope dynamics of free-air CO₂-enriched cotton and soils. *Agricultural and Forest Meteorology* **70**: 87–101.

Liao, J.D., Boutton, T.W., and Jastrow, J.D. 2006. Storage and dynamics of carbon and nitrogen in soil physical fractions following woody plant invasion of grassland. *Soil Biology and Biochemistry* **38**: 3184–3196.

Lichter, J., Barron, S.H., Bevacqua, C.E., Finzi, A.C., Irving, K.F., Stemmler, E.A., and Schlesinger, W.H. 2005. Soil carbon sequestration and turnover in a pine forest after six years of atmospheric CO₂ enrichment. *Ecology* **86**: 1835–1847.

Liski, J., Ilvesniemi, H., Makela, A., and Westman, C.J. 1999. CO₂ emissions from soil in response to climatic warming are overestimated—The decomposition of old soil organic matter is tolerant of temperature. *Ambio* **28**: 171–174.

Lopez-Pintor, A., Sal, A.G., and Benayas, J.M. R. 2006. Shrubs as a source of spatial heterogeneity—the case of *Retama sphaerocarpa* in Mediterranean pastures of central Spain. *Acta Oecologia* **29**: 247–255.

Marhan, S., Demin, D., Erbs, M., Kuzyakov, Y.,

Fangmeier, A., and Kandeler, E. 2008. Soil organic matter mineralization and residue decomposition of spring wheat grown under elevated CO₂ atmosphere. *Agriculture, Ecosystems and Environment* **123**: 63–68.

Martens, R., Heiduk, K., Pacholski, A., and Weigel, H.-J. 2009. Repeated $^{14}\text{CO}_2$ pulse-labeling reveals an additional net gain of soil carbon during growth of spring wheat under free air carbon dioxide enrichment (FACE). *Soil Biology & Biochemistry* **41**: 2422–2429.

Martin, A. 1991. Short- and long-term effects of the endogenic earthworm *Millsonia anomala* (Omodeo) (Megascolecidae, Oligochaeta) of tropical savannas on soil organic matter. *Biology and Fertility of Soils* **11**: 234–238.

McCulley, R.L., Archer, S.R., Boutton, T.W., Hons, F.M., and Zuberer, D.A. 2004. Soil respiration and nutrient cycling in wooded communities developing in grassland. *Ecology* **85**: 2804–2817.

Melillo, J.M., Steudler, P.A., Aber, J.D., Newkirk, K., Lux, H., Bowles, F.P., Catricala, C., Magill, A., Ahrens, T., and Morrisseau, S. 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* **298**: 2173–2176.

Morison, J.I.L. 1985. Sensitivity of stomata and water use efficiency to high CO₂. *Plant, Cell and Environment* **8**: 467–474.

Mutuo, P.K., Cadisch, G., Albrecht, A., Palm, C.A., and Verchot, L. 2005. Potential of agroforestry for carbon sequestration and mitigation of greenhouse gas emissions from soils in the tropics. *Nutrient Cycling in Agroecosystems* **71**: 45–54.

Neilsen, C.B., Groffman, P.M., Hamburg, S.P., Driscoll, C.T., Fahey, T.J., and Hardy, J.P. 2001. Freezing effects on carbon and nitrogen cycling in northern hardwood forest soils. *Soil Science Society of America Journal* **65**: 1723–1730.

Nitschelm, J.J., Lüscher, A., Hartwig, U.A., and van Kessel, C. 1997. Using stable isotopes to determine soil carbon input differences under ambient and elevated atmospheric CO₂ conditions. *Global Change Biology* **3**: 411–416.

Norby, R.J., Todd, D.E., Fults, J., and Johnson, D.W. 2001. Allometric determination of tree growth in a CO₂-enriched sweetgum stand. *New Phytologist* **150**: 477–487.

Owensby, C.E., Coyne, P.I., Ham, J.M., Auen, L.M., and Knapp, A.K. 1993. Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO₂. *Ecological Applications* **3**: 644–653.

Pendall, E. and King, J.Y. 2007. Soil organic matter dynamics in grassland soils under elevated CO₂: Insights from long-term incubations and stable isotopes. *Soil Biology & Biochemistry* **39**: 2628–2639.

Climate Change Reconsidered II: Biological Impacts

- Polley, H.W. 1997. Implications of rising atmospheric carbon dioxide concentration for rangelands. *Journal of Range Management* **50**: 561–577.
- Pregitzer, K.S., Zak, D.R., Maziasz, J., DeForest, J., Curtis, P.S., and Lussenhop, J. 2000. Interactive effects of atmospheric CO₂ and soil-N availability on fine roots of *Populus tremuloides*. *Ecological Applications* **10**: 18–33.
- Prior, S.A., Rogers, H.H., Runion, G.B., Torbert, H.A., and Reicosky, D.C. 1997. Carbon dioxide-enriched agroecosystems: Influence of tillage on short-term soil carbon dioxide efflux. *Journal of Environmental Quality* **26**: 244–252.
- Prior, S.A., Runion, G.B., Rogers, H.H., Torbert, H.A., and Reeves, D.W. 2005. Elevated atmospheric CO₂ effects on biomass production and soil carbon in conventional and conservation cropping systems. *Global Change Biology* **11**: 657–665.
- Prior, S.A., Runion, G.B., Torbert, H.A., and Rogers, H.H. 2004. Elevated atmospheric CO₂ in agroecosystems: Soil physical properties. *Soil Science* **169**: 434–439.
- Prior, S.A., Torbert, H.A., Runion, G.B., and Rogers, H.H. 2003. Implications of elevated CO₂-induced changes in agroecosystem productivity. *Journal of Crop Production* **8**: 217–244.
- Pritchard, S.G., Rogers, H.H., Davis, M.A., Van Santen, E., Prior, S.A., and Schlesinger, W.H. 2001. The influence of elevated atmospheric CO₂ on fine root dynamics in an intact temperate forest. *Global Change Biology* **7**: 829–837.
- Prospero, J.M. 2001. African dust in America. *Geotimes* **46** (11): 24–27.
- Reynolds, J.F., Virginia, R.A., Kemp, P.R., de Soyza, A.G., and Tremmel, D.C. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monographs* **69**: 69–106.
- Rillig, M.C., Treseder, K.K., and Allen, M.F. 2002. Global change and mycorrhizal fungi. In: van der Heijden, M.G.A. and Sanders, I.R. (Eds.) *Mycorrhizal Ecology*. Springer-Verlag, New York, NY, USA, pp. 135–160.
- Rillig, M.C., Wright, S.F., Allen, M.F., and Field, C.B. 1999. Rise in carbon dioxide changes soil structure. *Nature* **400**: 628.
- Ritchie, J.C., Hawks, P.H., and McHenry, J.R. 1975. Deposition rates in valleys determined using fallout Cs-137. *Geological Society of America Bulletin* **86**: 1128–1130.
- Ritchie, J.C. and McCarty, G.W. 2001. Sediment deposition rates and carbon content in the soils of an agricultural riparian ecosystem. *Proceedings of the Seventh Federal Interagency Sedimentation Conference* **2**: IX41–IX46.
- Ritchie, J.C. and McCarty, G.W. 2003. ¹³⁷Cesium and soil carbon in a small agricultural watershed. *Soil & Tillage Research* **69**: 45–51.
- Rosenzweig, C. and Hillel, D. 2000. Soils and global climate change: Challenges and opportunities. *Soil Science* **165**: 47–56.
- Ross, D.J., Tate, K.R., Newton, P.C.D., Wilde, R.H., and Clark, H. 2000. Carbon and nitrogen pools and mineralization in a grassland gley soil under elevated carbon dioxide at a natural CO₂ spring. *Global Change Biology* **6**: 779–790.
- Rouhier, H. and Read, D. 1999. Plant and fungal responses to elevated atmospheric CO₂ in mycorrhizal seedlings of *Betula pendula*. *Environmental and Experimental Botany* **42**: 231–241.
- Schade, J.D. and Hobbie, S.E. 2005. Spatial and temporal variation in islands of fertility in the Sonoran Desert. *Biogeochemistry* **73**: 541–553.
- Schipper, L.A., Baisden, T., Parfitt, R.L., Ross, C., and Claydon, J.J. 2007. Large losses of soil C and N from soil profiles under pasture in New Zealand during the past 20 years. *Global Change Biology* **13**: 1138–1144.
- Schlesinger, W.H. (Ed.) 1997. *Biogeochemistry: An Analysis of Global Change*. Academic Press, San Diego, California, USA.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Ross, V.A., and Whitford, W.G. 1990. Biological feedbacks in global desertification. *Science* **247**: 1043–1048.
- Schulze, E.D. and Freibauer, A. 2005. Carbon unlocked from soils. *Nature* **437**: 205–206.
- Skovsgaard, J.P. and Henriksen, H.A. 1996. Increasing site productivity during consecutive generations of naturally regenerated and planted beech (*Fagus sylvatica* L.) in Denmark. *European Forest Institute Research Report* **5**: 91–97.
- Springsteen, A., Loya, W., Liebig, M., and Hendrickson, J. 2010. Soil carbon and nitrogen across a chronosequence of woody plant expansion in North Dakota. *Plant and Soil* **328**: 369–379.
- Stallard, R.F. 1998. Terrestrial sedimentation and the carbon cycle: coupling weathering and erosion to carbon burial. *Global Biogeochemical Cycles* **12**: 231–257.
- Treseder, K.K., Egerton-Warburton, L.M., Allen, M.F., Cheng, Y., and Oechel, W.C. 2003. Alteration of soil carbon pools and communities of mycorrhizal fungi in chaparral exposed to elevated carbon dioxide. *Ecosystems* **6**: 786–796.
- Tuba, Z., Csintalan, Z., Szente, K., Nagy, Z., and Grace,

J. 1998. Carbon gains by desiccation-tolerant plants at elevated CO₂. *Functional Ecology* **12**: 39–44.

van Ginkel, J.H. and Gorissen, A. 1998. In situ decomposition of grass roots as affected by elevated atmospheric carbon dioxide. *Soil Science Society of America Journal* **62**: 951–958.

van Ginkel, J.H., Whitmore, A.P., and Gorissen, A. 1999. *Lolium perenne* grasslands may function as a sink for atmospheric carbon dioxide. *Journal of Environmental Quality* **28**: 1580–1584.

Verburg, P.S.J., Gorissen, A., and Arp, W.J. 1998. Carbon allocation and decomposition of root-derived organic matter in a plant-soil system of *Calluna vulgaris* as affected by elevated CO₂. *Soil Biology and Biochemistry* **30**: 1251–1258.

Vucetich, J.A., Reed, D.D., Breymeyer, A., Degorski, M., Mroz, G.D., Solon, J., Roo-Zielinska, E., and Noble, R. 2000. Carbon pools and ecosystem properties along a latitudinal gradient in northern Scots pine (*Pinus sylvestris*) forest. *Forest Ecology and Management* **136**: 135–145.

Waelbroeck, C.P., Monfray, W.C., Oechel, W.C., Hastings, S., and Vourlius, G. 1997. The impact of permafrost thawing on the carbon dynamics of tundra. *Geophysical Research Letters* **24**: 229–232.

Walling, D.E., Owens, P.N., and Leeks, G.J.L. 1999. Rates of contemporary overbank sedimentation and sediment storage on the floodplains of the main channel systems of the Yorkshire Ouse and River Tweed, UK. *Hydrological Processes* **13**: 993–1009.

Yang, Y., Fang, J., Ma, W., Smith, P., Mohammat, A., Wang, S., and Wang, W. 2010. Soil carbon stock and its changes in northern China's grasslands from 1980s to 2000s. *Global Change Biology* **16**: 3036–3047.

Zaller, J.G. and Arnone III, J.A. 1997. Activity of surface-casting earthworms in a calcareous grassland under elevated atmospheric CO₂. *Oecologia* **111**: 249–254.

Zaller, J.G. and Arnone III, J.A. 1999. Interactions between plant species and earthworm casts in a calcareous grassland under elevated CO₂. *Ecology* **80**: 873–881.

Zhou, X., Chen, C., Wang, Y., Smaill, S., and Clinton, P. 2013. Warming rather than increased precipitation increases soil recalcitrant organic carbon in a semiarid grassland after 6 years of treatments. *PLOS ONE* **8**: e53761.

1.2.5.3 Erosion

- The historical increase in the atmosphere's CO₂ concentration has significantly reduced the erosion

of Earth's valuable topsoil over the past several decades, and the continuing increase in atmospheric CO₂ can maintain this trend, and perhaps even accelerate it, throughout the foreseeable future.

More than two decades ago, Idso (1989) predicted, “as a result of the direct effects of atmospheric CO₂ enrichment upon the primary plant processes of photosynthesis and transpiration ... many plants will greatly expand their ranges with augmented water use efficiencies, stabilizing the soil and protecting it from erosion.” Prior to that time (and continuing well past it), study after study had concluded (and continued to conclude) soil erosion by both wind and water was running at a high sustained rate. In an article published in *Science*, Trimble and Crosson (2000) wrote, “some sources have suggested that recent erosion is as great as or greater than that of the 1930s.”

Remarkably, this long-held belief in continued high or even increasing soil erosion “was based mostly on models,” write Trimble and Crosson. Enlarging on this thesis, the two researchers report little physical field-based evidence other than anecdotal statements has been offered to verify the high soil erosion estimates. They note, “it is questionable whether there has ever been another perceived public problem for which so much time, effort, and money were spent in light of so little scientific evidence.” The good news, according to Trimble and Crosson, is “available field evidence suggests declines of soil erosion, some very precipitous, during the past six decades.”

The problem was largely a failure to realize most of the soil particles removed from one part of the land, by either wind or water, were later deposited in nearby areas, so the net loss of soil was only a very small portion of the total that was moved about by the forces of nature.

Over the course of the data-driven shift in the public's perception of U.S. soil erosion, it has become evident perceptions of several ancillary phenomena also need adjusting. Trimble and Crosson note, for example, certain studies once warned “increasingly eroded soil profiles will allow less rainfall to be infiltrated and stored,” leading to “increased overland flow, erosion, and flooding.” However, they note, detailed hydrologic studies indicate just the opposite was occurring: “runoff is decreasing, flood peaks are smaller, and in some places, the base flow is greater.” In addition, they write, “these field studies show that more water is infiltrating into the soil and, in some

cases ... significantly more water is being transpired by plants.”

These real-world observations follow what would be expected on the basis of Idso’s 1989 prediction. With gradually increasing atmospheric CO₂ concentrations gradually enhancing plant water use efficiencies, more plants should have gradually been spreading over the surface of the land, reducing rates of surface runoff and allowing more water to infiltrate the soil, thereby providing more water to be extracted from the soil by more plants for subsequent transpiration. These hydrologic improvements, in turn, should have improved the status of still other aspects of the planet’s natural resource base, for example by increasing the stability of streams.

A pair of photographs in the Trimble and Crosson article provided a visual testament to the reality of this phenomenon. Both photos showed the same view of a portion of Bohemian Creek in La Crosse County, Wisconsin, USA. The first of the pictures, taken in 1940, showed an “eroded, shallow channel composed of gravel and cobbles, with coarse sediment deposited by overflows on the floodplain.” The second, taken 34 years later in 1974, indicates the stream channel was “narrower, smaller, and more stable.” In addition, Trimble and Crosson note, “the coarse sediment has been covered with fine material, and the flood plain is vegetated to the edge of the stream.” And conditions improved even more over the following quarter-century, they observe.

In addition to this broad introduction to the issue of soil erosion, a number of scientific studies have focused on other specific effects of rising temperatures and atmospheric CO₂ concentrations on soil erosion.

Allen *et al.* (1999) analyzed sediment cores extracted from a lake in southern Italy and from the Mediterranean Sea, deriving a high-resolution climate and vegetation dataset for this region that covered the last 102,000 years. Rapid changes in vegetation were found to be correlated with rapid changes in climate, such that complete shifts in natural ecosystems sometimes occurred over periods of less than 200 years. Throughout the warmest portion of this record—the current interglacial or Holocene—the total organic carbon content of the vegetation reached its highest level, more than doubling values experienced over the rest of the record. Other proxy indicators revealed the increased vegetative cover typically was associated with less soil erosion during the more productive woody plant period of the Holocene.

Rillig *et al.* (2000) examined several charac-

teristics of beneficial arbuscular mycorrhizal fungi (AMF) associated with the roots of plants growing for at least 20 years along a natural CO₂ gradient near a CO₂-emitting spring in New Zealand. Enriching the air’s CO₂ concentration from 370 to 670 ppm increased percent root colonization by AMF in a linear fashion—and by nearly fourfold. Similarly, fungal hyphal length experienced a more-than-threefold linear increase along the same CO₂ gradient, and total soil glomalin (a protein secreted by fungal hyphae that increases soil aggregation and stability) experienced a linear increase of approximately fivefold. Consequently, as the air’s CO₂ concentration rises, the positive responses of AMF identified in this study likely will become increasingly pronounced, significantly reducing soil losses via wind and water erosion by way of CO₂-induced glomalin-mediated increases in soil aggregate stability, which should benefit terrestrial ecosystems throughout the world.

In a closely allied free-air CO₂-enrichment (FACE) study of adequately fertilized sorghum, where daylight atmospheric CO₂ concentration was increased by approximately 50%, Rillig *et al.* (2001) studied plants grown under both well-watered and water-stressed irrigation treatments, focusing on the effects of elevated CO₂ on the hyphal growth of AMF, two fractions of glomalin, and the production of water-stable soil aggregates. They found the 50% increase in the air’s CO₂ concentration dramatically increased fungal hyphae lengths—by about 120% in the wet irrigation treatment and 240% in the dry treatment. The biological effects of the extra CO₂ in the air also increased the mass of water-stable soil aggregates—by 40% in the wet treatment and 20% in the dry treatment. In addition, the researchers write, the “two fractions of glomalin and AMF hyphal lengths were all positively correlated with soil aggregate water stability.” Hence they say their study “demonstrated for the first time that elevated CO₂ can affect soil aggregation in an agricultural system,” where “a soil stabilizing effect of CO₂ would be clearly advantageous.”

Knox (2001) determined how the conversion of the United States’ Upper Mississippi River Valley from prairie and forest to crop and pasture land by settlers in the early 1800s influenced subsequent watershed runoff and soil erosion rates. They found conversion of the region’s natural landscape to agricultural uses boosted surface erosion rates to values three to eight times greater than those characteristic of pre-settlement times. In addition, the land-use conversion increased peak discharges from high-frequency floods by 200 to 400%. Since the late

1930s, however, surface runoff has been decreasing; but this decrease was “not associated with climatic causes,” Knox writes, as “an analysis of temporal variation in storm magnitudes for the same period showed no statistically significant trend.”

It is important to note the decreases in soil erosion rates and extreme streamflow conditions that began in the late 1930s in the Upper Mississippi River Valley were the exact opposite of predictions, which suggest these phenomena should have been increasing as a result of unprecedented CO₂-induced global warming. However, they likely were not related to climate factors, Knox argues, instead attributing them to the introduction of soil conservation measures such as contour plowing, strip-cropping, terracing, and minimum tillage, to which list could be added the concomitant rise in atmospheric CO₂ concentration and its impacts on the various beneficial phenomena discussed in this subsection.

Olafsdottir and Gudmundsson (2002) studied spatial and temporal patterns of land degradation in northeastern Iceland over the past 7,500 years based on data from excavations of 67 soil profiles, comparing their results with climatic variations known to have occurred over the same period. These activities revealed, in their words, “the deterioration in vegetation and soil cover noted coincides with the recorded deterioration in climate.” During every major cold period of their record, land degradation was classified as “severe.” During every major warm period, however, this condition was reversed, and soils were built up as vegetation cover expanded.

The primary implication of these findings, according to the two researchers, is “climate has a significant role in altering land cover *per se* and may trigger land degradation without the additional influence of men.” Thus they conclude, “in Iceland severe land degradation could commence without anthropogenic influence—simply as a result of the cold periods.”

In a FACE study conducted on the North Island of New Zealand, Newton *et al.* (2003) measured the water repellency of a grassland soil—which contained about 20 species of legumes, C₃ grasses, C₄ grasses, and forbs, and was grazed periodically by adult sheep—after five years of exposure to an extra 100 ppm of CO₂. They found a significant reduction in the water repellency of the soil in the elevated CO₂ treatment. The researchers note, “at field moisture content the repellence of the ambient soil was severe and significantly greater than that of the elevated [CO₂] soil.”

Newton *et al.* say water repellency “is a soil

property that prevents free water from entering the pores of dry soil (Tillman *et al.*, 1989),” and they report it “has become recognized as a widespread problem, occurring under a range of vegetation and soil types (agricultural, forestry and amenity; sand, loam, clay, peat and volcanic) (Bachmann *et al.*, 2001) and over a large geographical range (Europe, USA, Asia, Oceania) (Bauters *et al.*, 1998).” Specifically, they note water-repellency-induced problems for land managers include “increased losses of pesticides and fertilizers, reduced effectiveness of irrigation, increased rates of erosion, and increased runoff,” and there are water-repellency-induced problems “in the establishment and growth of crops (Bond, 1972; Crabtree and Gilkes, 1999) and implications for the dynamics of natural ecosystems, particularly those subject to fire (DeBano, 2000).” The CO₂-induced reduction of soil water repellency discovered in this study portends a wide range of very important benefits for both agro- and natural ecosystems as the air’s CO₂ content rises in the future.

Prior *et al.* (2004) note “enhanced aboveground crop growth under elevated CO₂, leading to more soil surface residue and greater percent ground cover (Prior *et al.*, 1997), coupled with positive shifts in crop root systems (Prior *et al.*, 2003), may have the potential to alter soil structural characteristics.” They decided to see whether this inference was indeed true, and if true, whether elevated atmospheric CO₂ concentrations tend to enhance or degrade soil physical properties.

The researchers grew plots of soybean and sorghum plants from seed to maturity for five consecutive growing seasons in open-top chambers maintained at atmospheric CO₂ concentrations of either 360 or 720 ppm. The soil in which the plants grew had been fallow for more than 25 years prior to the start of the study and was located in a huge outdoor bin. There, at the end of each growing season, the researchers allowed aboveground non-yield residues (stalks, soybean pod hulls, and sorghum chaff), including 10% of the grain yield, to remain on the surfaces of the plots to simulate no-tillage farming. Measurements of various soil properties made at the beginning of the experiment were compared with similar measurements conducted at its conclusion.

They found elevated CO₂ had no effect on soil bulk density in the sorghum plot, but lowered it in the soybean plot by approximately 5%. Elevated CO₂ also had no effect on soil saturated hydraulic conductivity in the sorghum plot, but increased it in the soybean plot by about 42%. Soil aggregate stability was

increased in both plots, but by a greater amount in the soybean plot, and total soil carbon content was increased by 16% in the sorghum plot and 29% in the soybean plot. Consequently, the soils of both plots experienced some improvements in response to the experimental doubling of the atmosphere's CO₂ concentration, although there were more and greater improvements in the soybean plot than in the sorghum plot. Prior *et al.* conclude their results "indicate potential for improvements in soil carbon storage, water infiltration and soil water retention, and reduced erosion," which are positive consequences they described as "CO₂-induced benefits."

Zhang and Liu (2005) report using the general circulation model of the UK Meteorological Office's Hadley Centre to calculate expected changes in temperature and precipitation throughout the Chinese Loess Plateau over the next century. They found 2.3–4.3°C increases in daily maximum temperature, 3.6–5.3°C increases in daily minimum temperature, and 23–37% increases in annual precipitation. They used a stochastic weather generator to downscale these monthly projections to daily values, after which they ran the Water Erosion Prediction Project model of Flanagan and Nearing (1995), as modified to account for CO₂ effects on evapotranspiration and biomass production by Favis-Mortlock and Savabi (1996), for a wheat-wheat-corn rotation utilizing either conventional or conservation tillage.

Zhang and Liu determined the climate-change scenarios they investigated led to 29–79% more water runoff and 2–81% greater soil loss under conventional tillage practices, but "adoption of conservation tillage could reduce runoff by 18–38% and decrease soil loss by 56–68% as compared to the conventional tillage under the present climate." They conclude "the use of the conservation tillage would be sufficient to maintain low runoff and erosion levels and thus protect agro-ecosystems under projected climate changes." As for crop productivity, they determined the warmer, wetter, CO₂-enriched environment projected to prevail on the Chinese Loess Plateau a hundred years from now would boost yields by significant amounts: 15–44% for wheat and 40–58% for corn. Zhang and Liu express great optimism about the future, noting "the significant increases in predicted wheat and maize yields [that] were results of increased precipitation and CO₂ concentration ... outweighed the negative effect of temperature rise on crop growth."

Shifting from the physiological effects of atmospheric CO₂ enrichment on groundcover plants to the immediate impacts of certain climatic

phenomena on soil erosivity, D'Asaro *et al.* (2007) begin the report of their study by stating "warmer atmospheric temperatures associated with greenhouse warming are expected to lead to a more variable hydrological cycle, including more extreme rainfall events (IPCC, 1995)," adding "this change is expected to influence the erosive power, or erosivity, of rainfall and, hence, soil erosion rates (Nearing, 2001)." As a test of this "expectation," D'Asaro *et al.* set out "to assess changes in annual and seasonal rainfall erosivity that occurred in Sicily during the twentieth century," the hundred-year period typically described by IPCC and others as having experienced an increase in global temperature unprecedented over the past two millennia (Mann and Jones, 2003; Mann *et al.*, 2003) or more (Hansen *et al.* 2006). The scientists generated long-term series (from 1916 to 1999 in most cases) of a storm erosion index based on storm rainfall amounts and intensities and then applied that index at 17 Sicilian locations (representative of different climatic zones) where the latter two parameters were routinely measured. The three Italian researchers found "the annual erosivity did not increase during the twentieth century." In fact, they write, it "decreased at a few locations."

Diodato *et al.* (2008) conducted a detailed analysis of Calore River Basin (South Italy) erosive rainfall using data from 425-year-long series of both observations (1922–2004) and proxy-based reconstructions (1580–1921). The more recent of these two series was based on a scheme that employed the Revised Universal Soil Loss Equation; documentary descriptions provided the basis for the earlier series. They write the results of this work revealed pronounced interdecadal variations, with "multi-decadal erosivity reflecting the mixed population of thermo-convective and cyclonic rainstorms with large anomalies." In addition, they report, "the so-called Little Ice Age (16th to mid-19th centuries) was identified as the stormiest period, with mixed rainstorm types and high frequency of floods and erosive rainfall."

In the concluding section of their paper, the three researchers note, "in recent years, climate change (generally assumed as synonymous with global warming) has become a global concern and is widely reported in the media." One of the chief of these concerns is that extreme weather phenomena, such as droughts and floods, will become both more frequent and more severe as the planet warms, which would lead to more soil erosion. However, Diodato *et al.* say their study indicates "climate in the Calore River Basin has been largely characterized by naturally

occurring weather anomalies in past centuries (long before industrial CO₂ emissions), not only in recent years,” and there has been a “relevant smoothing” of such events during the modern era.

Stankoviansky (2003) employed topographical maps and aerial photographs, field geomorphic investigation, and the study of historical documents, including those from local municipal and church sources, to determine the spatial distribution of gully landforms and the temporal history of their creation in the Myjava Hill Land of Slovakia, situated in the western part of the country near its border with the Czech Republic. This work revealed “the central part of the area, settled between the second half of the 16th and the beginning of the 19th centuries, was affected by gully formation in two periods, the first between the end of the 16th century and the 1730s and the second roughly between the 1780s and 1840s.” Stankoviansky notes the gullies were formed “during periods of extensive forest clearance and expansion of farmland,” and “the triggering mechanism of gullying was extreme rainfalls during the Little Ice Age.” More specifically, he writes, “the gullies were formed relatively quickly by repeated incision of ephemeral flows concentrated during extreme rainfall events, which were clustered in periods that correspond with known climatic fluctuations during the Little Ice Age.”

From the mid-nineteenth century to the present, Stankoviansky affirms, “there has been a decrease in gully growth because of the afforestation of gullies and especially climatic improvements since the termination of the Little Ice Age.” These observations suggest extreme and destructive rainfall events were much more common in the Myjava Hill Land of Slovakia during the Little Ice Age than they have been subsequently. This view, in his words (and in many of the references he cites), “is often regarded as generally valid for Central Europe.” This evidence-derived view runs counter to that of most climate alarmists, who tend to blame global warming for such destructive precipitation events and the erosive flooding they cause.

In the course of a long-term field experiment at the Kessler Farm Field Laboratory in McClain County, Oklahoma, USA, Xue *et al.* (2011) explored how annual clipping for biofuel feedstock production and warming caused soil erosion and accompanying carbon and nitrogen losses in tallgrass prairie. The researchers provided warming by infrared heaters suspended 1.5 m above the ground, as described by Kimball (2005), raising air temperatures by an average of 1.47°C and soil temperatures in the

clipping plots by 1.98°C. The results of this experiment revealed the average relative depth of erosion caused by clipping was 1.65 and 0.54 mm/year, respectively, in the warmed and control plots from November 21, 1999 to April 21, 2009; the soil erosion rate was 2148 g/m²/year in the warmed plots and 693 g/m²/year in the control plots; soil organic carbon was lost at a rate of 69.6 g/m²/year in the warmed plots and 22.5 g/m²/year in the control plots; and total nitrogen was lost at a rate of 4.6 g/m²/year in the warmed plots and 1.4 g/m²/year in the control plots. Xue *et al.* note, “the amount of carbon and nitrogen loss caused by clipping is equivalent to, or even larger than, changes caused by global change factors.”

The five researchers state their results indicate “clipping for biofuel harvest results in significant soil erosion and accompanying losses of soil carbon and nitrogen, which is aggravated by warming.” Also, “soil erosion is one of the most pressing global environmental challenges facing the world today, causing declining soil productivity and crop yields, which may create difficulties in meeting the rising demand for food and energy (Brink *et al.*, 1977; Brown, 1981; Lal, 2004; MEA, 2005).” Consequently, the biofuel “cure” for the global warming “disease” might be worse than the malady itself.

Tape *et al.* (2011) state “recent changes in the climate of Arctic Alaska, including warmer temperatures and a lengthened growing season (Chapin *et al.*, 2005; Serreze and Francis, 2006; Shulski and Wendler, 2007), are linked with ... increased vegetation productivity, as measured using time series of satellite vegetation indices such as Normalized Difference Vegetation Index (NDVI),” as documented by Myneni *et al.* (1997), Jia *et al.* (2003), Goetz *et al.* (2005), and Bhatt *et al.*, 2010). This phenomenon, they note, “has been partly attributed to the expansion of shrubs, which has been documented using time series of aerial photography (Sturm *et al.*, 2001; Tape *et al.*, 2006), plot studies (Joly *et al.*, 2007), and shrub growth ring chronologies (Forbes *et al.*, 2010; Hallinger *et al.*, 2010).” In light of these observations they ask, “Is the current warming and concurrent shrub expansion on older Arctic landscapes associated with increased or decreased erosion?”

Working with time series imagery from Landsat thematic mapper data covering the period 1986–2009, Tape *et al.* (2011) examined the landscape pattern of tall shrub distribution and expansion in the Arctic foothills, located on the north side of the Brooks Range, Alaska, and they studied sediments obtained

Climate Change Reconsidered II: Biological Impacts

from cores of four lakes near the Chandler River on the central North Slope of Alaska (where shrub expansion is occurring), to compare relationships among shrub cover, erosion, and runoff over the past quarter-century. Their results reveal “a background decline in erosion since 1980, superimposed by episodic erosional events,” and “the background decline in erosion is associated with trends of increasing shrubs and declining peak runoff events.”

The results of the many studies discussed in this review suggest the historical increase in the atmosphere’s CO₂ concentration has reduced significantly the erosion of valuable topsoil worldwide over the past several decades, and the continuing increase in atmospheric CO₂ can maintain this trend, and perhaps even accelerate it, throughout the foreseeable future.

References

- Allen, J.R.M., Brandt, U., Brauer, A., Hubberten, H.-W., Huntley, B., Keller, J., Kraml, M., Mackensen, A., Mingram, J., Negendank, J.F.W., Nowaczyk, N.R., Oberhansli, H., Watts, W.A., Wulf, S., and Zolitschka, B. 1999. Rapid environmental changes in southern Europe during the last glacial period. *Nature* **400**: 740–743.
- Bachmann, J., Horton, R., and van der Ploeg, R.R. 2001. Isothermal and non-isothermal evaporation from four sandy soils of different water repellency. *Soil Science Society of America Journal* **65**: 1599–1607.
- Bauters, T.W.J., DiCarlo, D.A., Steenhuis, T.S., and Parlange, J.-Y. 1998. Preferential flow in water-repellent soils. *Soil Science Society of America Journal* **62**: 1185–1190.
- Bhatt, U.S., Walker, D., Raynolds, M., Comiso, J., Epstein, H., Jia, G., Gens, R., Pinzon, J., Tucker, C., Tweedie, C., and Webber, P. 2010. Circumpolar Arctic tundra vegetation change is linked to sea ice decline. *Earth Interactions* **14**: 120.
- Bond, R.D. 1972. Germination and yield of barley when grown in a water-repellent sand. *Agronomy Journal* **64**: 402–403.
- Brink, R.A., Densmore, J.W., and Hill, G.A. 1977. Soil deterioration and the growing world demand for food. *Science* **197**: 625–630.
- Brown, L.R. 1981. World population growth, soil erosion, and food security. *Science* **214**: 995–1002.
- Chapin III, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P., Beringer, J., Chapman, W.L., Epstein, H.E., Euskirchen, E.S., Hinzman, L.D., Jia, G., Ping, C.-L., Tape, K.D., Thompson, C.D.C., Walker, D.A., and Welker, J.M. 2005. Role of land-surface changes in Arctic summer warming. *Science* **310**: 657–660.
- Crabtree, W.L. and Gilkes, R.J. 1999. Improved pasture establishment and production on water-repellent soils. *Agronomy Journal* **91**: 467–470.
- D’Asaro, F., D’Agostino, L., and Bagarello, V. 2007. Assessing changes in rainfall erosivity in Sicily during the twentieth century. *Hydrological Processes* **21**: 2862–2871.
- DeBano, L.F. 2000. The role of fire and soil heating on water repellency in wildland environments: a review. *Journal of Hydrology* **231–232**: 195–206.
- Diodato, N., Ceccarelli, M., and Bellocchi, G. 2008. Decadal and century-long changes in the reconstruction of erosive rainfall anomalies in a Mediterranean fluvial basin. *Earth Surface Processes and Landforms* **33**: 2078–2093.
- Favis-Mortlock, D.T. and Savabi, M.R. 1996. Shifts in rates and spatial distribution of soil erosion and deposition under climate change. In: Anderson, M.G. and Brooks, S.M. (Eds.) *Advances in Hillslope Processes*. John Wiley, New York, New York, USA, pp. 529–560.
- Flanagan, D.C. and Nearing, M.A. (Eds.) 1995. *USDA-Water Erosion Prediction Project: Hillslope Profile and Watershed Model Documentation*. National Soil Erosion Research Laboratory Report No. 10. NSERL, West Lafayette, Indiana, USA.
- Forbes, B.C., Fauria, M.M., and Zetterberg, P. 2010. Russian Arctic warming and ‘greening’ are closely tracked by tundra shrub willows. *Global Change Biology* **16**: 1542–1554.
- Goetz, S.J., Bunn, A.G., Fiske, G.J., and Houghton, R.A. 2005. Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Sciences USA* **102**: 13,521–13,525.
- Hallinger, M., Manthey, M., and Wilmking, M. 2010. Establishing a missing link: Warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist* **186**: 890–899.
- Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D.W., and Medina-Elizade, M. 2006. Global temperature change. *Proceedings of the National Academy of Sciences USA* **103**: 14,288–14,293.
- Idso, S.B. 1989. *Carbon Dioxide and Global Change: Earth in Transition*. IBR Press, Tempe, AZ.
- Intergovernmental Panel on Climate Change (IPCC). 1995. *Second Assessment Synthesis of Scientific-Technical Information Relevant to Interpreting Article 2 of the U.N. Framework Convention on Climate Change*. Geneva, Switzerland.

- Jia, G., Epstein, H.E., and Walker, D.A. 2003. Greening of arctic Alaska, 1981–2001. *Geophysical Research Letters* **30**: 10.1029/2003GL018268.
- Joly, K., Jandt, R.R., Meyers, C.R., and Cole, M.J. 2005. Changes in vegetative cover on Western Arctic Herd winter range from 1981 to 2005: Potential effects of grazing and climate change. *Rangifer* **27**: 199–206.
- Kimball, B.A. 2005. Theory and performance of an infrared heater for ecosystem warming. *Global Change Biology* **11**: 2041–2056.
- Knox, J.C. 2001. Agricultural influence on landscape sensitivity in the Upper Mississippi River Valley. *Catena* **42**: 193–224.
- Lal, R. 2004. Soil carbon sequestration impacts on global climate change and food security. *Science* **304**: 1623–1627.
- Mann, M., Amman, C., Bradley, R., Briffa, K., Jones, P., Osborn, T., Crowley, T., Hughes, M., Oppenheimer, M., Overpeck, J., Rutherford, S., Trenberth, K., and Wigley, T. 2003. On past temperatures and anomalous late-20th century warmth. *EOS, Transactions, American Geophysical Union* **84**: 256–257.
- Mann, M.E. and Jones, P.D. 2003. Global surface temperatures over the past two millennia. *Geophysical Research Letters* **30**: 10.1029/2003GL017814.
- MEA. 2005. *Millennium Ecosystem Assessment—Ecosystems and Human Well-being: Desertification Synthesis*. World Resources Institute, Washington, DC, USA.
- Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G., and Nemani, R.R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* **386**: 698–702.
- Nearing, M.A. 2001. Potential changes in rainfall erosivity in the U.S. with climate change during the 21st century. *Journal of Soil and Water Conservation* **56**: 229–232.
- Newton, P.C.D., Carran, R.A., and Lawrence, E.J. 2003. Reduced water repellency of a grassland soil under elevated atmospheric CO₂. *Global Change Biology* **10**: 1–4.
- Olafsdottir, R. and Gudmundsson, H.J. 2002. Holocene land degradation and climatic change in northeastern Iceland. *The Holocene* **12**: 159–167.
- Prior, S.A., Rogers, H.H., Runion, G.B., Torbert, H.A., and Reicosky, D.C. 1997. Carbon dioxide-enriched agroecosystems: Influence of tillage on short-term soil carbon dioxide efflux. *Journal of Environmental Quality* **26**: 244–252.
- Prior, S.A., Runion, G.B., Torbert, H.A., and Rogers, H.H. 2004. Elevated atmospheric CO₂ in agroecosystems: Soil physical properties. *Soil Science* **169**: 434–439.
- Prior, S.A., Torbert, H.A., Runion, G.B., and Rogers, H.H. 2003. Implications of elevated CO₂-induced changes in agroecosystem productivity. *Journal of Crop Production* **8**: 217–244.
- Rillig, M.C., Hernandez, G.Y., and Newton, P.C.D. 2000. Arbuscular mycorrhizae respond to elevated atmospheric CO₂ after long-term exposure: evidence from a CO₂ spring in New Zealand supports the resource balance model. *Ecology Letters* **3**: 475–478.
- Rillig, M.C., Wright, S.F., Kimball, B.A., Pinter, P.J., Wall, G.W., Ottman, M.J., and Leavitt, S.W. 2001. Elevated carbon dioxide and irrigation effects on water stable aggregates in a *Sorghum* field: a possible role for arbuscular mycorrhizal fungi. *Global Change Biology* **7**: 333–337.
- Serreze, M.C. and Francis, J. 2006. The Arctic amplification debate. *Climatic Change* **76**: 241–264.
- Shulski, M. and Wendler, G. 2007. *The Climate of Alaska*. University of Alaska Press, Fairbanks, Alaska, USA.
- Sturm, M., Racine, C., and Tape, K. 2001. Increasing shrub abundance in Arctic. *Nature* **411**: 546–547.
- Stankoviansky, M. 2003. Historical evolution of permanent gullies in the Myjava Hill Land, Slovakia. *Catena* **51**: 223–239.
- Tape, K.D., Sturm, M., and Racine, C. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* **12**: 686–702.
- Tape, K.D., Verbyla, D., and Welker, J.M. 2011. Twentieth century erosion in Arctic Alaska foothills: The influence of shrubs, runoff, and permafrost. *Journal of Geophysical Research* **116**: 10.1029/2011JG001795.
- Tilman, R.W., Scotter, D.R., and Wallis, M.G., et al. 1989. Water-repellency and its measurement by using intrinsic sorptivity. *Australian Journal of Soil Research* **27**: 637–644.
- Trimble, S.W. and Crosson, P. 2000. U.S. soil erosion rates—myth and reality. *Science* **289**: 248–250.
- Xue, X., Luo, Y., Zhou, X., Sherry, R., and Jia, X. 2011. Climate warming increases soil erosion, carbon and nitrogen loss with biofuel feedstock harvest in tallgrass prairie. *GCB Bioenergy* **3**: 198–207.
- Zhang, X.-C. and Liu, W.-Z. 2005. Simulating potential response of hydrology, soil erosion, and crop productivity to climate change in Changwu tableland region on the Loess Plateau of China. *Agricultural and Forest Meteorology* **131**: 127–142.

2

Plant Characteristics

Key Findings

Introduction

2.1 Acclimation

- 2.1.1 Agricultural Species
- 2.1.2 Chaparral and Desert Species
- 2.1.3 Grassland Species
- 2.1.4 Tree Species
- 2.1.5 Source/Sink Relations

2.2 Antioxidants

2.3 Chlorophyll

2.4 Early Spring Growth

2.5 Flowers

2.6 Fluctuating Asymmetry

2.7 Hormones

2.8 Glomalin

2.9 Isoprene

2.10 Leaves

- 2.10.1 Agricultural Species
- 2.10.2 Trees
- 2.10.3 Other

2.11 Lignin

2.12 Lipids

2.13 Low Temperature

2.14 Monoterpenes

2.15 Nectar

2.16 Nitrogen Fixation

- 2.16.1 Herbaceous Plants
- 2.16.2 Woody Plants

2.17 Nitrogen Use Efficiency

2.18 Nutrient Acquisition

2.19 Phenolics

- 2.19.1 Herbaceous Species
- 2.19.2 Woody Species

2.20 Phenology

2.21 Protein

2.22 Respiration

- 2.22.1 Herbaceous Plants
- 2.22.2 Woody Plants

2.23 Roots

- 2.23.1 Crops
- 2.23.2 Grasses
- 2.23.3 Trees
- 2.23.4 Other

2.24 Rubisco

- 2.24.1 Agricultural Species
- 2.24.2 Grassland Species
- 2.24.3 Tree Species

2.25 Seeds

- 2.25.1 Crops
- 2.25.2 Grasslands
- 2.25.3 Trees

2.26 Starch

2.27 Stomatal Density

- 2.27.1 Herbaceous Plants
- 2.27.2 Woody Plants

2.28 Sugars

2.29 Tannins

- 2.29.1 Aspen Trees
- 2.29.2 Birch Trees
- 2.29.3 Oak Trees
- 2.29.4 Other

2.30 Thylakoid Membranes

2.31 Transpiration

- 2.31.1 Herbaceous Plants
- 2.31.2 Woody Plants

2.32 Vegetative Storage Proteins

2.33 Water Use efficiency

- 2.33.1 Agricultural Species
- 2.33.2 Grasslands
- 2.33.3 Trees

2.34 Wood Density

Key Findings

The key findings of this chapter are presented in the bullet points below.

- As the CO₂ content of the air rises, plant species may not experience photosynthetic acclimation—lower long-term rates of photosynthesis than occur when CO₂ concentrations are first increased—even under conditions of low soil nitrogen. In the event a plant cannot balance its carbohydrate sources and sinks, CO₂-induced acclimation can shift limiting resources away from the site of photosynthesis to strengthen sink development or enhance other important plant processes.
- Atmospheric CO₂ enrichment may increase, decrease, or have no effect on leaf chlorophyll concentration. Even when leaf chlorophyll concentration is decreased, the reallocation of its nitrogen generally occurs without any adverse consequences, as most plants displaying this response typically continue to exhibit significant increases in photosynthesis and biomass production.
- Studies of several different tree species suggest enhanced carbohydrates stored in terminal branchlets or nitrogen stored in second-year leaves may be remobilized to facilitate greater first-flush needle or leaf growth the following year as a result of atmospheric CO₂ enrichment.
- At higher atmospheric CO₂ concentrations, plants tend to produce more and larger flowers, as well as other flower-related changes having significant implications for plant productivity and survival, almost all of which are positive.
- Higher concentrations of atmospheric CO₂ tend to reduce fluctuating asymmetry in plant leaves, leading to more symmetrical leaves that appear to be less susceptible to attack by herbivores.
- Atmospheric CO₂ enrichment enhances plant growth, development, and ultimate yield (in the case of agricultural crops) by increasing the concentrations of plant hormones that stimulate cell division, cell elongation, and protein synthesis.
- Atmospheric CO₂ enrichment increases the production of glomalin, a protein created by fungi living in symbiotic association with the roots of 80% of the planet's vascular plants, which is being released to almost every soil in the world in ever-greater quantities with the passage of time, where it is having a positive impact on the biosphere.
- Increasing atmospheric CO₂ concentrations likely will affect many leaf characteristics of agricultural plants, with the majority of the changes leading to higher rates and efficiencies of photosynthesis and growth, as well as numerous other changes in leaf characteristics that help promote increased resistances to herbivory and pathogen attack.
- Atmospheric CO₂ enrichment stimulates photosynthesis in nearly all plants, enabling them to produce more nonstructural carbohydrates that can be used to create important carbon-based secondary compounds, one of which is lignin.
- The highly positive impacts of atmospheric CO₂ enrichment on lipid concentrations and characteristics in various terrestrial and aquatic plants portend nothing but good for the managed and unmanaged components of Earth's biosphere as the air's CO₂ content continues to climb.
- The stresses of low temperature have been shown to be both alleviated and enhanced in plants growing under elevated CO₂ concentrations. It appears far more plants are benefiting from such stress alleviation than experience stress augmentation.
- The diverse results of several experimental studies do not paint a clear picture of what should be expected in the way of plant monoterpene emissions in a CO₂-enriched and possibly warmer world of the future. Until a better understanding is obtained, it would be unwise to conclude much more about the situation.
- As the air's CO₂ content continues to rise, plant fitness, flower pollination, and nectar production should be enhanced, leading to increases in fruit, grain, and vegetable yields of agricultural crops, as well as similar increases in the productivity of the world's natural vegetation.
- Increases in the air's CO₂ content likely will stimulate nitrogen fixation in most herbaceous

Plant Characteristics

species that form symbiotic relationships with nitrogen-fixing soil bacteria—i.e., legumes—and this phenomenon likely will lead to increased nitrogen availability in soils and large increases in agricultural and natural ecosystem productivity. Likewise, increases in the air's CO₂ content will enhance the growth of Earth's leguminous trees, stimulating their fixation of nitrogen and their exudation of the resultant nitrogenous substances to the soils in which they grow, where they become available to neighboring non-leguminous vegetation, all of which promotes biospheric productivity.

- As the air's CO₂ content continues to rise, Earth's plants likely will reduce the amount of nitrogen invested in rubisco and other photosynthetic proteins while maintaining enhanced rates of photosynthesis and thereby increasing their photosynthetic nitrogen-use efficiencies.
- As the CO₂ content of the air increases, much of Earth's vegetation likely will display increases in biomass, and the larger plants likely will develop more extensive root systems and extract greater amounts of mineral nutrients from the soils in which they are rooted, enabling them to sustain their enhanced growth.
- Herbaceous plants often experience increases in foliar and fruit phenolic concentrations in response to atmospheric CO₂ enrichment, and these responses appear to have numerous positive implications for man and the biosphere. Similarly, future increases in the air's CO₂ concentration likely will enhance foliar phenolic concentrations in many trees and shrubs. This phenomenon should enhance woody-plant defense mechanisms that help deter herbivory, thereby improving forest health, robustness, and longevity.
- The wide range of results obtained by many past and current methods of detecting each year's start of spring has led to premature claims of spring's increasingly earlier annual occurrence over the course of the twentieth century. While these claims are used to support the associated claim of twentieth century CO₂-induced global warming, real-world data fail to support the bulk of these contentions.
- With respect to managed agricultural crops and the wild plants of Earth's natural ecosystems, it appears the ongoing rise of the air's CO₂ concentration will have few negative impacts of any consequence on the nutritive value of their grains and foliage in terms of protein concentration. In tree crops such as citrus, CO₂-induced changes in the activities of certain foliar proteins could lead to vast increases in yield potential.
- The growth and biomass production of herbaceous crops are generally enhanced by CO₂-induced decreases in respiration during the dark (nighttime) period. However, scientists lack fundamental information on how respiration and the processes supported by it are physiologically controlled, thereby preventing sound interpretations of what seem to be species-specific responses of respiration to elevated CO₂. Thus the precise role of plant respiration in augmenting the sink capacity of herbaceous plants remains uncertain.
- Both above and below the soil surface, coniferous trees appear to exhibit significant reductions in respiration in CO₂-enriched air. However, deciduous trees exhibit increases and decreases, as well as cases of no change in respiration. Other studies of multiple tree species also suggest atmospheric CO₂ enrichment may either increase or decrease woody-plant respiration, but not to any great degree. The net result for Earth's trees generally likely would be of little significance.
- Elevated CO₂ nearly always increases root biomass, often even more than shoot biomass, by increasing the size of taproots and the number and size of lateral roots, along with fine-root biomass and a number of other important root properties.
- There is a reduced need for nitrogen investment in leaf rubisco in most plants growing in CO₂-enriched air, because under such conditions plants typically reallocate some of their "surplus" nitrogen to other processes essential for optimal growth and development without compromising enhanced carbon gains via photosynthesis.
- Atmospheric CO₂ enrichment has been shown to increase the amount, size, weight, carbohydrate content, lipid content, protein content, earlier production, earlier germination, and greater percent germination of various plant seeds. All of these improvements bode well for the future of Earth's biosphere.

Climate Change Reconsidered II: Biological Impacts

- As the air's CO₂ content rises, most of Earth's vegetation responds by exhibiting enhanced rates of photosynthesis and greater production of carbohydrates. Many of these carbohydrates are exported from leaves and needles to provide energy or carbon skeletons to facilitate increased biomass production, after which remaining carbohydrates generally are converted into starch and stored within leaves or roots for future use.
- In addition to sequentially reducing the openness of their stomata to restrict unnecessary water loss via excessive transpiration as the air's CO₂ content rises, some plants also reduce the density (number per area) of stomates on their leaves, but only to a certain degree, beyond which this latter phenomenon would be counterproductive.
- Atmospheric CO₂ enrichment typically increases plants' ability to produce greater amounts of various forms of sugar.
- Atmospheric CO₂ enrichment significantly enhances the condensed tannin concentrations of the vast majority of Earth's trees and grasses, providing them with stronger defenses against various herbivores both above and below ground. By reducing the amount of methane released to the atmosphere via ruminants browsing on tree leaves and grass, this phenomenon should reduce the rate of rise of the air's methane concentration and thereby decrease the impetus for methane-induced global warming.
- Thylakoid membranes of chloroplasts perform a host of important functions that influence the process of carbon fixation in plants, and in CO₂-enriched air, they generally perform these functions more efficiently, enabling plants to overcome some of the deleterious effects of a host of plant stresses, including insufficient soil moisture, abnormally cold temperatures, abnormally hot temperatures, and ozone pollution.
- As the atmosphere's CO₂ concentration rises, most plants tend to exhibit increased rates of net photosynthesis and biomass production; on a per-unit-leaf-area basis, plants exposed to elevated CO₂ concentrations are likely to lose less water via transpiration because they tend to exhibit lower stomatal conductances. Therefore, the amount of carbon gained per unit of water lost per unit leaf area—water use efficiency—should

increase significantly as the air's CO₂ content rises.

- Atmospheric CO₂ enrichment appears to enhance the between-cuttings savings of vegetative storage proteins (VSPs) in the roots of alfalfa crops, as well as the between-years storage of VSPs in the leaves of sour orange trees (and possibly other citrus species), so that when the next crop's or tree's growing season begins, the first flush of foliage gets a head start.
- Atmospheric CO₂ enrichment tends to increase wood density in both seedlings and mature trees, thereby also increasing a number of strength properties of their branches and trunks. However, different species of trees may respond somewhat differently to atmospheric CO₂ enrichment, and they can respond with still greater variety under different environmental conditions.

Introduction

According to a draft of IPCC Working Group II's Summary for Policymakers (SPM) to accompany its 2014 report, "without adaptation, local temperature increases of 1°C or more above preindustrial levels are projected to negatively impact yields for the major crops (wheat, rice, maize) in tropical and temperate regions, although individual locations may benefit (*medium confidence*). With or without adaptation, climate change will reduce median yields by 0 to 2% per decade for the rest of the century, as compared to a baseline without climate change" (IPCC 2014, p. 10).

The research and analysis summarized in Chapter 1 of the current report challenged IPCC's predictions by showing how rising levels of atmospheric CO₂ help plants overcome abnormally hot temperatures and other plant stresses that might accompany a warming planet. It referenced tabular presentations in Appendices 3 and 4 reporting more than 5,000 individual plant biomass and photosynthetic responses reported in the peer-reviewed literature. That chapter went on to show how elevated atmospheric CO₂ and warmer temperatures benefit various important ecosystems including forests, grasslands, peatlands, wetlands, and soils.

The current chapter continues the analysis, presenting research on the effects of elevated CO₂ on a long list of plant characteristics ranging (in alphabetical order) from antioxidants and chlorophyll to water use efficiency and wood density. The sections

Plant Characteristics

and subsections that follow report the results of hundreds of experiments involving plants grown in air enriched with carbon dioxide to levels expected to be experienced in the future as well as examination of yearly growth rings of long-lived trees revealing how they grew over prior years, decades, and even centuries as atmospheric CO₂ concentrations have risen. In the case of agricultural crops, grassland vegetation, and chaparral and desert species, the first of these techniques is typically employed, as it also is in the study of young tree seedlings. Growth-ring studies are reserved for more mature trees, some of which may have lived for several centuries.

The primary information being sought in these studies is rates of photosynthesis and biomass production and the efficiency with which the plants and trees utilize water. These studies also can provide information about substances produced in the growth process that affect how well it proceeds; substances deposited in the parts of agricultural crops that are harvested for human and animal consumption; and substances that determine whether the foliage or fruit of a certain crop or tree will be attractive to insect pests. Finally, these studies also can help determine whether forest soils will have sufficient nitrogen to sustain the long-term CO₂-enhanced growth rates of long-lived trees.

This chapter powerfully rebuts claims that plant species typically experience photosynthetic acclimation—a decline in rates of photosynthesis over time to less than what would have been expected based on measurements made during short-term exposure to CO₂-enriched air—even under conditions of low soil nitrogen. In the event a plant cannot balance its carbohydrate sources and sinks, CO₂-induced acclimation represents a way of achieving that balance by shifting limiting resources away from the site of photosynthesis to strengthen sink development or enhance other important plant processes. This is especially important because many estimates of the costs and benefits of future global warming assume acclimation will limit the benefits of carbon dioxide fertilization or even turn carbon sinks into net emitters. The research that follows shows convincingly that this is not the case.

Similarly, this chapter addresses head-on the claim that water shortages in a warmer world will eventually stop the higher CO₂-induced increase in plant growth and foreshadow declining plant productivity, with corresponding negative effects on food supply and human welfare. It seems Mother Nature anticipated the greater need for moisture that faster-growing plants would exhibit by minimizing

their loss of water via transpiration by lowering stomatal conductances. The amount of carbon gained per unit of water lost per unit of leaf area—water use efficiency—should increase significantly as the air's CO₂ concentration rises.

This chapter also looks closely at the impact of higher CO₂ levels on plants that are significant sources of nutrition for humans directly or indirectly as feed for cattle, sheep, and other domesticated animals. The evidence is overwhelmingly positive: Higher levels of atmospheric CO₂ already are enhancing crop yields of alfalfa, citrus, rice, soybeans, and wheat. Carbon dioxide fertilization promotes the production of more and larger flowers, more symmetrical leaves (which appears to reduce herbivory), more nonstructural carbohydrates, and positive impacts on lipid concentrations and characteristics, plant fitness, flower pollination, nectar production, and more. Rising levels of CO₂ in the air will have few negative impacts of any consequence on the nutritive value of grains and foliage in terms of protein concentration, and in some tree crops such as citrus, CO₂-induced changes in the activities of certain foliar proteins could lead to vast increases in yield potential.

In short, IPCC's conclusions about the impact of future global warming on agriculture are far too pessimistic. Trends in the twentieth century and experimental research all point to a continued flourishing of crops important to human welfare as well as virtually all plants.

Reference

IPCC. 2014. Summary for Policymakers. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability*. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Draft dated October 28, 2013.

2.1 Acclimation

Plants grown in elevated CO₂ environments often exhibit photosynthetic acclimation or down-regulation, typically characterized by somewhat lower long-term rates of photosynthesis than would have been expected based on measurements made during short-term exposure to CO₂-enriched air. These downward adjustments result from modest long-term decreases in the activities and/or amounts of the

primary plant carboxylating enzyme rubisco.

Acclimation is said to have occurred when the photosynthetic rates of long-term CO₂-enriched plants are found to be lower than those of long-term non-CO₂-enriched plants when the normally CO₂-enriched plants are measured during brief exposures to ambient CO₂ concentrations. The subsections below review research published on acclimation in agricultural, desert, grassland, and woody tree species.

2.1.1 Agricultural Species

- As the CO₂ content of the air rises, agricultural species may not experience photosynthetic acclimation, even under conditions of low soil nitrogen, but in the event a plant cannot balance its carbohydrate sources and sinks, CO₂-induced acclimation represents a beneficial means of achieving that balance by shifting limiting resources away from the site of photosynthesis to strengthen sink development or enhance other important plant processes.

Several studies have examined the effects of elevated CO₂ on acclimation in agricultural crops. Ziska (1998), for example, reports soybeans grown at an atmospheric CO₂ concentration of 720 ppm initially exhibited photosynthetic rates 50% greater than those observed in control plants grown at 360 ppm. After the onset of photosynthetic acclimation, the CO₂-enriched plants displayed subsequent photo-synthetic rates only 30% greater than their ambiently grown counterparts. Theobald *et al.* (1998) grew spring wheat at twice-ambient atmospheric CO₂ concentrations and determined elevated CO₂ reduced the amount of rubisco required to sustain enhanced rates of photosynthesis, which led to a significant increase in plant photosynthetic nitrogen-use efficiency. CO₂-induced increases in photosynthetic nitrogen-use efficiency also have been reported in spring wheat by Osborne *et al.* (1998).

In a study incorporating both hydroponically and pot-grown wheat plants, Farage *et al.* (1998) demonstrated low nitrogen fertilization does not lead to photosynthetic acclimation in elevated CO₂ environments, as long as the nitrogen supply keeps pace with the relative growth rate of the plants. When spring wheat was grown at an atmospheric CO₂ concentration of 550 ppm in a free-air CO₂ enrichment (FACE) experiment with optimal soil nutrition and unlimited rooting volume, Garcia *et al.* (1998) found no evidence of photosynthetic

acclimation.

CO₂-induced photosynthetic acclimation often results from insufficient plant sink strength, which can lead to carbohydrate accumulation in source leaves and the triggering of photosynthetic end-product feedback inhibition, which reduces net photosynthetic rates. Gesch *et al.* (1998) report rice plants, which have relatively limited potential for developing additional carbon sinks, grown at an atmospheric CO₂ concentration of 700 ppm exhibited increased leaf carbohydrate contents, which likely reduced *rbcS* mRNA levels and rubisco protein content. Similarly, Sims *et al.* (1998) report photosynthetic acclimation was induced in CO₂-enriched soybean plants from the significant accumulation of nonstructural carbohydrates in their leaves. However, in growing several different *Brassica* species at 1,000 ppm CO₂, Reekie *et al.* (1998) demonstrated CO₂-induced acclimation was avoided in species having well-developed carbon sinks (broccoli and cauliflower) and appeared only in species lacking significant sink strength (rape and mustard).

Thus, photosynthetic acclimation does not appear to be a direct consequence of atmospheric CO₂ enrichment but rather an indirect effect of low sink strength, which results in leaf carbohydrate accumulation that can trigger acclimation.

In some cases, plants can effectively increase their sink strength, and thus reduce the magnitude of CO₂-induced acclimation, by forming symbiotic relationships with certain species of soil fungi. Under such conditions, photosynthetic down-regulation is not triggered as rapidly, or as frequently, by end-product feedback inhibition, as excess carbohydrates are mobilized out of source leaves and sent belowground to symbiotic fungi. Louche-Tessandier *et al.* (1999) found photosynthetic acclimation in CO₂-enriched potatoes was less apparent when plants were simultaneously colonized by a mycorrhizal fungus. Thus, CO₂-induced acclimation appears to be closely related to the source:sink balance that exists within plants, being triggered when sink strength falls below, and source strength rises above, critical thresholds in a species-dependent manner.

Acclimation is generally regarded as a process that reduces the amount of rubisco and/or other photosynthetic proteins, which effectively increases the amount of nitrogen available for enhancing sink development or stimulating other nutrient-limited processes. Watling *et al.* (2000), for example, report a 50% CO₂-induced reduction in the concentration of PEP-carboxylase, the primary carboxylating enzyme

Plant Characteristics

in C₄ plants, within sorghum leaves. Maroco *et al.* (1999) documented CO₂-induced decreases in both PEP-carboxylase and rubisco in leaves of the C₄ crop maize.

In some cases, acclimation to elevated CO₂ is manifested by an “up-regulation” of certain enzymes. When Gesch *et al.* (2002) took rice plants from ambient air and placed them in air enriched to 700 ppm CO₂, for example, they noticed a significant increase in the activity of sucrose-phosphate synthase (SPS), a key enzyme involved in the production of sucrose. Similarly, Hussain *et al.* (1999) report rice plants grown at an atmospheric CO₂ concentration of 660 ppm displayed 20% more SPS activity during the growing season than did ambiently grown rice plants. Such increases in the activity of this enzyme could allow CO₂-enriched plants to avoid the onset of photosynthetic acclimation by synthesizing and subsequently exporting sucrose from source leaves into sink tissues before they accumulate and trigger end product feedback inhibition.

Gesch *et al.* (2000) took ambiently growing rice plants and placed them in an atmospheric CO₂ concentration of 175 ppm, which reduced photosynthetic rates by 45%. After five days’ exposure to this sub-ambient CO₂ concentration, the plants manifested an up-regulation of rubisco, which stimulated photosynthetic rates by 35%. Thus, plant acclimation responses can involve both an increase or decrease in specific enzymes, depending on the atmospheric CO₂ concentration.

Many peer-reviewed studies suggest that as the CO₂ content of the air slowly but steadily rises, agricultural species may not exhibit photosynthetic acclimation, even under conditions of low soil nitrogen. If a plant can maintain a balance between its sources and sinks for carbohydrates at the whole-plant level, for example, acclimation should not be necessary; for if Earth’s atmospheric CO₂ content is rising by an average of only 1.5 ppm per year, most plants should be able to adjust their relative growth rates by the small amount that would be needed to prevent low nitrogen-induced acclimation from ever occurring, or expand their root systems by the small amount that would be needed to supply the extra nitrogen required to take full advantage of the CO₂-induced increase in leaf carbohydrate production. And if a plant cannot initially balance its sources and sinks for carbohydrates at the whole-plant level, CO₂-induced acclimation represents a beneficial secondary mechanism for achieving that balance through redistributing limiting resources away from the plant’s photosynthetic machinery to strengthen sink

development or enhance other important plant processes.

References

- Farage, P.K., McKee, I.F., and Long, S.P. 1998. Does a low nitrogen supply necessarily lead to acclimation of photosynthesis to elevated CO₂? *Plant Physiology* **118**: 573–580.
- Garcia, R.L., Long, S.P., Wall, G.W., Osborne, C.P., Kimball, B.A., Nie, G.Y., Pinter Jr., P.J., LaMorte, R.L., and Wechsung, F. 1998. Photosynthesis and conductance of spring-wheat leaves: field response to continuous free-air atmospheric CO₂ enrichment. *Plant, Cell and Environment* **21**: 659–669.
- Gesch, R.W., Boote, K.J., Vu, J.C.V., Allen Jr., L.H., and Bowes, G. 1998. Changes in growth CO₂ result in rapid adjustments of ribulose-1,5-bisphosphate carboxylase/oxygenase small subunit gene expression in expanding and mature leaves of rice. *Plant Physiology* **118**: 521–529.
- Gesch, R.W., Vu, J.C.V., Boote, K.J., Allen Jr., L.H., and Bowes, G. 2000. Subambient growth CO₂ leads to increased Rubisco small subunit gene expression in developing rice leaves. *Journal of Plant Physiology* **157**: 235–238.
- Gesch, R.W., Vu, J.C.V., Boote, K.J., Allen Jr., L.H., and Bowes, G. 2002. Sucrose-phosphate synthase activity in mature rice leaves following changes in growth CO₂ is unrelated to sucrose pool size. *New Phytologist* **154**: 77–84.
- Hussain, M.W., Allen Jr., L.H., and Bowes, G. 1999. Up-regulation of sucrose phosphate synthase in rice grown under elevated CO₂ and temperature. *Photosynthesis Research* **60**: 199–208.
- Louche-Tessandier, D., Samson, G., Hernandez-Sebastia, C., Chagvardieff, P., and Desjardins, Y. 1999. Importance of light and CO₂ on the effects of endomycorrhizal colonization on growth and photosynthesis of potato plantlets (*Solanum tuberosum*) in an *in vitro* tripartite system. *New Phytologist* **142**: 539–550.
- Maroco, J.P., Edwards, G.E., and Ku, M.S.B. 1999. Photosynthetic acclimation of maize to growth under elevated levels of carbon dioxide. *Planta* **210**: 115–125.
- Osborne, C.P., LaRoche, J., Garcia, R.L., Kimball, B.A., Wall, G.W., Pinter Jr., P.J., LaMorte, R.L., Hendrey, G.R., and Long, S.P. 1998. Does leaf position within a canopy affect acclimation of photosynthesis to elevated CO₂? *Plant Physiology* **117**: 1037–1045.
- Reekie, E.G., MacDougall, G., Wong, I., and Hicklenton, P.R. 1998. Effect of sink size on growth response to elevated atmospheric CO₂ within the genus *Brassica*. *Canadian Journal of Botany* **76**: 829–835.

Sims, D.A., Luo, Y., and Seeman, J.R. 1998. Comparison of photosynthetic acclimation to elevated CO₂ and limited nitrogen supply in soybean. *Plant, Cell and Environment* **21**: 945–952.

Theobald, J.C., Mitchell, R.A.C., Parry, M.A.J., and Lawlor, D.W. 1998. Estimating the excess investment in ribulose-1,5-bisphosphate carboxylase/oxygenase in leaves of spring wheat grown under elevated CO₂. *Plant Physiology* **118**: 945–955.

Watling, J.R., Press, M.C., and Quick, W.P. 2000. Elevated CO₂ induces biochemical and ultrastructural changes in leaves of the C4 cereal sorghum. *Plant Physiology* **123**: 1143–1152.

Ziska, L.H. 1998. The influence of root zone temperature on photosynthetic acclimation to elevated carbon dioxide concentrations. *Annals of Botany* **81**: 717–721.

2.1.2 Chaparral and Desert Species

- The few studies of acclimation that have been conducted on chaparral and desert plants indicate that although acclimation can sometimes be quite severe, other physiological changes, such as the reductions in stomatal conductance that typically produce large increases in water use efficiency, often more than compensate for the increases in photosynthesis caused by acclimation.

Roberts *et al.* (1998) conducted a FACE experiment in southern California, USA, exposing *Adenostoma fasciculatum* shrubs to atmospheric CO₂ concentrations of 360 and 550 ppm while they studied the nature of gas-exchange in this chaparral species. After six months of CO₂ fumigation, photosynthetic acclimation occurred. However, because of reductions in stomatal conductance and transpirational water loss, the CO₂-enriched shrubs exhibited leaf water potentials less negative (and hence less stressful) than those of control plants. This CO₂-induced water conservation phenomenon should enable this woody perennial to better withstand the periods of drought that commonly occur in this southern California region, and the photosynthetic down-regulation it exhibits should allow it to more equitably distribute the limiting resources it possesses among different essential plant physiological processes.

Huxman and Smith (2001) measured seasonal gas exchange during an unusually wet El Niño year in an annual grass (*Bromus madritensis* ssp. *rubens*) and a perennial forb (*Eriogonum inflatum*) growing within FACE plots established in the Mojave Desert, USA,

which they maintained at atmospheric CO₂ concentrations of 350 and 550 ppm. The elevated CO₂ consistently increased net photosynthetic rates in the annual grass without inducing photosynthetic acclimation. Even as seasonal photosynthetic rates declined post-flowering, the reduction was much less in the CO₂-enriched plants. Elevated CO₂ had no consistent effect on stomatal conductance in this species. In contrast, *Eriogonum* plants growing at 550 ppm CO₂ exhibited significant photosynthetic acclimation, especially late in the season, which led to similar rates of net photosynthesis in these plants in both CO₂ treatments. But in this species, elevated CO₂ reduced stomatal conductance over most of the growing season. And, therefore, although the two desert plants exhibited different stomatal and photosynthetic responses to elevated CO₂, both experienced significant CO₂-induced increases in water use efficiency and biomass production, highlighting the existence of different, but equally effective, species-specific mechanisms for responding positively to atmospheric CO₂ enrichment in a desert environment.

In another study conducted at the Mojave Desert FACE site, Hamerlynck *et al.* (2002) determined plants of the deciduous shrub *Lycium andersonii* grown in elevated CO₂ displayed photosynthetic acclimation, as maximum rubisco activity in the plants growing in the CO₂-enriched air was 19% lower than in the plants growing in ambient air. The elevated CO₂ did not significantly impact rates of photosynthesis. Leaf stomatal conductance, by contrast, was consistently about 27% lower in the plants grown in the CO₂-enriched air. During the last month of the spring growing season, the plants in the elevated CO₂ plots displayed leaf water potentials less negative than those exhibited by the control plants growing in ambient air. Hence, as the CO₂ content of the air increases, *Lycium andersonii* likely will respond by exhibiting significantly enhanced water use efficiency, which should greatly increase its ability to cope with the highly variable precipitation and temperature regimes of the Mojave Desert. The acclimation observed within the shrub's photosynthetic apparatus should allow it to reallocate more resources to sustaining greater amounts of biomass. Thus it is likely future increases in the air's CO₂ content will favor a “greening” of the American Mojave Desert.

References

Hamerlynck, E.P., Huxman, T.E., Charlet, T.N., and Smith,

Plant Characteristics

S.D. 2002. Effects of elevated CO₂ (FACE) on the functional ecology of the drought-deciduous Mojave Desert shrub, *Lycium andersonii*. *Environmental and Experimental Botany* **48**: 93–106.

Huxman, T.E. and Smith, S.D. 2001. Photosynthesis in an invasive grass and native forb at elevated CO₂ during an El Niño year in the Mojave Desert. *Oecologia* **128**: 193–01.

Roberts, S.W., Oechel, W.C., Bryant, P.J., Hastings, S.J., Major, J., and Nosov, V. 1998. A field fumigation system for elevated carbon dioxide exposure in chaparral shrubs. *Functional Ecology* **12**: 708–719.

2.1.3 Grassland Species

- As the air's CO₂ content rises, grassland species may not exhibit photosynthetic acclimation if they can maintain a balance between their carbohydrate sources and sinks. But if this balancing act is not possible, acclimation represents a beneficial way of achieving that balance by redistributing limiting resources away from a plant's photosynthetic machinery to strengthen its sink development and/or its nutrient-gathering activities.

In nearly every reported case of photosynthetic acclimation in CO₂-enriched grassland species, rates of photosynthesis displayed by plants grown and measured at elevated concentrations of CO₂ are typically greater than those exhibited by control plants grown and measured at ambient CO₂ concentrations (Davey *et al.*, 1999; Bryant *et al.*, 1998). But as mentioned in prior sections, CO₂-induced photosynthetic acclimation often results from insufficient plant sink strength that can lead to carbohydrate accumulation in source leaves and the triggering of photosynthetic end-product feedback inhibition, which reduces rubisco activity and rates of net photosynthesis (Roumet *et al.*, 2000).

As one example of this phenomenon, Rogers *et al.* (1998) report perennial ryegrass grown at an atmospheric CO₂ concentration of 600 ppm and low soil nitrogen content exhibited leaf carbohydrate contents and rubisco activities 100% greater and 25% less, respectively, than those observed in control plants grown at 360 ppm CO₂ prior to a cutting event. But following the cutting, which effectively reduced the source:sink ratio of the plants, leaf carbohydrate contents in CO₂-enriched plants decreased and rubisco activities increased, completely ameliorating the photosynthetic acclimation in this species.

However, at high soil nitrogen, photo-synthetic acclimation to elevated CO₂ did not occur. Thus, photosynthetic acclimation appears to result from the inability of plants to develop adequate sinks at low soil nitrogen, and is not necessarily induced directly by atmospheric CO₂ enrichment.

In some cases, plants can effectively increase their sink strength and thus reduce the magnitude of CO₂-induced acclimation by forming symbiotic relationships with certain species of soil fungi. Under such conditions, photosynthetic down-regulation is not triggered as rapidly, or as frequently, by end-product feedback inhibition, as excess carbohydrates are mobilized out of source leaves and sent below-ground to the symbiotic fungi. Staddon *et al.* (1999), for example, report photosynthetic acclimation was not induced in CO₂-enriched *Plantago lanceolata* plants inoculated with a mycorrhizal fungus, but it was induced in control plants that were not inoculated with the fungus. Thus, CO₂-induced acclimation appears to be closely related to the source:sink balance that exists within plants, and which is triggered when sink strength falls below, and source strength rises above, certain critical thresholds in a species-dependent manner.

As the air's CO₂ content slowly but steadily rises, therefore, these peer-reviewed studies suggest grassland species may not exhibit photosynthetic acclimation if they can maintain a balance between their sources and sinks for carbohydrates at the whole-plant level. But in the event this balancing act is not possible, acclimation represents a beneficial secondary means of achieving that balance by redistributing limiting resources away from a plant's photosynthetic machinery to strengthen its sink development and/or its nutrient-gathering activities.

References

- Bryant, J., Taylor, G., and Frehner, M. 1998. Photo-synthetic acclimation to elevated CO₂ is modified by source:sink balance in three component species of chalk grassland swards grown in a free air carbon dioxide enrichment (FACE) experiment. *Plant, Cell and Environment* **21**: 159–168.
- Davey, P.A., Parsons, A.J., Atkinson, L., Wadge, K., and Long, S.P. 1999. Does photosynthetic acclimation to elevated CO₂ increase photosynthetic nitrogen-use efficiency? A study of three native UK grassland species in open-top chambers. *Functional Ecology* **13**: 21–28.
- Rogers, A., Fischer, B.U., Bryant, J., Frehner, M., Blum, H., Raines, C.A., and Long, S.P. 1998. Acclimation of

photosynthesis to elevated CO₂ under low-nitrogen nutrition is affected by the capacity for assimilate utilization. Perennial ryegrass under free-air CO₂ enrichment. *Plant Physiology* **118**: 683–689.

Roumet, C., Garnier, E., Suzor, H., Salager, J.-L., and Roy, J. 2000. Short and long-term responses of whole-plant gas exchange to elevated CO₂ in four herbaceous species. *Environmental and Experimental Botany* **43**: 155–169.

Staddon, P.L., Fitter, A.H., and Robinson, D. 1999. Effects of mycorrhizal colonization and elevated atmospheric carbon dioxide on carbon fixation and below-ground carbon partitioning in *Plantago lanceolata*. *Journal of Experimental Botany* **50**: 853–860.

2.1.4 Tree Species

Aspen/poplar trees, growing out-of-doors and rooted in the ground, generally show little long-term photosynthetic acclimation (gradual reduction in initial experimental CO₂-induced growth stimulation), and sometimes none at all. Although there can be a steep multiyear decline in the initial huge CO₂-induced growth stimulation of citrus trees, the subsequent long-term equilibrium growth enhancement can be quite substantial. And in oak trees, both long-term and total-lifetime CO₂ enhancement of the air surrounding various species have provided evidence for a total lack of photosynthetic acclimation, indicating the many positive and enduring benefits of atmospheric CO₂ enrichment. Also, even though there may be a partial acclimation of the photosynthetic process in pine trees in some CO₂-enrichment experiments, the down-regulation is typically neither complete nor wholly detrimental, for it transfers nitrogen from the sites of photosynthesis to the sinks for photosynthates, where it is most needed when soil infertility is limiting primary productivity. Finally, studies of spruce trees reveal atmospheric CO₂ enrichment increases their photo-synthetic rates, even in the case of partial photo-synthetic acclimation, which enables them to transport greater amounts of soluble carbohydrates, including glucose, to active sink tissues to support their enhanced growth and development even on nutrient-poor soils.

2.1.4.1 Aspen/Poplar

- Aspen/poplar trees, growing out-of-doors and rooted in the ground, generally show little long-term acclimation (reduction in CO₂-induced growth stimulation), and sometimes none at all.

Trees grown for long periods of time in elevated CO₂ environments sometimes exhibit some degree of photosynthetic acclimation or down-regulation, typically characterized by modestly reduced rates of photosynthesis compared to what might be expected on the basis of short-term exposure to CO₂-enriched air. These reductions result from a long-term decrease in the activity and/or amount of the primary plant carboxylating enzyme *rubisco*. This section explores this phenomenon as it applies to various species of aspen/poplar trees.

Takeuchi *et al.* (2001) grew quaking aspen (*Populus tremuloides*) trees for two years in 30-meter-diameter free-air CO₂ enrichment (FACE) plots near Rhinelander, Wisconsin (USA), maintained at atmospheric CO₂ concentrations of either 360 or 560 ppm. They found elevated CO₂ stimulated the growth and closure of the trees' canopies, as indicated by light intensities measured near the seedlings' lowermost branches only 17% and 9% of values observed near their uppermost branches in the ambient and CO₂-enriched environments, respectively, which led to the light availability for photosynthesis decreasing with canopy depth, but more so for the CO₂-enriched seedlings. Nevertheless, seasonal photosynthetic rates were always greater in the CO₂-enriched seedlings, although the growth stimulation was much greater in the upper canopy than in the lower (26 and 3%, respectively). Photosynthetic acclimation also occurred in the CO₂-enriched seedlings in a depth-dependent manner, with less acclimation occurring in the upper as opposed to the lower canopy, as indicated by decreases in foliar *rubisco* content of 28 and 50%, respectively, in those two locations. Yet in spite of this significant acclimation, the elevated CO₂ still led to a greater total net carbon uptake, and the CO₂-enriched seedlings grew 18% taller than the seedlings exposed to ambient air.

At the EuroFACE facility near Viterbo in Central Italy, Wittig *et al.* (2005) grew stands of closely spaced (1 m x 1 m) individuals of three *Populus* species—white poplar (*P. alba*), black poplar (*P. nigra*), and robusta poplar (*P. x euramericana*)—from the time of planting through canopy closure to coppice (aboveground tree harvest) at atmospheric CO₂ concentrations of 370 and 550 ppm for three full years. Based on measurements of leaf area index and various photosynthetic parameters made at regular intervals, photosynthetic rates of different leaf classes were determined for monthly intervals and summed to obtain annual canopy photosynthesis or gross primary production (GPP) in each of the three years of the

study.

The 10 researchers note, “significant stimulation of GPP driven by elevated CO₂ occurred in all 3 years, and was greatest in the first year (223-251%), but markedly lower in the second (19-24%) and third years (5-19%).” The decline in CO₂-induced growth stimulation was *not* due to photosynthetic acclimation; it was simply a consequence of canopy closure and the increased shading of leaves that accompanied it.

Averaged across all species and plots, the CO₂-induced stimulation of annual GPP was 234%, 22%, and 11% in 1999, 2000, and 2001, respectively. Averaged over the full three-year period, the GPP enhancements for *P. alba*, *P. nigra*, and *P. x euramericana* were, respectively, 17%, 17%, and 25%. The scientists note these results “were consistent with independent measurements of net primary production, determined independently from biomass increments and turnover.” Thus, Wittig *et al.* say their results suggest, “with selection, nutrient and moisture supply, coppice managed plantation poplars have the potential for large and sustained increases in GPP” in response to atmospheric CO₂ enrichment.

Over the following year, as the trees sent up new sprouts and renewed their growth after coppicing, Davey *et al.* (2006) measured total daily photosynthetic carbon assimilation together with several other related physiological parameters and processes. They found “diurnal photosynthesis in poplar trees grown in elevated CO₂ over four growing seasons showed a sustained increase in photosynthesis of between 35 and 60% prior to coppicing,” and “this increase in daily photosynthesis is maintained during the re-growth following coppicing in *P. x euramericana*.”

These observations and their other data indicate, as the seven scientists describe it, “no long-term photosynthetic acclimation to CO₂ occurred in these plants,” and “poplar trees are able to ‘escape’ from long-term, acclamatory down-regulation of photosynthesis through a high capacity for starch synthesis and carbon export.” They also note, “Wittig *et al.* (2005) showed that the canopy photosynthetic carbon gain in these species is proportional to wood increment, implying that the increased photosynthesis will result in more carbon in wood.” Therefore, the seven scientists say their findings “show that the acclamatory loss of the initial increase in photosynthetic rate under elevated CO₂ is not inevitable,” and “poplar species, selected for rapid growth, may be well suited to a future elevated CO₂ environment and particularly suited to afforestation

projects aimed to increase carbon uptake into wood in the near term.”

Throughout the same year and over one additional year, Liberloo *et al.* (2005) studied the regrowth of the trees under unfertilized and fertilized conditions. During those first and second growing seasons after coppicing, they found the elevated CO₂ treatment significantly increased the trees’ leaf area index, with relative differences between the CO₂-enriched and control trees ranging from +1.7 to +38.7%, +4.7 to +38.5%, and +3.9 to +45% for *P. alba*, *P. nigra*, and *P. x euramericana*, respectively, for unfertilized and fertilized conditions, respectively. In addition, they report the increased leaf area index “supported increased aboveground biomass production,” but only in the fertilized treatment. In light of these findings, they remark that if the CO₂-induced growth enhancement after canopy closure continues to hold true in subsequent years, it “will have important implications for the carbon balance of terrestrial ecosystems, because forests could behave as a larger carbon sink under future atmospheric conditions.”

Liberloo *et al.* (2006) report results for the second three-year growth rotation of the trees. They found fertilization did not affect the growth of the second-rotation trees, “likely because of the high rates of fertilization during the previous agricultural land use.” In contrast, they write, “elevated CO₂ enhanced biomass production by up to 29%, and this stimulation did not differ between above- and below-ground parts.” They also report the net rate of carbon assimilation was “on average for all species stimulated up to 30% during the third year of the second rotation,” and “after six years of fumigation, measurements of photosynthetic parameters along the canopy profile could not detect any clear sign of acclimation to elevated CO₂” for any of the three species. Thus, they conclude, “poplar trees are able to optimally profit from future high CO₂ concentrations, provided that they are intensively managed, planted in regions with high incident radiation and supplied with sufficient nutrients and water.” Such “high-density poplar coppice cultures,” in their opinion, “offer possibilities to mitigate the rise of atmospheric CO₂ by producing renewable bio-energy in an economically feasible way, whereby the elevated CO₂ stimulation might sustain over several rotation cycles.”

Working at the same site but studying only robusta poplar that had been growing there for five years, Calfapietra *et al.* (2005) measured the trees’ photosynthetic responses to an approximate 200-ppm

increase in the air's CO₂ concentration in mid-July of the study's fifth year, comparing their results with what was observed at the beginning of the experiment, both with and without supplemental nitrogen fertilization. As they describe their findings, "even after such a long period of exposure, leaves of *Populus x euramericana* have not shown clear signs of photosynthetic acclimation." They also report CO₂ enrichment "significantly decreased stomatal conductance both on upper and lower canopy leaves," which together with the CO₂-induced stimulation of photosynthesis implies a significant sustained increase in leaf water use efficiency throughout the trees' canopies. They say their results "suggest that the photosynthetic acclimation of poplar plantations is unlikely to occur in an atmosphere enriched in CO₂ and thereby will not influence the response of poplar plantations to increasing atmospheric CO₂ concentrations either over the long term or under conditions of nitrogen deposition."

At the Aspen FACE site near Rhinelander, Wisconsin (USA), Kets *et al.* (2010) measured diurnal changes in light-saturated net photosynthesis (P_n) rate under both ambient and elevated atmospheric CO₂ and/or ozone (O₃) concentrations over wide ranges of stomatal conductance, water potential, intercellular CO₂, leaf temperature, and vapor pressure difference between leaf and air in two clones (271 and 42E) of quaking aspen (*Populus tremuloides* Michx.) trees that differed in their sensitivity to ozone and had been growing under the aforementioned experimental conditions for seven to eight years. This work revealed P_n was typically enhanced by 33 to 46% in the CO₂-enriched treatment over the course of the study, and there was a small increase in leaf chlorophyll concentration as well.

Noting "previous Aspen FACE studies have reported 25–36% increases in P_n (Noormets *et al.*, 2001; Takeuchi *et al.*, 2001; Sharma *et al.*, 2003; Ellsworth *et al.*, 2004)," the six scientists emphasize the aerial fertilization effect of atmospheric CO₂ enrichment on P_n observed in their study "has rather been increasing in time than decreasing," stating this phenomenon may be caused by the "slight but significant increase in leaf chlorophyll content per leaf area, which is rather positive acclimation in photosynthetic apparatus than negative acclimation." They cite the studies of Centritto and Jarvis (1999) and Eichelmann *et al.* (2004) in support of this conclusion.

Darbah *et al.* (2010) analyzed photosynthesis data they and others had collected at the Aspen FACE site over a period of 11 years for the same two quaking

aspen clones, which were exposed to all combinations of ambient and elevated (560 ppm) CO₂ and ambient and elevated (1.5 times ambient) ozone (O₃). In addition, they studied leaf stomatal conductance under the same conditions. This work revealed, as they describe it, "no long-term photosynthetic and stomatal acclimation to elevated CO₂, O₃ or CO₂ + O₃ in aspen trees exposed to elevated CO₂ and/or O₃ gases for 11 years," and the aspen trees "have sustained their maximum instantaneous photosynthesis stimulation for over a decade." In discussing their findings, Darbah *et al.* say they support the observations of Liberloo *et al.* (2007), who measured a 49% increase in net photosynthetic rate in poplar trees after six years of exposure to elevated CO₂; Sholtis *et al.* (2004), who reported a 44% stimulation of net photosynthesis in sweetgum trees after three years of exposure to elevated CO₂; Crous and Ellsworth (2004), who found a photosynthetic enhancement of 51 to 69% in *Pinus taeda* trees after six years of exposure to elevated CO₂; and Davey *et al.* (2006) and Paoletti *et al.* (2007), of whose work Darbah *et al.* state, "there was no photosynthetic acclimation (down-regulation) occurring in *Quercus ilex* under long-term CO₂ enrichment." In addition, they remark, even in white clover (*Trifolium repens*), Ainsworth *et al.* (2003) found photosynthetic stimulation "remained after nine years of exposure to elevated CO₂."

Thus, as more long-term experiments are conducted on long-lived woody plants growing out-of-doors and rooted in the ground, where their roots are not artificially confined to a limited volume of soil, it is becoming abundantly clear they generally do not experience a complete cessation of the initial photosynthetic stimulation provided them by the extra CO₂ to which they are exposed in CO₂ enrichment studies. They often show very little long-term reduction in CO₂-induced growth stimulation, and sometimes no reduction at all, as is evidenced in these several studies of aspen/poplar trees.

References

- Ainsworth, A.E., Rogers, A., Blum, H., Nosberger, J., and Long, S.P. 2003. Variation in acclimation of photosynthesis in *Trifolium repens* after eight years of exposure to free air CO₂ enrichment (FACE). *Journal of Experimental Botany* 54: 2769–2774.
- Calfapietra, C., Tulva, I., Eensalu, E., Perez, M., De Angelis, P., Scarascia-Mugnozza, G., and Kull, O. 2005. Canopy profiles of photosynthetic parameters under

elevated CO₂ and N fertilization in a poplar plantation. *Environmental Pollution* **137**: 525–535.

Centritto, M. and Jarvis, P.G. 1999. Long-term effects of elevated carbon dioxide concentration and provenance on four clones of Sitka spruce (*Picea sitchensis*). II. Photosynthetic capacity and nitrogen use efficiency. *Tree Physiology* **19**: 807–814.

Crous, K.Y. and Ellsworth, D.S. 2004. Canopy position affects photosynthetic adjustments to long-term elevated CO₂ concentration (FACE) in aging needles in a mature *Pinus taeda* forest. *Tree Physiology* **24**: 961–970.

Darbah, J.N.T., Kubiske, M.E., Nelson, N., Kets, K., Riikonen, J., Sober, A., Rouse, L., and Karnosky, D.F. 2010. Will photosynthetic capacity of aspen trees acclimate after long-term exposure to elevated CO₂ and O₃? *Environmental Pollution* **158**: 983–991.

Davey, P.A., Olcer, H., Zakhleniuk, O., Bernacchi, C.J., Calfapietra, C., Long, S.P., and Raines, C.A. 2006. Can fast-growing plantation trees escape biochemical down-regulation of photosynthesis when grown throughout their complete production cycle in the open air under elevated carbon dioxide? *Plant, Cell and Environment* **29**: 1235–1244.

Eichelmann, H., Oja, V., Rasulov, B., Padu, E., Bichele, I., Pettai, H., Mols, T., Kasparova, I., Vapaavuori, E., and Laisk, A. 2004. Photosynthetic parameters of birch (*Betula pendula* Roth) leaves growing in normal and in CO₂- and O₃-enriched atmospheres. *Plant, Cell and Environment* **27**: 479–495.

Ellsworth, D.S., Reich, P.B., Naumburg, E.S., Koch, G.W., Kubiske, M.E., and Smith, S.D. 2004. Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO₂ across four free-air CO₂ enrichment experiments in forest, grassland and desert. *Global Change Biology* **10**: 2121–2138.

Kets, K., Darbah, J.N.T., Sober, A., Riikonen, J., Sober, J., and Karnosky, D.F. 2010. Diurnal changes in photosynthetic parameters of *Populus tremuloides*, modulated by elevated concentrations of CO₂ and/or O₃ and daily climatic variation. *Environmental Pollution* **158**: 1000–1007.

Liberloo, M., Calfapietra, C., Lukac, M., Godbold, D., Luo, Z.-B., Polle, A., Hoosbeek, M.R., Kull, O., Marek, M., Raines, C., Rubino, M., Taylor, G., Scarascia-Mugnozza, G., and Ceulemans, R. 2006. Woody biomass production during the second rotation of a bio-energy *Populus* plantation increases in a future high CO₂ world. *Global Change Biology* **12**: 1094–1106.

Liberloo, M., Dillen, S.Y., Calfapietra, C., Marinari, S., Luo, Z.B., De Angelis, P., and Ceulemans, R. 2005. Elevated CO₂ concentration, fertilization and their interaction: growth stimulation in a short-rotation poplar coppice (EUROFACE). *Tree Physiology* **25**: 179–189.

Liberloo, M., Tulva, I., Raim, O., Kull, O., and Ceulemans, R. 2007. Photosynthetic stimulation under long-term CO₂ enrichment and fertilization is sustained across a closed *Populus* canopy profile (EUROFACE). *New Phytologist* **173**: 537–549.

Noormets, A., Sober, A., Pell, E.J., Dickson, R.E., Podila, G.K., Sober, J., Isebrands, J.G., and Karnosky, D.F. 2001. Stomatal and non-stomatal limitation to photosynthesis in two trembling aspen (*Populus tremuloides* Michx.) clones exposed to elevated CO₂ and O₃. *Plant, Cell and Environment* **24**: 327–336.

Paoletti, E., Seufert, G., Della Rocca, G., and Thomsen, H. 2007. Photosynthetic response to elevated CO₂ and O₃ in *Quercus ilex* leaves at a natural CO₂ spring. *Environmental Pollution* **147**: 516–524.

Sharma, P., Sober, A., Sober, J., Podila, G.K., Kubiske, M.E., Mattson, W.J., Isebrands, J.G., and Karnosky, D.F. 2003. Moderation of CO₂-induced gas exchange responses by elevated tropospheric O₃ in trembling aspen and sugar maple. *Ekologia* **22** (S1): 304–317.

Sholtis, J.D., Gunderson, C.A., Norby, R.J., and Tissue, D.T. 2004. Persistent stimulation of photosynthesis by elevated CO₂ in a sweetgum (*Liquidambar styraciflua*) forest stand. *New Phytologist* **162**: 243–254.

Takeuchi, Y., Kubiske, M.E., Isebrands, J.G., Pregitzer, K.S., Hendrey, G., and Karnosky, D.F. 2001. Photosynthesis, light and nitrogen relationships in a young deciduous forest canopy under open-air CO₂ enrichment. *Plant, Cell and Environment* **24**: 1257–1268.

Wittig, V.E., Bernacchi, C.J., Zhu, X.-G., Calfapietra, C., Ceulemans, R., DeAngelis, P., Gielens, B., Miglietta, F., Morgan, P.B., and Long, S.P. 2005. Gross primary production is stimulated for three *Populus* species grown under free-air CO₂ enrichment from planting through canopy closure. *Global Change Biology* **33**: 644–656.

2.1.4.2 Citrus

- Although there can be a steep multiyear decline in the initial CO₂-induced growth stimulation of citrus trees, the subsequent long-term equilibrium growth enhancement can be substantial.

Trees grown for long periods of time in air enriched with CO₂ sometimes exhibit photosynthetic acclimation or down-regulation. This phenomenon is characterized by modestly reduced rates of photosynthesis (compared to what is observed during short-term exposure to CO₂-enriched air), which result from a slow decline in the activity and/or amount of the primary plant carboxylating enzyme *rubisco*. This

section reports what has been learned about this phenomenon in the few experiments that have studied it in citrus trees.

Jifon *et al.* (2002) grew seedlings of sour orange (*Citrus aurantium* L.) and sweet orange (*Citrus sinensis* L.) for nearly three months in glasshouses maintained at atmospheric CO₂ concentrations of either 360 or 700 ppm, where they were either inoculated with arbuscular mycorrhizal fungi or left non-inoculated as control plants. Thus they studied the effects of both elevated CO₂ and fungal presence on photosynthesis and growth in these two citrus species of contrasting fungal acceptance: sour orange, which displays strong associations with mycorrhizal symbionts, and sweet orange, which exhibits relatively weaker relationships with such fungi.

This protocol revealed elevated CO₂ increased photosynthetic rates in non-mycorrhizal and mycorrhizal sour orange tree seedlings by 18% and 118%, respectively. Elevated CO₂ enhanced photosynthetic rates in non-mycorrhizal and mycorrhizal sweet orange seedlings by 50% and 67%, respectively.

In terms of biomass production, the mycorrhizal sour orange seedlings exposed to ambient CO₂ displayed 18% less growth than the non-mycorrhizal control seedlings, but at elevated CO₂, the mycorrhizal seedlings displayed 15% more growth than the non-mycorrhizal seedlings. Thus atmospheric CO₂ enrichment more than compensated for the carbon costs associated with maintaining the mycorrhizal fungal symbiosis in the sour orange seedlings, and sweet orange seedlings exposed to elevated CO₂ exhibited the same increase in biomass with or without fungal inoculation, indicating this species is less dependent upon fungal symbiosis in eliciting CO₂-induced growth responses.

As the air's CO₂ content continues to rise, therefore, both of these citrus species likely will respond by exhibiting enhanced rates of photosynthesis and biomass production. In sour orange trees, photosynthetic and growth responses to elevated CO₂ will likely be greater when seedlings are involved in symbiotic relationships with soil fungi. Jifon *et al.* found the degree of CO₂-induced photosynthetic acclimation or down-regulation in sour orange tree seedlings was significantly reduced when mycorrhizal fungi were present, as they served as a carbon sink for excess carbohydrates produced by photosynthesis, thereby alleviating the notorious end-product inhibition of photosynthesis. Thus, it is likely increasing atmospheric CO₂ concentrations may increase growth in nearly all tree species throughout

their normal life spans, for most are involved in symbiotic relationships with one or more types of mycorrhizal fungi.

Adam *et al.* (2004) measured numerous plant physiological processes and properties throughout the fourteenth year of a long-term study of the effects of a 75% increase (from 400 ppm to 700 ppm) in the air's CO₂ concentration on the growth and development of sour orange trees that had been grown from the seedling stage to maturity under well-watered and fertilized conditions out-of-doors at Phoenix, Arizona (USA) in clear-plastic-wall open-top enclosures. They then compared their results with those of similar measurements made in earlier years of the study.

In the second year of the experiment, net photosynthesis rates were 2.84 times greater in the CO₂-enriched enclosures than in the ambient-air enclosures. By the sixth year of the study, however, this enhancement ratio had declined to 1.75, and in the fourteenth year it had dropped to 1.45. Plotting similarly declining above-ground woody biomass ratios against these net photosynthesis ratios, Adam *et al.* derived a linear relationship with an r^2 value of 0.997 that yielded a CO₂-induced woody biomass enhancement ratio of 1.78 at the 14-year point of the study. This value for the woody biomass ratio previously had been found by Idso and Kimball (2001) to have been essentially constant from year 10 to year 14, leading Adam *et al.* to conclude the CO₂-induced net photosynthesis ratio they derived (1.45) likely also had been essentially constant over this period, indicating the final equilibrium level at which it had apparently stabilized.

Other evidence for the down-regulation of photosynthesis in the CO₂-enriched sour orange tree leaves was provided by the observation that in year 14 of the study, the pooled mean of the concentration of the large subunit of rubisco in the CO₂-enriched leaves was only 78% of that observed in the ambient-air leaves, and the concentration of the small subunit of rubisco was reduced by 34% in the CO₂-enriched leaves compared to the ambient-air leaves. In addition, the full and initial activities of rubisco under CO₂ enrichment were reduced, as were leaf chlorophyll *a* and total nitrogen concentrations.

Adam *et al.* conclude, "long-term CO₂ enrichment can result in photosynthetic down-regulation in leaves of trees, even under non-limiting nitrogen conditions." At the final equilibrium level of acclimation experienced in the sour orange trees of this long-term study, the 75% enhancement of the air's CO₂ concentration still produced an equivalent percentage increase (or possibly slightly more) in

Plant Characteristics

both wood and fruit production (78 and 80%, respectively).

Three years later, Kimball *et al.* (2007) described the final state of the Phoenix sour orange trees at the termination of that 17-year-long CO₂ enrichment experiment. In terms of total biomass production, which was the primary focus of their summary report, they state the CO₂-enriched to ambient-treatment ratio of annual wood plus fruit production peaked in years 2–4 of the experiment at a value of approximately 2.4, and following that peak “there was a decline through year 8.” Thereafter, however, they found the annually produced-biomass ratios were, as they describe it, “more or less at a plateau that corresponded with the value of the ratio at final harvest of 1.69.”

In terms of harvestable yield, the four researchers write, “the cumulative amount of biomass due to fruit production over the duration of the experiment was increased 85% due to elevated CO₂,” and this increase “was entirely from an increase in fruit number.” In addition, they report, “the vitamin C content of the fruit was increased 7% based on samples taken from the fourth through the 12th years of the experiment,” citing the study of Idso *et al.* (2002). Not only were many more oranges produced by the trees in the CO₂-enriched chambers, but many more better-quality oranges were produced.

In the concluding discussion of one of the major implications of the study, Kimball *et al.* write, “rather than a continual acclimation”—i.e., rather than a gradual long-term decline in the aerial fertilization effect of the extra 300 ppm of CO₂ supplied to the CO₂-enriched trees—“there was a sustained enhancement of about 70% in annual fruit and incremental wood production over the last several years of the experiment.” This observation led them to conclude, “the effects of elevated CO₂ on trees can be large and sustained for many years,” as they demonstrated to be the case with the sour orange trees they studied: Over the entire last decade of the experiment, there was a 70% sustained increase in total biomass production and an 85% increase in fruit production in response to the 75% increase in the air’s CO₂ content employed throughout the study.

References

Adam, N.R., Wall, G.W., Kimball, B.A., Idso, S.B., and Webber, A.N. 2004. Photosynthetic down-regulation over long-term CO₂ enrichment in leaves of sour orange (*Citrus aurantium*) trees. *New Phytologist* **163**: 341–347.

Idso, S.B. and Kimball, B.A. 2001. CO₂ enrichment of sour

orange trees: 13 years and counting. *Environmental and Experimental Botany* **46**: 147–153.

Idso, S.B., Kimball, B.A., Shaw, P.E., Widmer, W., Vanderslice, J.T., Higgs, D.J., Montanari, A., and Clark, W.D. 2002. The effect of elevated atmospheric CO₂ on the vitamin C concentration of (sour) orange juice. *Agriculture, Ecosystems and Environment* **90**: 1–7.

Jifon, J.L., Graham, J.H., Drouillard, D.L., and Syvertsen, J.P. 2002. Growth depression of mycorrhizal Citrus seedlings grown at high phosphorus supply is mitigated by elevated CO₂. *New Phytologist* **153**: 133–142.

Kimball, B.A., Idso, S.B., Johnson, S., and Rillig, M.C. 2007. Seventeen years of carbon dioxide enrichment of sour orange trees: final results. *Global Change Biology* **13**: 2171–2183.

2.1.4.3 Oak

- Both long-term and total-lifetime CO₂ enhancement of the air surrounding various species of oak trees have provided evidence for a lack of photosynthetic acclimation, indicative of the many positive and enduring benefits of atmospheric CO₂ enrichment.

Working in Italy with mature downy oak (*Quercus pubescens*) trees located at two distances from natural CO₂-emitting springs, Stylinski *et al.* (2000) measured various physiological and biochemical properties of trees that had been exposed to atmospheric CO₂ concentrations of approximately 370 and 700 ppm for their entire 40- to 50-year life spans. The oak trees exposed to the elevated CO₂ concentration exhibited net photosynthetic rates 36 to 77% greater than those exhibited by the trees growing at the ambient CO₂ concentration. The CO₂-enriched trees showed no signs of photosynthetic down-regulation. There were no significant differences between the CO₂-enriched and ambient trees with respect to their leaves’ rubisco activity, rubisco content, total nitrogen content, chlorophyll content, and carotenoid content.

Polle *et al.* (2001) collected acorns from mature holly oak (*Quercus ilex*) trees that had been growing under the same set of conditions in Italy, exposed to ambient and twice-ambient atmospheric CO₂ concentrations for their entire lifetimes. After germinating those acorns, the seedlings they produced were grown for eight months at both atmospheric CO₂ concentrations to see if atmospheric CO₂ enrichment of the parent trees had any effect on their offspring’s

response to atmospheric CO₂ enrichment.

The researchers found elevated CO₂ increased whole-plant biomass by 158 and 246% in seedlings derived from acorns produced in ambient and twice-ambient atmospheric CO₂ concentrations, respectively, and the final biomass of the CO₂-enriched seedlings derived from the acorns produced in the CO₂-enriched air was 25% greater than that of the CO₂-enriched seedlings derived from the acorns produced in ambient air. In addition, their gas exchange measurements indicated the CO₂-enriched seedlings derived from the acorns produced on the CO₂-enriched trees exhibited less-pronounced photosynthetic acclimation to elevated CO₂ than did the CO₂-enriched seedlings derived from the acorns produced on the trees exposed to ambient air.

Blaschke *et al.* (2001) studied the effects of long-term atmospheric CO₂ enrichment on gas exchange in both species of mature oak trees—*Quercus ilex* (a strongly drought-tolerant evergreen species) and *Quercus pubescens* (a less drought-tolerant deciduous species)—both of which were growing near CO₂-emitting springs in Italy. They made physiological and biochemical measurements on trees that had been exposed to atmospheric CO₂ concentrations of approximately 370 and 700 ppm for their 30- to 50-year lifetimes. The CO₂-enriched *Q. pubescens* and *Q. ilex* trees exhibited net photosynthetic rates 69% and 26% greater, respectively, than those displayed by trees exposed to ambient CO₂, in spite of CO₂-induced decreases of 30% and 15% in their respective foliar rubisco concentrations. In addition, stomatal conductances of CO₂-enriched *Q. pubescens* trees were approximately 23% lower than those of ambient trees, and stomatal conductances of *Q. ilex* trees displayed no CO₂-sensitivity. Both species exhibited increased water use efficiencies in the elevated CO₂ environment closest to the CO₂-emitting springs. Blaschke *et al.*'s results clearly demonstrate fully mature trees continue to exhibit enhanced rates of photosynthesis and increases in water use efficiency even after decades of exposure to elevated atmospheric CO₂ concentrations.

Marek *et al.* (2001) employed open-top chambers to boost the air's CO₂ content approximately twofold for five years around 30-year-old *Quercus ilex* trees growing in perennial evergreen stands. They found the extra CO₂ increased rates of net photosynthesis in sun-exposed and shaded leaves by 68% and 59%, respectively. After measuring short-term photosynthetic rates at various atmospheric CO₂ concentrations, they found no evidence of photosynthetic acclimation in the leaves of the mature

trees. In addition, they determined the trees' light compensation point—the light level at which photosynthetic carbon uptake is matched by respiratory carbon loss—was 24% and 30% lower in sun-exposed and shaded leaves, respectively, of CO₂-enriched trees than it was in corresponding leaves of the trees growing in ambient air.

As the atmosphere's CO₂ concentration continues to increase, therefore, the work of Marek *et al.* suggests its stimulatory effect on oak tree photosynthesis will persist over the long term. In addition, because elevated CO₂ significantly lowered the light compensation point in mature oak trees, which would allow them to exhibit net carbon gains earlier in the morning and maintain them later into the evening, the stimulatory effect of elevated CO₂ on daily carbon uptake will be further enhanced. Together, these observations suggest carbon sequestration by oak trees, and perhaps other tree species, may be more substantial in future CO₂-enriched air than has been projected.

After burning a Florida (USA) scrub-oak ecosystem (dominated by *Quercus myrtifolia*, *Q. chapmanii*, and *Q. geminata*) to the ground, Ainsworth *et al.* (2002) erected open-top chambers on the site and fumigated them with ambient (380 ppm) and CO₂-enriched (700 ppm) air to study the effects of elevated CO₂ on community regeneration. During the third and fourth years of the study, they found elevated CO₂ consistently increased photosynthetic rates in *Q. myrtifolia* and *Q. chapmanii* by as much as 150% without inducing any degree of photosynthetic acclimation, although acclimation was observed in *Q. geminata*. After three years of exposure to elevated CO₂, the three oak species taken together exhibited an average increase in their rates of photosynthesis of 53%. Thus, at higher CO₂ concentrations, regenerating scrub-oak communities likely will exhibit enhanced rates of photosynthesis that will persist throughout canopy closure and maturity. These increases in photosynthesis likely will enhance community biomass production. The five researchers conclude the sustained increases in photosynthesis exhibited by *Q. myrtifolia* and *Q. chapmanii* have "translated to increased growth in these species, and there is no suggestion that this trend is changing." Carbon sequestration in regenerating and maturing scrub-oak ecosystems is likely to continue to increase with future increases in the air's CO₂ concentration.

Paoletti *et al.* (2007) measured rates of net photosynthesis in upper sunlit leaves of mature *Quercus ilex* trees growing close to (5 m) and further away from (130 m) a CO₂-emitting spring, where the

Plant Characteristics

trees had experienced lifetime exposure to atmospheric CO₂ concentrations of approximately 1,500 and 400 ppm, respectively. This was done during a two-week period in June 2002 at the end of the spring rains, when midday air temperatures rose above 40°C. The net photosynthetic rates of the leaves on the trees growing closest to the CO₂ spring were approximately 250% greater than those of the leaves on the trees growing 125 meters further away, where the air's CO₂ concentration was 1,100 ppm less than it was in the vicinity of the trees nearest the spring. The four Italian researchers conclude, "the considerable photosynthetic stimulation at the very high CO₂ site suggests no photosynthetic down-regulation over long-term CO₂ enrichment."

References

Ainsworth, E.A., Davey, P.A., Hymus, G.J., Drake, B.G., and Long, S.P. 2002. Long-term response of photosynthesis to elevated carbon dioxide in a Florida scrub-oak ecosystem. *Ecological Applications* **12**: 1267–1275.

Blaschke, L., Schulte, M., Raschi, A., Slee, N., Rennenberg, H., and Polle, A. 2001. Photosynthesis, soluble and structural carbon compounds in two Mediterranean oak species (*Quercus pubescens* and *Q. ilex*) after lifetime growth at naturally elevated CO₂ concentrations. *Plant Biology* **3**: 288–297.

Marek, M.V., Sprtova, M., De Angelis, P., and Scarascia-Mugnozza, G. 2001. Spatial distribution of photosynthetic response to long-term influence of elevated CO₂ in a Mediterranean *macchia* mini-ecosystem. *Plant Science* **160**: 1125–1136.

Paoletti, E., Seufert, G., Della Rocca, G., and Thomsen, H. 2007. Photosynthetic responses to elevated CO₂ and O₃ in *Quercus ilex* leaves at a natural CO₂ spring. *Environmental Pollution* **147**: 516–524.

Polle, A., McKee, I., and Blaschke, L. 2001. Altered physiological and growth responses to elevated [CO₂] in offspring from holm oak (*Quercus ilex* L.) mother trees with lifetime exposure to naturally elevated [CO₂]. *Plant, Cell and Environment* **24**: 1075–1083.

Stylinski, C.D., Oechel, W.C., Gamon, J.A., Tissue, D.T., Miglietta, F., and Raschi, A. 2000. Effects of lifelong [CO₂] enrichment on carboxylation and light utilization of *Quercus pubescens* Willd. examined with gas exchange, biochemistry and optical techniques. *Plant, Cell and Environment* **23**: 1353–1362.

2.1.4.4 Pine

- Even though there may be a partial acclimation of the photosynthetic process in pine trees in some CO₂-enrichment experiments, the down-regulation is typically neither complete nor wholly detrimental, for it transfers nitrogen from the sites of photosynthesis to the sinks for photosynthates, where it is most needed when soil infertility is limiting primary productivity.

Studies of the effects of atmospheric CO₂ enrichment on the growth and development of pine trees over the past several years have focused chiefly on three species: *Pinus radiata* (Monterey pine), *Pinus sylvestris* (Scots pine), and *Pinus taeda* (Loblolly pine).

Turnbull *et al.* (1998) grew seedlings of *P. radiata* in open-top chambers near Bromley, Christchurch (New Zealand) for four years at atmospheric CO₂ concentrations of 360 and 650 ppm. Near the conclusion of this period they measured photosynthetic parameters in current-year and one-year-old needles at each of the CO₂ concentrations to determine the effects of elevated CO₂ and leaf age on photosynthesis. This work revealed CO₂-induced increases in needle photosynthetic rate of 63% and 31% in current and one-year-old needles, respectively, suggesting needle age might be an important determinant of photosynthetic acclimation in this species. As further evidence for this hypothesis, they found atmospheric CO₂ enrichment did not induce changes in rubisco content or activity in current-year needles, but it did reduce rubisco content and activity by about 40% in one-year-old needles. After four years of CO₂ enrichment, the CO₂-induced photosynthetic enhancement persisted in each year's new flush of needles, while it experienced a partial down-regulation in older needles.

Reporting further on the same experiment, Griffin *et al.* (2000) noted a decline in older-needle rubisco content in the elevated CO₂ treatment, as well as a 40% reduction in needle stomatal conductance. The first of these changes implies that with the redistribution of nitrogen away from rubisco (which allows it to perform other vital functions), it is likely *P. radiata* will maintain high rates of net carbon uptake while using less nitrogen and other resources in doing so. Coupling these observations with the reduction in water loss due to CO₂-induced decreases in stomatal conductance, *P. radiata* seedlings probably will grow more efficiently with less water inputs in future atmospheres containing greater con-

centrations of CO₂.

At the conclusion of the four-year study of *P. radiata* in Christchurch, New Zealand, Greenep *et al.* (2003) took cuttings from the four-year-old Monterey pines that had experienced lifetime exposure to either ambient or elevated atmospheric CO₂ concentrations and grew them for one year in their respective CO₂ treatments in open-top chambers, where they were irrigated daily and fertilized every three months. They found the “photosynthetic rate in young needles during summer, autumn and spring was 34, 43 and 38% higher, respectively, in trees grown at elevated CO₂ than in trees grown at ambient CO₂,” and “in older needles, the corresponding photosynthetic rate increases were 26, 47 and 49%.” In addition, water use efficiency was 49% higher in the foliage of the elevated CO₂ treatment, although there was no change in needle stomatal conductance.

These responses were comparable to those observed in the parent trees when they were approximately the same size and age as the second-generation trees. However, there were signs of photosynthetic acclimation in the older needles of the parent trees when they were larger (in their third and fourth years) but physiologically younger than the second-generation trees, which by the time of this study (having been derived from four-year-old trees and grown for an additional year) were in their fifth year of life. Thus, the researchers suggested the down-regulation of photosynthesis observed in the parent trees in their third and fourth years “was a result of a shift in the proportion of young to old needles as the trees increased in size.”

In concluding, they hypothesize, “in small trees, close proximity of active sinks, such as developing buds, to a proportionally small reservoir of source tissue (mature foliage) would increase the overall sink strength and reduce the extent of photosynthetic acclimation (down-regulation) at elevated CO₂.” They note, for example, “within an immature *P. radiata* canopy, young needles may represent as much as 4 to 10 times the biomass of older needles,” but “as the canopy matures this ratio approaches equality (Turnbull *et al.*, 1998).” Hence, they conclude, “down-regulation of photosynthesis at elevated CO₂ is related to tree size rather than tree age or duration of exposure,” and “the capacity for enhanced photosynthesis in trees growing in elevated CO₂ is unlikely to be lost in subsequent generations.”

Jach and Ceulemans (2000) studied three-year-old *Pinus sylvestris*, Scots pine, seedlings rooted in the ground and grown in open-top chambers maintained at atmospheric CO₂ concentrations of 350

and 750 ppm for two additional years to determine the long-term effects of elevated CO₂ on photosynthesis in this important European timber species. To make the experimental results more representative of the natural world, no nutrients or irrigation water were applied to the soils during their investigation.

During the second year of atmospheric CO₂ enrichment, the photosynthetic rates of the current-year and one-year-old CO₂-enriched needles were 62% and 65% greater, respectively, than the rates displayed by the needles on the seedlings growing in ambient air. When photosynthesis was measured at atmospheric CO₂ concentrations reciprocal to growth CO₂ concentrations, the researchers detected photosynthetic acclimation in the CO₂-enriched seedlings, as evidenced by a 21% reduction in their photosynthetic rates. However, Jach and Ceulemans note, “the stimulatory effect of elevated CO₂ on photosynthesis substantially exceeded the magnitude of down-regulation.” Even with photosynthetic acclimation, the rate of net photosynthesis in the CO₂-enriched seedlings was more than 40% greater than the rate measured in the control seedlings exposed to ambient air.

In a parallel study of Scots pine, Gielen *et al.* (2000) worked with six-year-old seedlings rooted in the ground within open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 750 ppm for three years to determine the long-term effects of elevated CO₂ on chlorophyll fluorescence and needle characteristics. No nutrients or irrigation water were applied to the soil. At the end of the period, a detailed seasonal analysis indicated elevated CO₂ did not significantly impact the photochemical quantum efficiency of photosystem II, nor did it affect any parameters associated with chlorophyll fluorescence. This indicates atmospheric CO₂ enrichment did not modify the light-dependent reactions of photosynthesis in this species.

With respect to needle characteristics, on the other hand, elevated CO₂ reduced needle nitrogen and chlorophyll contents by 33% and 26%, respectively. These observations suggest the light-independent reactions of photosynthesis were being modified by long-term exposure to elevated CO₂ in a manner indicating photosynthetic acclimation. But this acclimation of the photosynthetic process allows for the redistribution of limiting resources—such as nitrogen—away from what thus becomes a more efficient photosynthetic apparatus, so this important nutrient can be utilized in other areas of the tree where it is needed more. Thus, this CO₂-induced phenomenon can have a positive effect on growth

because it allows trees to produce more biomass under conditions of low soil fertility than would otherwise be possible under ambient CO₂ concentrations, due to the mobilization of nitrogen out of photosynthetically active leaves and into actively expanding sink tissues.

Maier *et al.* (2002) constructed open-top chambers around 13-year-old *Pinus taeda*, loblolly pines, growing on infertile sandy soil and fumigated them for two more years with air containing either 350 ppm or 550 ppm of CO₂, while half of the trees at each CO₂ concentration received supplemental soil fertilization. They found the elevated CO₂ increased branch needle area by 13%, and soil fertilization increased it by 38%. Applied together, the two treatments enhanced branch needle area by 56%. In addition, the extra CO₂ enhanced the trees' net photosynthesis rates by 82%, with the trees showing no signs of photosynthetic acclimation over the two-year duration of the study.

Crous and Ellsworth (2004) studied the photosynthetic rates of different-age needles measured at different crown positions on the 19-year-old (in 2002) loblolly pine trees at the Duke Forest FACE facility in the sixth year of that long-term study, comparing them with the results of similar measurements made over the prior five years. Although there was some evidence of photosynthetic down-regulation in one-year-old needles across the fifth to sixth year of CO₂ exposure, the two researchers report "strong photosynthetic enhancement in response to elevated CO₂ (e.g., +60% across age classes and canopy locations) was observed across the years."

Looking at the concept of acclimation from a somewhat different perspective, Lichter *et al.* (2008) noted progressive nitrogen limitation (PNL) may "accompany carbon sequestration in plants and soils stimulated by CO₂ fertilization, gradually attenuating the CO₂ response," after which they described what they learned about the PNL hypothesis from a nine-year CO₂ enrichment study.

The nine researchers report their data pertaining to forest-floor carbon pools indicate the existence of "a long-term steady-state sink" of about 30 g C per m² per year, which represents, they write, "a substantial increase in forest-floor C storage under elevated CO₂ (i.e. 29%)," and which they attribute to "increased litterfall and root turnover during the first 9 years of the study." Of the mineral soil C formed over this period, they note "approximately 20% has been allocated to stable pools that will likely remain protected from microbial activity and associated release as CO₂."

The research team also found "a significant widening of the C:N ratio of soil organic matter in the upper mineral soil under both elevated and ambient CO₂." This suggests, as they describe it, "enhanced rates of soil organic matter decomposition are increasing mineralization and uptake to provide the extra N required to support the observed increase in primary productivity under elevated CO₂." At the Duke Forest FACE site, for example, Pritchard *et al.* (2008) say this CO₂-induced increase in productivity amounts to approximately 30% annually, and they add there is "little evidence to indicate a diminished response through time," citing Finzi *et al.* (2007), who found the same to be true at the long-term forest FACE studies being conducted at Rhinelander, Wisconsin (USA), Oak Ridge National Laboratory (USA), and Tuscania (Italy).

It thus appears several of Earth's forests thought to have access to less-than-adequate soil nitrogen supplies may be able to acquire the extra nitrogen they need to maintain the sizable increases in their growth rates that are driven by elevated concentrations of atmospheric CO₂. In the case of North Carolina's Duke Forest, for example, "even after nine years of experimental CO₂ fertilization," as Lichter *et al.* describe it, "attenuation of the CO₂-induced productivity enhancement has not been observed," as also has been noted by Finzi *et al.* (2006). This finding at this location is extremely significant, because the growth of pine-hardwood forests in the southeastern United States often removes so much nitrogen from the soils in which they grow that they induce what Finzi and Schlesinger (2003) have described as "a state of acute nutrient deficiency that can only be reversed with fertilization," which was not employed in the Duke Forest FACE study.

Even though there may sometimes be a partial acclimation of the photosynthetic process in pine trees in some CO₂-enrichment experiments, the research described above suggests the down-regulation seems never to be complete. The phenomenon may even play a positive role in shifting much-needed nitrogen from the sites of photosynthesis to the sinks for photosynthates in situations where soil fertility is a limiting factor to primary productivity.

References

Crous, K.Y. and Ellsworth, D.S. 2004. Canopy position affects photosynthetic adjustments to long-term elevated CO₂ concentration (FACE) in aging needles in a mature *Pinus taeda* forest. *Tree Physiology* 24: 961–970.

Climate Change Reconsidered II: Biological Impacts

Finzi, A.C., Moore, D.J.P., DeLucia, E.H., Lichter, J., Hofmockel, K.S., Jackson, R.B., Kim, H.-S., Matamala, R., McCarthy, H.R., Oren, R., Phippen, J.S., and Schlesinger, W.H. 2006. Progressive nitrogen limitation of ecosystem processes under elevated CO₂ in a warm-temperate forest. *Ecology* **87**: 15–25.

Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., and Ceulemans, R. 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂. *Proceedings of the National Academy of Sciences, USA* **104**: 14,014–14,019.

Finzi, A.C. and Schlesinger, W.H. 2003. Soil-nitrogen cycling in a pine forest exposed to 5 years of elevated carbon dioxide. *Ecosystems* **6**: 444–456.

Gielen, B., Jach, M.E., and Ceulemans, R. 2000. Effects of season, needle age and elevated atmospheric CO₂ on chlorophyll fluorescence parameters and needle nitrogen concentration in (*Pinus sylvestris* L.). *Photosynthetica* **38**: 1321.

Greenep, H., Turnbull, M.H., and Whitehead, D. 2003. Response of photosynthesis in second-generation *Pinus radiata* trees to long-term exposure to elevated carbon dioxide partial pressure. *Tree Physiology* **23**: 569–576.

Griffin, K.L., Tissue, D.T., Turnbull, M.H., and Whitehead, D. 2000. The onset of photosynthetic acclimation to elevated CO₂ partial pressure in field-grown *Pinus radiata* D. Don. after 4 years. *Plant, Cell and Environment* **23**: 1089–1098.

Jach, M.E. and Ceulemans, R. 2000. Effects of season, needle age and elevated atmospheric CO₂ on photosynthesis in Scots pine (*Pinus sylvestris* L.). *Tree Physiology* **20**: 145–157.

Lichter, J., Billings, S.A., Ziegler, S.E., Gaindh, D., Ryals, R., Finzi, A.C., Jackson, R.B., Stemmler, E.A., and Schlesinger, W.H. 2008. Soil carbon sequestration in a pine forest after 9 years of atmospheric CO₂ enrichment. *Global Change Biology* **14**: 2910–2922.

Maier, C.A., Johnsen, K.H., Butnor, J., Kress, L.W., and Anderson, P.H. 2002. Branch growth and gas exchange in 13-year-old loblolly pine (*Pinus taeda*) trees in response to elevated carbon dioxide concentration and fertilization. *Tree Physiology* **22**: 1093–1106.

Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., and Oren, R. 2008. Mycorrhizal and rhizomorph dynamics in a loblolly pine forest during 5 years of free-air-CO₂-enrichment. *Global Change Biology* **14**: 1–13.

Turnbull, M.H., Tissue, D.T., Griffin, K.L., Rogers,

G.N.D., and Whitehead, D. 1998. Photosynthetic acclimation to long-term exposure to elevated CO₂ concentration in *Pinus radiata* D. Don. is related to age of needles. *Plant, Cell and Environment* **21**: 1019–1028.

2.1.4.5 Spruce

- Studies of spruce trees reveal atmospheric CO₂ enrichment increases their photosynthetic rates, even in the case of partial photosynthetic acclimation, which enables them to transport greater amounts of soluble carbohydrates, including glucose, to active sink tissues to support their enhanced growth and development even on nutrient-poor soils.

The large increases in net photosynthesis exhibited by trees growing in CO₂-enriched air have been claimed to disappear gradually over extended periods of time, in a process known as acclimation or down-regulation. The following section reviews the findings of several studies of spruce trees that bear on this question.

Spunda *et al.* (1998) monitored 15-year-old Norway spruce trees in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm for four additional years, to study the long-term effects of elevated CO₂ on photosynthetic acclimation. When they measured the trees' photosynthetic rates at reciprocal growth CO₂ concentrations, they found the CO₂-enriched shoots displayed a reduction of 18% compared to shoots grown in ambient air, indicating the presence of CO₂-induced photosynthetic acclimation. Likewise, when analyzing photosynthetic pigments, they found the total amounts of chlorophylls and carotenoids in needles produced in CO₂-enriched air to be 17% and 14% less, respectively, than the amounts found in needles produced in ambient air. Nevertheless, when measured at growth CO₂ concentrations, current-year CO₂-enriched shoots still displayed rates of net photosynthesis 78% greater than those exhibited by shoots of trees grown in ambient air.

Egli *et al.* (1998) rooted several saplings of different Norway spruce genotypes directly into calcareous or acidic soils in open-top chambers and exposed them to atmospheric CO₂ concentrations of 370 or 570 ppm and low or high soil nitrogen contents, in order to determine the effects of elevated CO₂ and soil quality on the saplings' photosynthesis and growth rates. They found the elevated CO₂ stimulated light-saturated rates of net photosynthesis

under all conditions, with all genotypes exhibiting stimulations as great as 35%. Elevated CO₂ also led to a down-regulation of photosynthesis. Rates of leaf photosynthesis still remained higher for the trees grown in the CO₂-enriched air, despite the occurrence of this phenomenon. This increase in photosynthesis ultimately contributed to greater instantaneous water-use efficiencies of the trees grown in elevated CO₂, which were also promoted by CO₂-induced decreases in needle stomatal conductance. All these processes operating together consistently led to increased aboveground biomass production, regardless of genotype, soil type, and nitrogen content.

Wiemken and Ineichen (2000) grew Norway spruce seedlings for three years in growth chambers maintained at atmospheric CO₂ concentrations of 280, 420, and 560 ppm. In addition, the seedlings received either low, medium, or high levels of nitrogen fertilization. This work revealed nitrogen fertilization did not affect the concentrations of any sugars within mature needles of the seedlings, but atmospheric CO₂ enrichment significantly enhanced needle glucose contents in a season-dependent manner.

In the highly productive growing phases characteristic of spring and early summer, for example, glucose contents in mature needles of the CO₂-enriched trees were not significantly different from those observed in needles of the trees exposed to atmospheric CO₂ concentrations of 280 and 420 ppm. In late summer, fall, and winter, however, glucose concentrations in needles on the CO₂-enriched trees were 40% to 50% higher than those of needles on trees subjected to ambient and sub-ambient CO₂ concentrations (420 and 280 ppm, respectively). These seasonal fluctuations in needle glucose concentrations suggested to the two researchers glucose levels may be mediating a seasonal photosynthetic down-regulation in spruce needles, as had been noted previously by others.

It would appear that as the air's CO₂ content continues to rise, Norway spruce trees likely will increase their photosynthetic rates, which should result in greater needle concentrations of soluble carbohydrates, including glucose. During favorable growing conditions associated with spring and early summer, the additional glucose produced by trees growing in CO₂-enriched air likely will be mobilized and sent to active sinks to support their growth and development. As growing conditions become less favorable in late summer, glucose may not be mobilized from needles as rapidly as it was during the spring and early summer, which may lead to a seasonal photosynthetic down-regulation in this species.

In spite of this intimation of a temporary seasonal down-regulation of photosynthesis in Norway spruce seedlings, it seems logical to expect they will still exhibit greater biomass production at higher atmospheric CO₂ concentrations, as demonstrated by the findings of Spanda *et al.* (1998) and Egli *et al.* (1998) and the work of Tjoelker *et al.* (1998). The latter scientists studied *Picea mariana* (black spruce) together with quaking aspen, paper birch, tamarack, and jack pine in controlled-environment chambers for three months at atmospheric CO₂ concentrations of 370 ppm or 580 ppm and day/night temperatures ranging from 18/12°C to 30/24°C. They found the 57% increase in the CO₂ content of the air significantly stimulated net photosynthesis in all of the studied species by an average of 28%, regardless of temperature, over the three-month study period. Elevated CO₂ decreased leaf nitrogen levels in all species, causing differing degrees of photosynthetic down-regulation. However, the mobilization of nitrogen from the trees' leaves or needles, coupled with the sustained enhancement of photosynthetic rates, led to increased photosynthetic nitrogen-use efficiencies in all plants grown in elevated CO₂. In addition, the elevated CO₂ decreased stomatal conductance by 10% to 25% in all species, leading to 40% to 80% increases in their instantaneous water-use efficiencies. As in essentially all such studies conducted to date, these benefits of atmospheric CO₂ enrichment more than compensated for the incomplete acclimation that sometimes occurs.

References

- Egli, P., Maurer, S., Gunthardt-Goerg, M.S., and Korner, C. 1998. Effects of elevated CO₂ and soil quality on leaf gas exchange and aboveground growth in beech-spruce model ecosystems. *New Phytologist* **140**: 185–196.
- Spanda, V., Kalina, J., Cajanek, M., Pavlickova, H., and Marek, M.V. 1998. Long-term exposure of Norway spruce to elevated CO₂ concentration induces changes in photosystem II mimicking an adaptation to increased irradiance. *Journal of Plant Physiology* **152**: 413–419.
- Tjoelker, M.G., Oleksyn, J., and Reich, P.B. 1998. Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO₂ and temperature. *Tree Physiology* **18**: 715–726.
- Wiemken, V. and Ineichen, K. 2000. Seasonal fluctuations of the levels of soluble carbohydrates in spruce needles exposed to elevated CO₂ and nitrogen fertilization and glucose as a potential mediator of acclimation to elevated CO₂. *Journal of Plant Physiology* **156**: 746–750.

2.1.5 Source/Sink Relations

- Plants with large sink capacity typically respond strongly to atmospheric CO₂ enrichment by increasing their photosynthetic rates; but when sink capacity is low, they reduce their rates of photosynthesis via photosynthetic acclimation, yielding up more of the nitrogen and other nutrients they possess to help build sink structures such as roots, tubers, or aboveground fruit.

Plants grown in elevated CO₂ for extended durations often, but not always, exhibit some degree of photosynthetic acclimation or down-regulation, typically characterized by reduced rates of photosynthesis resulting from decreased activity and/or amount of the primary plant carboxylating enzyme rubisco. When this phenomenon occurs, leaf nitrogen content often decreases, as nitrogen previously invested in rubisco is transferred to other parts of the plant. Photosynthetic acclimation to elevated CO₂ can be induced by insufficient plant sink strength, which often leads to carbohydrate accumulation in source leaves and reductions in net rates of photosynthesis. Acclimation also can result from the physical constraints of growing plants in pots or by limiting their access to important nutrients such as nitrogen. This section reviews the results of various studies of source:sink relationships on plant growth responses to atmospheric CO₂ enrichment.

In a simple experiment designed to determine how sink size naturally influences plant growth response to elevated CO₂, Reekie *et al.* (1998) grew various *Brassica* species of differing sink capacity in growth chambers receiving atmospheric CO₂ concentrations of 350 and 1,000 ppm. After four weeks, elevated CO₂ had increased the total dry weights of all *Brassica* species. However, at final harvests made after six or 12 weeks of CO₂ fumigation, significant CO₂-induced increases in total dry weight persisted only in species possessing well-developed carbon sinks. Thus, the authors' data suggest species with inherently low sink strength are more likely to experience CO₂-induced acclimation than are species with inherently large sink strength that can naturally utilize the additional carbohydrates produced under CO₂-enriched conditions to progressively increase their biomass.

In a non-invasive manipulation of plant source:sink ratios, Gesch *et al.* (1998) grew rice plants for one month in growth chambers having atmospheric CO₂ concentrations of 350 and 700 ppm before switching half of the plants in each chamber to

the other CO₂ growth concentration. Within 24 hours of switching, plants moved into the elevated CO₂ environment displayed a mean 15% increase in photosynthetic rate and a mean 19% reduction in *rbcS* mRNA, whereas previously CO₂-enriched plants switched to ambient CO₂ exhibited photosynthetic rates 10% lower than those of plants grown continuously at ambient CO₂ and an analogous 19% increase in the amount of *rbcS* transcript. These observations suggest rice plants grown continuously in elevated CO₂ experienced sink limitations to growth.

In the FACE experiment of Rogers *et al.* (1998), perennial ryegrass growing at atmospheric CO₂ concentrations of 360 and 600 ppm was frequently cut to determine how physical changes in source:sink relationships influence transient growth responses to elevated CO₂. Regardless of cutting events, plants grown in elevated CO₂ with high soil nitrogen availability exhibited no signs of CO₂-induced photosynthetic acclimation. In contrast, when measured one day prior to cutting, plants grown in elevated CO₂ with low soil nitrogen availability exhibited 25% reductions in leaf rubisco content. One day after cutting, this acclimation response was completely eliminated, probably in response to rapid carbohydrate utilization to repair cut leaves. Similarly, Bryant *et al.* (1998) report simulated grazing events reversed CO₂-induced decreases in rubisco activity in leaves of chalk grassland species growing on nutrient-poor soils. The results of these studies suggest photosynthetic acclimation likely results from an indirect effect of low soil nitrogen on sink development, rather than from a direct effect of elevated CO₂ on leaf photosynthetic capacity.

Farage *et al.* (1998) investigated the role of nitrogen supply in inducing photosynthetic acclimation in CO₂-enriched wheat. In one experiment, plants were grown in pots placed within growth chambers receiving 350 ppm or 650 ppm CO₂ and were irrigated with fixed amounts of low- or high-nitrogen solutions on a regular basis, which is standard protocol for experiments utilizing potted plants. In the other experiment, plants were grown hydroponically at 350 ppm or 650 ppm CO₂ to eliminate any root restriction effects on growth. The plants were placed in nutrient solutions containing low or high concentrations of nitrogen, which were continually increased to match the rising demand of the growing plants. All plants were grown for approximately five weeks and then harvested.

Wheat plants grown in pots exhibited photosynthetic acclimation when supplied with low fixed

amounts of nitrogen, and elevated CO₂ exacerbated this effect. In contrast, hydroponically grown wheat that received gradually increasing nutrient supplies, which became ever-larger with increasing plant size, exhibited no signs of photosynthetic acclimation when grown at elevated CO₂ even at low nitrogen availability. These observations led the authors to conclude low nitrogen fertilization may not lead to photosynthetic acclimation in elevated CO₂, as long as the nitrogen supply keeps pace with the relative growth rate of the plants. Consequently, it is important for researchers who use potted plants to increase plant nutrient supply in proportion to plant growth as their experiments progress, in order to avoid inducing photosynthetic acclimation via the dilution of tissue nitrogen contents that typically results from enhanced carbohydrate and biomass production in elevated CO₂.

It appears plants with inherently large sink capacity have the ability to respond strongly and persistently to atmospheric CO₂ enrichment. In other plants, a short-term reduction in source strength often overcomes sink-induced limitations on growth responses to atmospheric CO₂ enrichment. Foliar reductions resulting from clipping events—or non-invasive reductions in source strength—nearly always eliminated CO₂-induced photosynthetic acclimation. Moreover, acclimation to elevated CO₂ may actually be an indirect effect induced by insufficient amounts of soil nitrogen; if soil nitrogen content is too low, additional sink strength cannot be developed in some plants, which consequently allows carbohydrate accumulation in source leaves that can induce photosynthetic acclimation by feedback inhibition processes. As the CO₂ content of the air rises and increases plant photosynthetic rates, many plants will respond by reducing rubisco contents, which frees up large quantities of nitrogen that may be used to enhance sink strength to keep plants from exhibiting photosynthetic acclimation.

References

- Bryant, J., Taylor, G., and Frehner, M. 1998. Photosynthetic acclimation to elevated CO₂ is modified by source:sink balance in three component species of chalk grassland swards grown in a free air carbon dioxide enrichment (FACE) experiment. *Plant, Cell and Environment* **21**: 159–168.
- Farage, P.K., McKee, I.F., and Long, S.P. 1998. Does a low nitrogen supply necessarily lead to acclimation of photosynthesis to elevated CO₂? *Plant Physiology* **118**: 573–580.

Gesch, R.W., Boote, K.J., Vu, J.C.V., Allen Jr., L.H., and Bowes, G. 1998. Changes in growth CO₂ result in rapid adjustments of ribulose-1,5-bisphosphate carboxylase/oxygenase small subunit gene expression in expanding and mature leaves of rice. *Plant Physiology* **118**: 521–529.

Reekie, E.G., MacDougall, G., Wong, I., and Hicklenton, P.R. 1998. Effect of sink size on growth response to elevated atmospheric CO₂ within the genus *Brassica*. *Canadian Journal of Botany* **76**: 829–835.

Rogers, A., Fischer, B.U., Bryant, J., Frehner, M., Blum, H., Raines, C.A., and Long, S.P. 1998. Acclimation of photosynthesis to elevated CO₂ under low-nitrogen nutrition is affected by the capacity for assimilate utilization. Perennial ryegrass under free-air CO₂ enrichment. *Plant Physiology* **118**: 683–689.

2.2 Antioxidants

Oxidation is a chemical process that occurs naturally in plants, animals, and humans. Although the process is vital for life, it can produce free radicals, including reactive oxygen species (ROS), in a series of chain reactions that lead to cell damage and cell death. In humans, oxidative stress has been linked to cardiovascular disease, cancer, neurodegenerative disorders, and other chronic diseases. Nature's way of responding to the threats posed by such radicals is to neutralize and inhibit their reactions via complex systems of multiple types of antioxidants.

Plants, animals, and humans each harbor defense systems comprised of various types of antioxidants, including vitamin A, vitamin C, and vitamin E, and enzymes such as catalase, superoxide dismutase, and various peroxidases. Inadequate levels of antioxidants, or inhibition of antioxidant enzymes, can lead to oxidative stress.

The impact of rising atmospheric CO₂ on antioxidant compounds and enzymes found in plants is examined in Section 7.3.1.1 of Chapter 7, *Human Health*, this volume, where it is noted higher levels of atmospheric CO₂ tend to reduce oxidative stress, resulting in a reduction in antioxidant enzyme activity because fewer such enzymes are needed to counter the stress. As a result, plants are able to direct more of their limited resources into the production of other plant tissues or processes essential to their continued growth and development. In some cases, such resources are invested into the production and enhancement of antioxidative compounds, which are known to provide health benefits to animals and humans that ingest them.

2.3 Chlorophyll

- Atmospheric CO₂ enrichment may either increase, decrease, or have no effect on leaf chlorophyll concentration. Even when it is decreased, the reallocation of its nitrogen generally occurs without any adverse consequences, as most plants displaying this response typically continue to exhibit significant increases in photosynthesis and biomass production.

Plants of all types that are grown in elevated CO₂ environments often exhibit some degree of physiological adaptation. The most common of these is photosynthetic acclimation or down-regulation, which is characterized by reductions in the activity and/or amount of the primary plant carboxylating enzyme rubisco (see Section 2.1 Acclimation). In addition, plant acclimation to elevated atmospheric CO₂ may lead to reductions in leaf nitrogen and chlorophyll concentrations, the latter of which is discussed below.

Photosynthetic acclimation to elevated CO₂ is not a detrimental phenomenon, but rather a positive phenomenon that facilitates the redistribution of nitrogen and other important resources away from a plant's photosynthetic apparatus toward other sites where growth-limiting processes also need these resources. In an open-top chamber experiment on spruce saplings that lasted three years, for example, CO₂-enriched trees exhibited photosynthetic rates 62% greater than those of their ambiently grown counterparts, in spite of their lower leaf chlorophyll contents (Centritto and Jarvis, 1999). Similar studies on herbaceous (Ong *et al.*, 1998; Pritchard *et al.*, 2000) and woody (Grams *et al.*, 1999; Ormrod *et al.*, 1999) species have yielded analogous results, indicating leaf chlorophyll concentrations in these species are often much greater than what are actually needed for adequate photosynthesis in CO₂-enriched atmospheres.

Nevertheless, atmospheric CO₂ enrichment does not always result in decreased leaf chlorophyll concentrations. In an open-top chamber experiment with alfalfa, for example, plants grown at an atmospheric CO₂ concentration of 600 ppm had greater leaf chlorophyll concentrations than those observed in plants grown at 340 ppm (Sgherri *et al.*, 1998). And exposure of an orchid to a super-elevated CO₂ concentration of 10,000 ppm led to a 64% increase in leaf chlorophyll concentration relative to that measured in leaves of plants grown at ambient CO₂ (Gouk *et al.*, 1999).

In between these two responses, increases in the

air's CO₂ content sometimes have been demonstrated to have no significant effect on leaf chlorophyll concentration. Sicher and Bunce (1999), for example, reported twice-ambient CO₂ concentrations elicited no change in leaf chlorophyll contents of potato plants during a three-year study. Even with higher CO₂ enrichment levels (870 ppm above ambient concentrations), Monje and Bugbee (1998) did not detect any CO₂-induced changes in leaf chlorophyll content of wheat. Similar results have been reported in woody plants, where a doubling of the atmospheric CO₂ concentration had no significant impact on leaf chlorophyll concentrations within sugar maple (Li *et al.*, 2000) and oak species (Carter *et al.*, 2000; Styliniski *et al.*, 2000).

These studies demonstrate atmospheric CO₂ enrichment may either increase, decrease, or have no effect on leaf chlorophyll concentrations, and even when leaf chlorophyll concentrations are decreased the reallocation of the nitrogen that is essential for producing chlorophyll and other photosynthetic components typically occurs without any adverse consequences. Most plants displaying this response almost always continue to exhibit significant increases in photosynthesis and biomass production.

References

- Carter, G.A., Bahadur, R., and Norby, R.J. 2000. Effects of elevated atmospheric CO₂ and temperature on leaf optical properties in *Acer saccharum*. *Environmental and Experimental Botany* **43**: 267–273.
- Centritto, M. and Jarvis, P.G. 1999. Long-term effects of elevated carbon dioxide concentration and provenance on four clones of Sitka spruce (*Picea sitchensis*). II. Photosynthetic capacity and nitrogen use efficiency. *Tree Physiology* **19**: 807–814.
- Gouk, S.S., He, J., and Hew, C.S. 1999. Changes in photosynthetic capability and carbohydrate production in an epiphytic CAM orchid plantlet exposed to super-elevated CO₂. *Environmental and Experimental Botany* **41**: 219–230.
- Grams, T.E.E., Anegg, S., Haberle, K.-H., Langebartels, C., and Matyssek, R. 1999. Interactions of chronic exposure to elevated CO₂ and O₃ levels in the photosynthetic light and dark reactions of European beech (*Fagus sylvatica*). *New Phytologist* **144**: 95–107.
- Li, J.-H., Dijkstra, P., Hymus, G.J., Wheeler, R.M., Piastuchi, W.C., Hinkle, C.R., and Drake, B.G. 2000. Leaf senescence of *Quercus myrtifolia* as affected by long-term CO₂ enrichment in its native environment. *Global Change Biology* **6**: 727–733.

Plant Characteristics

Monje, O. and Bugbee, B. 1998. Adaptation to high CO₂ concentration in an optimal environment: radiation capture, canopy quantum yield and carbon use efficiency. *Plant, Cell and Environment* **21**: 315–324.

Ong, B.-L., Koh, C.K.-K., and Wee, Y.-C. 1998. Effects of CO₂ on growth and photosynthesis of *Pyrrosia piloselloides* (L.) Price gametophytes. *Photosynthetica* **35**: 21–27.

Ormrod, D.P., Lesser, V.M., Olszyk, D.M., and Tingey, D.T. 1999. Elevated temperature and carbon dioxide affect chlorophylls and carotenoids in Douglas-fir seedlings. *International Journal of Plant Science* **160**: 529–534.

Pritchard, S.G., Ju, Z., van Santen, E., Qiu, J., Weaver, D.B., Prior, S.A., and Rogers, H.H. 2000. The influence of elevated CO₂ on the activities of antioxidative enzymes in two soybean genotypes. *Australian Journal of Plant Physiology* **27**: 1061–1068.

Sgherri, C.L.M., Quartacci, M.F., Menconi, M., Raschi, A., and Navari-Izzo, F. 1998. Interactions between drought and elevated CO₂ on alfalfa plants. *Journal of Plant Physiology* **152**: 118–124.

Sicher, R.C. and Bunce, J.A. 1999. Photosynthetic enhancement and conductance to water vapor of field-grown *Solanum tuberosum* (L.) in response to CO₂ enrichment. *Photosynthesis Research* **62**: 155–163.

Stylinski, C.D., Oechel, W.C., Gamon, J.A., Tissue, D.T., Miglietta, F., and Raschi, A. 2000. Effects of lifelong [CO₂] enrichment on carboxylation and light utilization of *Quercus pubescens* Willd. examined with gas exchange, biochemistry and optical techniques. *Plant, Cell and Environment* **23**: 1353–1362.

2.4 Early Spring Growth

- Studies conducted on several tree species suggest either enhanced carbohydrates stored in terminal branchlets or nitrogen stored in second-year leaves may be remobilized to facilitate greater first-flush needle or leaf growth the following year as a result of atmospheric CO₂ enrichment.

Each year in the spring, when vegetation awakens from its winter dormancy and begins to grow, producing new flushes of leaves and needles, the vegetative demand for carbon is so great that plant photosynthesis actually draws down the atmosphere's CO₂ concentration in the Northern Hemisphere by several ppm (in the Southern Hemisphere too, but to a much lesser extent due to the larger surface area of oceans). In the fall, when much of the new biomass produced over the spring and summer begins to

senesce and decay, large amounts of carbon are returned to the atmosphere, causing the air's CO₂ concentration to rise by several ppm. Hence, an annual oscillation is imposed on the ever-increasing CO₂ content of the atmosphere in each hemisphere, in which the CO₂ concentration first decreases with spring and summer growth and then increases with fall senescence.

In analyzing this annual atmospheric CO₂ oscillation, several scientists have noted the spring drawdown of the air's CO₂ content is beginning a few days earlier than it did several decades ago. Some have attributed this phenomenon to CO₂-induced global warming, but others have suggested the increasingly earlier occurrence of what may be called biological spring may result from an amplification of early spring branch growth that is provided by the ever-increasing aerial fertilization effect of the ongoing rise in the air's CO₂ content.

One of the first papers to anticipate this phenomenon was that of Lovelock *et al.* (1999), who enclosed branchlets of 30-m tall *Luehea seemannii* trees in open-top chambers suspended within the trees' upper canopies and fumigated them with air of either 360 or 750 ppm CO₂ for nearly 40 weeks in a study of the effects of elevated CO₂ on photosynthesis, growth, and reproduction in this deciduous tropical tree species. By these means they determined leaves of branchlets grown in CO₂-enriched air displayed net photosynthetic rates approximately 30% greater than those of leaves of branchlets grown in ambient air. The additional carbohydrates produced by this phenomenon were not used by CO₂-enriched branchlets to increase leaf growth or reproductive efforts. Instead, they were stored in terminal woody tissues. This observation led the authors to suggest enhanced carbohydrate storage in terminal branchlets may facilitate greater first-flush leaf growth the following year.

Documentation of this phenomenon was first provided by Idso *et al.* (2000), who periodically measured the lengths, dry weights, and leaf chlorophyll concentrations of new branches that each spring emerged from sour orange trees that had been growing out-of-doors in clear-plastic-wall open-top chambers for more than 10 years in air of either 400 or 700 ppm CO₂. Although new spring branch growth always began on exactly the same day in both the ambient and CO₂-enriched chambers, the initial rate of new-branch biomass production was vastly greater in the CO₂-enriched trees. Three weeks after branch growth began, for example, new branches on the CO₂-enriched trees were typically more than four times

more massive than their counterparts on the ambient-treatment trees, while on a per-tree basis, there was more than six times more new-branch biomass on the trees growing in the CO₂-enriched chambers than in the ambient-air chambers. Just as rapidly as this ultra-enhancement of new branch growth began, however, it also declined, and 10 weeks into the growing season the CO₂-enriched/ambient-treatment new-branch biomass ratio had leveled out at a value commensurate with seasonal standing biomass and fruit production ratios—just under a doubling.

Based on their experimentally observed results, Idso *et al.* calculated the length of time by which the new-branch dry weight of the CO₂-enriched trees led that of the ambient-treatment trees over the first two months of the growing season, determining the 300-ppm increase in the air's CO₂ concentration caused the trees to begin the significant portion of their spring drawdown of atmospheric CO₂ fully two weeks earlier than what otherwise would have been normal. They calculated that for the 43-ppm increase in the air's CO₂ concentration experienced between 1960 and 1994, biological spring for sour orange trees should have occurred two days earlier in 1994 than it did in 1960.

By way of comparison, there was an approximate seven-day advancement in the time of occurrence of the declining phase of the atmosphere's seasonal CO₂ cycle over this time period, and surface reflectance measurements made by satellites revealed a similar advancement in the springtime "greening of the Earth" in high northern latitudes. Idso *et al.*'s data thus suggest a significant portion of this advancement may have been due to the dramatic stimulation of initial new-branch growth provided by the increase in the air's CO₂ concentration experienced over that time interval. But where did the CO₂-enriched sour orange trees get the extra nitrogen needed to support the enhanced production of new branch and leaf tissue that occurred at the beginning of the growing season?

In an experiment bearing on this question, Idso *et al.* (2001) measured the concentrations of three soluble leaf proteins having molecular masses of 33, 31, and 21 kDa at weekly intervals for one full year in the foliage of the CO₂-enriched and ambient-treatment trees. During the central portion of the year, the abundances of the three proteins were generally lower in the leaves of the CO₂-enriched trees than they were in the leaves of the ambient-treatment trees; but in the latter part of the year and continuing for a short while into the next year, this relationship was reversed, as the leaf concentrations of the three

proteins in the CO₂-enriched trees surpassed those of the proteins in the trees growing in ambient air. Then in the spring, when new growth began to appear, the concentrations of the three proteins in the foliage of the CO₂-enriched trees plummeted, possibly as a result of giving up the nitrogen they had stored over winter to supply the needs of the newly developing branches and leaves.

According to Idso *et al.*, the N-terminal amino acid sequence of the 21-kDa protein has homology with sporamin B, an implicated vegetative storage protein (VSP) that can comprise 60 to 80% of the total soluble protein found in sweet potato tubers. They also determined it shares low sequence homology with trifoliatin, a soluble leaf protein from trifoliolate orange that shares 62% amino acid similarity with sporamin B and can comprise up to 65% of total leaf protein. In addition, they say "immunoelectron microscopy demonstrated the presence of the proteins within amorphous material in the vacuoles of mesophyll cells, where VSPs are commonly located."

Perhaps most telling, starting at about day-of-the-year 225, the CO₂-enriched trees experienced a period of leaf senescence and abscission that was not observed in the ambient-treatment trees. "This phenomenon," Idso *et al.* report, "peaked at about day 300, when the CO₂-enriched trees shed leaves at a rate 2.5–2.7 times greater than the normal background rate of the ambient-treatment trees, whereupon the enriched-tree leaf-fall rate diminished, returning to normal by the end of the year."

According to the hypothesis formulated by Idso *et al.*, nitrogen reabsorbed from these second-year leaves during the process of senescence became available for storage in first-year leaves of the CO₂-enriched trees, going into the 21-kDa protein starting at about day 225, into the 31-kDa protein starting at about day 265, and into the 33-kDa protein starting at about day 335, according to the trends defined by their weekly measurements of leaf protein concentrations. Then, when new branches and leaves began appearing in the spring, the stored nitrogen was remobilized from the prior first-year leaves (which now became second-year leaves) to supply the needs of the developing branch and leaf tissues, whereupon the concentrations of the three putative storage proteins in the now-second-year CO₂-enriched leaves rapidly dropped to levels once again less than those observed in similar-age ambient-treatment leaves, and they remained at that reduced level until the second-year leaves gave up even more nitrogen prior to their senescence in the fall.

Other experimental evidence for a CO₂-induced

Plant Characteristics

stimulation of new spring branch growth has been provided by Olszyk *et al.* (2001), who grew Ponderosa pine seedlings out-of-doors for two years in controlled-environment chambers maintained at atmospheric CO₂ concentrations of 390 and 670 ppm in combination with low (40 ppb) and high (60 ppb) ozone concentrations. They found the elevated CO₂ enhanced mean annual rates of net photosynthesis by 39% and increased bud lengths at the end of the second growing season in the low ozone treatment by 17%, which led to a transitory stimulation (+38%) of elongation and growth of terminal buds the following spring.

That super-stimulation of initial perennial plant growth in the early spring may be a ubiquitous phenomenon is suggested by the research of Bushway and Pritts (2002). They grew over-wintering strawberry plants in controlled environment chambers maintained at ambient (375 ppm) and elevated (700 to 1,000 ppm) atmospheric CO₂ concentrations until new blooms began to form on plants. They then moved the plants to a common greenhouse maintained at the ambient CO₂ concentration. The extra CO₂ stimulated rates of photosynthesis in the leaves of the over-wintering strawberry plants by more than 50%, which led to greater amounts of starch being found in key plant organs when new spring growth began. Plants grown in elevated CO₂ had two-, three-, and four-times the amount of starch in their crowns, leaves, and roots, respectively, than their ambiently grown counterparts. In addition, plants grown in elevated CO₂ flowered and fruited an average of four and seven days earlier than plants grown in ambient air, respectively.

Lim *et al.* (2004) correlated the monthly rate of relative change in normalized difference vegetation index (NDVI), which they derived from advanced very-high-resolution radiometer data, with the rate of change in atmospheric CO₂ concentration (δ CO₂) during the natural growing season within three eco-region zones of North America (the Arctic and Sub-Arctic Zone, the Humid Temperate Zone, and the Dry and Desert Zone, which they further subdivided into 17 regions) over the period 1982–1992. They explored the temporal progression of annual minimum NDVI over the period 1982–2001 throughout the eastern humid temperate zone of North America. In all 17 regions but one, “ δ CO₂ was positively correlated with the rate of change in vegetation greenness in the following month, and most correlations were high,” which they state is consistent with a CO₂ fertilization effect of the type observed in experimental manipulations of the air’s CO₂ content

that report a stimulation of photosynthesis and above-ground production at high CO₂. In addition, and most importantly, they determined the yearly “minimum vegetation greenness increased over the period 1982–2001 for all the regions of the eastern humid temperate zone in North America.”

Lim *et al.* opine rising CO₂ could “increase minimum greenness by stimulating photosynthesis at the beginning of the growing season,” citing Idso *et al.* (2000). Hence, by looking for a manifestation of the CO₂ fertilization effect at the time of year it is apt to be most strongly expressed, Lim *et al.* may have found it. Between 1982 and 2001, for example, the air’s CO₂ concentration rose by approximately 30 ppm. From Idso *et al.*’s findings of more than a 300% initial increase in the biomass of new sour orange tree branches for a 300-ppm increase in the air’s CO₂ concentration and more than a 500% initial increase in per-tree new-branch biomass, it can be calculated that yearly minimum greenness should have increased by a value between just over 30% and just over 50%, if other woody plants respond to atmospheric CO₂ enrichment as sour orange trees do. When the mean 19-year increase in NDVI for the seven regions for which Lim *et al.* present data is calculated, an increase of just over 40% is seen, indicating Lim *et al.*’s data are not only qualitatively consistent with the hypothesis of CO₂-induced ultra-stimulation of early spring branch growth, but quantitatively as well.

References

- Bushway, L.J. and Pritts, M.P. 2002. Enhancing early spring microclimate to increase carbon resources and productivity in June-bearing strawberry. *Journal of the American Society for Horticultural Science* **127**: 415–422.
- Idso, C.D., Idso, S.B., Kimball, B.A., Park, H.-S., Hooper, J.K., and Balling Jr., R.C. 2000. Ultra-enhanced spring branch growth in CO₂-enriched trees: Can it alter the phase of the atmosphere’s seasonal CO₂ cycle? *Environmental and Experimental Botany* **43**: 91–100.
- Idso, K.E., Hooper, J.K., Idso, S.B., Wall, G.W., and Kimball, B.A. 2001. Atmospheric CO₂ enrichment influences the synthesis and mobilization of putative vacuolar storage proteins in sour orange tree leaves. *Environmental and Experimental Botany* **48**: 199–211.
- Lim, C., Kafatos, M., and Megonigal, P. 2004. Correlation between atmospheric CO₂ concentration and vegetation greenness in North America: CO₂ fertilization effect. *Climate Research* **28**: 11–22.

Lovelock, C.E., Virgo, A., Popp, M., and Winter, K. 1999. Effects of elevated CO₂ concentrations on photosynthesis, growth and reproduction of branches of the tropical canopy trees species, *Luehea seemannii* Tr. & Planch. *Plant, Cell and Environment* **22**: 49–59.

Olszyk, D.M., Johnson, M.G., Phillips, D.L., Seidler, R.J., Tingey, D.T., and Watrud, L.S. 2001. Interactive effects of CO₂ and O₃ on a ponderosa pine plant/litter/soil mesocosm. *Environmental Pollution* **115**: 447–462.

2.5 Flowers

- At higher atmospheric CO₂ concentrations, plants often produce more and larger flowers, as well as a number of other flower-related changes having significant implications for plant productivity and survival, almost all of which are positive.

In one of the earliest papers to address the subject of atmospheric CO₂ enrichment effects on flowers, Idso *et al.* (1990) grew water lilies in sunken metal stock tanks located out-of-doors and enclosed within clear-plastic-wall open-top chambers through which air of either 350 or 650 ppm CO₂ was continuously circulated. Over the course of two growing seasons, he and his colleagues measured plant responses to these two environmental treatments. They found the water lilies in the CO₂-enriched enclosures grew better than the water lilies in the ambient CO₂ enclosures: the leaves in the CO₂-enriched tanks were larger and more substantial, and 75% more of them were produced over the course of the initial five-month growing season.

Each of the plants in the CO₂-enriched tanks also produced twice as many flowers as the plants growing in normal air, and the flowers that blossomed in the CO₂-enriched air were more substantial than those that bloomed in the air of normal CO₂ concentration: they had more petals, the petals were longer, they had a greater percentage of dry matter content, and each flower weighed about 50% more. In addition, the stems that supported the flowers were slightly longer in the CO₂-enriched tanks, and the percentage of dry matter contents of both the flower and leaf stems were greater, so the total dry matter in the flower and leaf stems in the CO₂-enriched tanks exceeded that of the flower and leaf stems in the ambient-air tanks by approximately 60%.

Deng and Woodward (1998) studied the direct and interactive effects of elevated CO₂ and nitrogen supply on strawberries by growing them in controlled-environment glasshouses maintained at

atmospheric CO₂ concentrations of either 390 or 560 ppm at three levels of nitrogen for nearly three months. They found strawberries growing at the elevated CO₂ concentration contained additional sugar and physical mass that enabled them to support significantly greater numbers of flowers and fruits than strawberry plants growing at 390 ppm CO₂. This effect ultimately led to total fresh fruit weights 42 and 17% greater in CO₂-enriched plants maintained at the highest and lowest nitrogen levels, respectively.

Lake and Hughes (1999) found a 380-ppm increase in the air's CO₂ content elicited a 35% increase in the total plant biomass of nasturtiums (*Tropaeolum majus*). Although it did not affect flower size in this species, the total flower nectar volume produced by the CO₂-enriched nasturtiums was 2.4-fold greater than that produced by ambient-grown control plants. Likewise, Dag and Eisikowitch (2000) reported atmospheric CO₂ enrichment up to 1,000 ppm doubled both the average nectar volume and sugar production per flower in greenhouse-grown melons (*Cucumis melo*).

Johnson and Lincoln (2000) report an annual plant native to the southeastern USA (*Heterotheca subaxillaris*) increased its total biomass by 20% in response to a 300-ppm increase in the air's CO₂ content. In addition, the elevated CO₂ increased reproductive flower biomass and induced flowering much earlier in the CO₂-enriched plants than in the ambient-air-grown plants. And in another experiment, Niu *et al.* (2000) found yellow and primrose pansies (*Viola x wittrockiana*) increased their total dry weights by 10 to 30% in response to a 600-ppm increase in the CO₂ content of the air, and atmospheric CO₂ enrichment increased flower size by 4 to 10%.

Carvalho and Heuvelink (2001) report atmospheric CO₂ enrichment positively influences several external quality characteristics of chrysanthemums, including increasing the plant's stem length, number of lateral branches, number of flowers, and size of flowers. Aloni *et al.* (2001) found a 450-ppm increase in the air's CO₂ content completely ameliorated a 75% high-temperature-induced reduction in bell pepper (*Capsicum annuum* L.) pollen production observed under ambient CO₂ concentrations. In addition, although high temperature reduced the number of seeds produced per fruit in ambient-grown plants by 68%, it reduced this parameter only by 9% in CO₂-enriched plants.

Deckmyn *et al.* (2001) grew white clover plants (*Trifolium repens* L., cv. Mervi) in four small greenhouses, two of which allowed 88% of the

Plant Characteristics

incoming UV-B radiation to pass through their roofs and walls, and two of which allowed 82% to pass through. One of the two greenhouses in each of the UV-B treatments was maintained at ambient CO₂ (371 ppm), and the other was maintained at elevated CO₂ (521 ppm). Midway through the four-month summer growing season, flower numbers were counted, revealing the 40% increase in atmospheric CO₂ concentration stimulated the production of flowers in the low UV-B treatment by 22% and in the slightly higher UV-B treatment by 43%.

By 2002, so many scientists had weighed in on the subject that Jablonski *et al.* (2002) conducted a meta-analysis of 159 peer-reviewed scientific journal articles published between 1983 and 2000 dealing with the effects of atmospheric CO₂ enrichment on the reproductive growth characteristics of several domesticated and wild plants. In calculating the mean responses reported in those papers, Jablonski *et al.* found for increases in the air's CO₂ concentration ranging from approximately 150 to 450 ppm (rough average of 300 ppm), across all species studied, the extra CO₂ supplied to the plants resulted in 19% more flowers, 18% more fruits, 16% more seeds, 4% greater individual seed mass, 25% greater total seed mass (equivalent to yield), and 31% greater total mass.

More studies demonstrating similar positive effects of atmospheric CO₂ enrichment on flowering characteristics followed. Silberbush *et al.* (2003), for example, grew small and large bulbs of *Hippeastrum* (which produces amaryllis flowers) in greenhouses receiving atmospheric CO₂ concentrations of 350 and 1000 ppm for about four hours of each day for 233 days with different combinations of nitrogen and potassium fertilization, in order to study the interactive effects of these parameters on bulb size. They found elevated CO₂ consistently increased bulb size across all nitrogen and potassium concentrations, with initially larger bulbs yielding the greatest size of final bulbs. On a percentage basis, smaller bulbs were slightly more responsive to atmospheric CO₂ enrichment than were larger bulbs. Under optimal nitrogen and potassium fertilization, the 650-ppm increase in the air's CO₂ concentration increased the size of smaller and larger bulbs by about 18 and 14%, respectively, suggesting as the CO₂ content of the air increases, *Hippeastrum* bulbs will increase their size, thus leading to enhanced bulb quality and flower (amaryllis) production.

Palacios and Zimmerman (2007) piped flue gas generated by the Duke Energy-North America Power Plant at Moss Landing, California (USA)

approximately 1 km to a site where it was bubbled through outdoor flow-through seawater aquaria at rates that produced four different aqueous CO₂ treatments characteristic of “(1) the present day atmosphere, with approximately 16 μ M CO₂(aq), (2) CO₂ projected for 2100 that increases the CO₂(aq) concentration of seawater to approximately 36 μ M CO₂(aq), (3) CO₂ projected for 2200 that increases the CO₂(aq) concentration of seawater to 85 μ M CO₂(aq), and (4) a dissolved aqueous CO₂ concentration of 1123 μ M CO₂(aq),” which in the earlier study of Zimmerman *et al.* (1997) had tripled the light-saturated photosynthesis rate of the eelgrass they had studied.

In their newer study, the researchers report the elevated CO₂ “led to significantly higher reproductive output, below-ground biomass and vegetative proliferation of new shoots in light-replete treatments,” i.e., those receiving light at 33% of the surface irradiance level. More specifically, they found “shoots growing at 36 μ M CO₂(aq) were 25% larger than those in the unenriched treatment [16 μ M CO₂(aq)],” and “at 85 μ M CO₂(aq) shoots were 50% larger than those in the unenriched treatment and at 1123 μ M CO₂(aq) shoots were almost twice as large as those in the unenriched treatment.” In addition, they found, at 1123 μ M CO₂(aq) “22% of the shoots differentiated into flowers, more than twice the flowering output of the other treatments at this light level.”

These findings have far-reaching implications. Noting “increased CO₂(aq) is capable of increasing eelgrass reproductive output via flowering, and area-specific productivity via vegetative shoot proliferation under naturally replete light regimes,” Palacios and Zimmerman state, “the resulting increases in eelgrass meadow density may initiate a positive feedback loop that facilitates the trapping of sediments and prevents their resuspension, thereby reducing turbidity and increasing light penetration in coastal habitats,” such that the resulting increased light penetration “may allow seagrass colonization depths to increase even further.”

The two researchers also suggest the CO₂-induced increase in the productivity of eelgrass may “enhance fish and invertebrate stocks as well.” They go so far as to suggest the “deliberate injection of CO₂ to seawater may facilitate restoration efforts by improving the survival rates of recently transplanted eelgrass shoots,” noting “it can buffer the negative effects of transplant shock by increasing rhizome reserve capacity and promoting shoot proliferation in light-replete environments.” In addition, they say it

“may also facilitate eelgrass survival in environments where conditions are periodically limiting, such as long dark winters or unusually warm summers that produce unfavorable productivity to respiration ratios,” and they write, “CO₂ injection may also promote flowering and seed production necessary for expansion and maintenance of healthy eelgrass meadows.” Finally, they suggest, “rising concentrations of CO₂(aq) may increase vegetative propagation and seed production of other seagrass populations besides eelgrass.”

In another review paper, Springer and Ward (2007) summarize “the results of 60 studies reporting flowering-time responses (defined as the time to first visible flower) of both crop and wild species at elevated CO₂.” They found “all possible responses have been observed both among species as well as within species, including accelerated, delayed and no change in flowering time in response to elevated CO₂.” However, they write, “flowering-time responses of wild species grown at elevated CO₂ are much more evenly distributed, in that a similar number of studies report accelerated, delayed, or no change in flowering time, whereas crops primarily showed accelerated flowering (approx. 80% exhibited accelerated flowering).” They also note, “plants utilizing both the C₃ and C₄ photosynthetic pathways show altered flowering time with elevated CO₂,” but “two crop species that account for a substantial portion of the world’s agricultural production, soybean [a C₃ crop] and maize [a C₄ crop], do not show consistent patterns in the response of flowering time at elevated CO₂.”

Springer and Ward additionally determined “studies performed within a genus also show a lack of consistent flowering-time response to elevated CO₂,” and among only 10 genotypes of a single well-studied species (*Arabidopsis thaliana*), “all possible flowering-time responses to elevated CO₂, including delayed, accelerated and unaltered flowering times, were observed.” Finally, they report, “a majority of multifactor studies that measured flowering time report no interaction between elevated CO₂ and other environmental factors, such as temperature, ... nutrient availability, ... light, ... and ozone,” although “a limited number of elevated CO₂ studies do show significant interactive effects with other environmental factors.”

Springer and Ward thus conclude the studies they reviewed “clearly show that future increases in atmospheric CO₂ will have major effects on the flowering time of both wild and crop species,” but “at this time it is not possible to account for the wide

variation in flowering-time responses because knowledge of the underlying physiological and molecular mechanisms is incomplete.”

Darbah *et al.* (2008) studied the effects of long-term exposure of birch (*Betula papyrifera*) trees to elevated CO₂ (an extra 200 ppm) on flower and pollen production at the Aspen FACE site in Rhinelander, Wisconsin (USA) in the eighth and ninth years (2006 and 2007) of that experiment. They found “an increase of 140% and 70% for 2006 and 2007, respectively, in the total number of trees that produced male flowers under elevated CO₂ and an increase of 260% in 2006 and 100% in 2007, respectively, in the quantity of male flowers produced under elevated CO₂.”

According to the six scientists, “the increases in the number of trees and in the quantity of male flowers produced under elevated CO₂ implies that more birch pollen will be produced.” They note, “these results support the findings of Curtis *et al.* (1994, 1996), Johnson and Lincoln (2000), Edwards *et al.* (2001), Jablonski *et al.* (2002), Bunce (2005) and Ladeau and Clark (2006a,b), which were that elevated CO₂ increases reproductive potential through increased pollination, and hence, fertilization and viable seed formation,” in harmony with the hypothesis of Herms and Mattson (1992), and “birch trees under adequate carbohydrate status [such as provided by atmospheric CO₂ enrichment] tend to favor male flower production.” They conclude by noting, “since sexual reproductive development is an important stage in the life cycle of plants, any change in the processes involved might have significant implications for the productivity of the plants and their survival.” The implications in the case of birch trees and atmospheric CO₂ enrichment clearly would be positive.

Johnston and Reekie (2008) write, “there have been marked changes in plant phenology over the past century” and these changes “have been interpreted as a consequence of the increase in temperature that has been observed over this time.” In addition, they speculate, “the concentration of atmospheric CO₂ may also directly affect time of flowering, even in the absence of temperature change.” They examined the effects of elevated atmospheric CO₂ concentration by itself (ambient and ambient + 330 ppm) and the combined effect of elevated CO₂ and elevated air temperature (ambient + 1.5°C) on the flowering phenology of 22 species of plants in the family Asteraceae, which were grown under natural seasonally varying temperature and day length in separate compartments of a glasshouse in Wolfville,

Nova Scotia, Canada.

They found, “on average, elevated CO₂ by itself advanced flowering by four days” and “increasing temperature as well as CO₂ advanced flowering by an additional three days.” They also found “CO₂ was more likely to hasten phenology in long- than in short-day species” and “early- and late-flowering species did not differ in response to elevated CO₂, but the combined effect of elevated CO₂ and temperature hastened flowering more in early- than late-flowering species.” Johnston and Reekie conclude, “the direct effect of CO₂ on phenology may be as important as its indirect effect through climate change.”

References

- Aloni, B., Peet, M., Pharr, M., and Karni, L. 2001. The effect of high temperature and high atmospheric CO₂ on carbohydrate changes in bell pepper (*Capsicum annuum*) pollen in relation to its germination. *Physiologia Plantarum* **112**: 505–512.
- Bunce, J.A. 2005. Seed yield of soybeans with daytime or continuous elevation of carbon dioxide under field conditions. *Photosynthetica* **43**: 435–438.
- Carvalho, S.M.P. and Heuvelink, E. 2001. Influence of greenhouse climate and plant density on external quality of chrysanthemum (*Dendranthema grandiflorum* (Ramat.) Kitamura): first steps toward a quality model. *Journal of Horticultural Science & Biotechnology* **76**: 249–258.
- Curtis, P.S., Klus, D.J., Kalisz, S., and Tonsor, S.J. 1996. Intraspecific variation in CO₂ responses in *Raphanus raphanistrum* and *Plantago lanceolata*: assessing the potential for evolutionary change with rising atmospheric change. In: Korner, C. and Bazzaz, F.A. (Eds.) *Carbon Dioxide, Populations and Communities*. Academic Press, New York, NY, USA, pp. 13–22.
- Curtis, P.S., Snow, A.A., and Miller, A.S. 1994. Genotype-specific effects of elevated CO₂ on fecundity in wild radish (*Raphanus raphanistrum*). *Oecologia* **97**: 100–105.
- Dag, A. and Eisikowitch, D. 2000. The effect of carbon dioxide enrichment on nectar production in melons under greenhouse conditions. *Journal of Apicultural Research* **39**: 88–89.
- Darbaj, J.N.T., Kubiske, M.E., Nelson, N., Oksanen, E., Vaapavuori, E., and Karnosky, D.F. 2008. Effects of decadal exposure to interacting elevated CO₂ and/or O₃ on paper birch (*Betula papyrifera*) reproduction. *Environmental Pollution* **155**: 446–452.
- Deckmyn, G., Caeyenberghs, E., and Ceulemans, R. 2001. Reduced UV-B in greenhouses decreases white clover response to enhanced CO₂. *Environmental and Experimental Botany* **46**: 109–117.
- Deng, X. and Woodward, F.I. 1998. The growth and yield responses of *Fragaria ananassa* to elevated CO₂ and N supply. *Annals of Botany* **81**: 67–71.
- Edwards, G.R., Clark, H., and Newton, P.C.D. 2001. The effects of elevated CO₂ on seed production and seedling recruitment in a sheep grazed pasture. *Oecologia* **127**: 383–394.
- Hermes, D.A. and Mattson, W.J. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology* **67**: 283–335.
- Idso, S.B., Allen, S.G., and Kimball, B.A. 1990. Growth response of water lily to atmospheric CO₂ enrichment. *Aquatic Botany* **37**: 87–92.
- Jablonski, L.M., Wang, X., and Curtis, P.S. 2002. Plant reproduction under elevated CO₂ conditions: a meta-analysis of reports on 79 crop and wild species. *New Phytologist* **156**: 9–26.
- Johnson, S.L. and Lincoln, D.E. 2000. Allocation responses to CO₂ enrichment and defoliation by a native annual plant *Heterotheca subaxillaris*. *Global Change Biology* **6**: 767–778.
- Johnston, A. and Reekie, E. 2008. Regardless of whether rising atmospheric carbon dioxide levels increase air temperature, flowering phenology will be affected. *International Journal of Plant Science* **169**: 1210–1218.
- LaDeau, S.L. and Clark, J.S. 2006a. Elevated CO₂ and tree fecundity: the role of tree size, interannual variability, and population heterogeneity. *Global Change Biology* **12**: 822–833.
- LaDeau, S.L. and Clark, J.S. 2006b. Pollen production by *Pinus taeda* growing in elevated atmospheric CO₂. *Functional Ecology* **20**: 541–547.
- Lake, J.C. and Hughes, L. 1999. Nectar production and floral characteristics of *Tropaeolum majus* L. grown in ambient and elevated carbon dioxide. *Annals of Botany* **84**: 535–541.
- Niu, G., Heins, R.D., Cameron, A.C., and Carlson, W.H. 2000. Day and night temperatures, daily light integral, and CO₂ enrichment affect growth and flower development of pansy (*Viola x wittrockiana*). *Journal of the American Society of Horticultural Science* **125**: 436–441.
- Palacios, S.L. and Zimmerman, R.C. 2007. Response of eelgrass *Zostera marina* to CO₂ enrichment: possible impacts of climate change and potential for remediation of coastal habitats. *Marine Ecology Progress Series* **344**: 1–13.
- Silberbush, M., Ephrath, J.E., Alekperov, Ch., and Ben-Asher, J. 2003. Nitrogen and potassium fertilization interactions with carbon dioxide enrichment in *Hippeastrum* bulb growth. *Scientia Horticulturae* **98**: 85–90.

Springer, C.J. and Ward, J.K. 2007. Flowering time and elevated atmospheric CO₂. *New Phytologist* **176**: 243–255.

Zimmerman, R.C., Kohrs, D.G., Steller, D.L., and Alberte, R.S. 1997. Impacts of CO₂-enrichment on productivity and light requirements of eelgrass. *Plant Physiology* **115**: 599–607.

2.6 Fluctuating Asymmetry

- Higher concentrations of atmospheric CO₂ tend to reduce fluctuating asymmetry in plant leaves, leading to more symmetrical leaves that appear to be less susceptible to attack by herbivores.

Fluctuating asymmetry (FA) is the terminology used to describe small variations from perfect symmetry in otherwise bilaterally symmetrical characters in an organism (Moller and Swaddle, 1997). It is believed to arise in consequence of developmental instability experienced during ontogeny that is caused by various stresses, including both genetic and environmental factors (Martel *et al.*, 1999; Cornelissen and Stiling, 2005); it has been studied extensively in animals but less so in plants (Moller and Shykoff, 1999).

In the first study to address the effects of atmospheric CO₂ enrichment on leaf asymmetry and how herbivores respond to these effects, Cornelissen *et al.* (2004) opened up a new window through which to view the potential effects of the ongoing rise in the air's CO₂ content on the plant and animal components of the biosphere. They conducted their study on a native scrub-oak community at the Kennedy Space Center, Titusville, Florida (USA), which is dominated by myrtle oak (*Quercus myrtifolia*) and sand live oak (*Quercus geminata*), under atmospheric CO₂ concentrations of approximately 370 and 700 ppm. Based on measurements of distances from the leaf midrib to the left and right edges of the leaf at its widest point and leaf areas on the left and right sides of the leaf midrib, Cornelissen *et al.* determined “asymmetric leaves were less frequent in elevated CO₂, and, when encountered, they were less asymmetric than leaves growing under ambient CO₂.” In addition, they found “*Q. myrtifolia* leaves under elevated CO₂ were 15.0% larger than in ambient CO₂ and *Q. geminata* leaves were 38.0% larger in elevated CO₂ conditions.” They also determined “elevated CO₂ significantly increased tannin concentration for both *Q. myrtifolia* and *Q. geminata* leaves” and “asymmetric leaves contained significantly lower concentrations of tannins than symmetric leaves for both *Q. geminata* and *Q. myrtifolia*.”

Commenting on their primary findings of reduced

percentages of leaves experiencing asymmetry in the presence of elevated levels of atmospheric CO₂ and the lesser degree of asymmetry exhibited by affected leaves in the elevated CO₂ treatment, Cornelissen *et al.* state, “a possible explanation for this pattern is the fact that, in contrast to other environmental stresses, which can cause negative effects on plant growth, the predominant effect of elevated CO₂ on plants is to promote growth with consequent reallocation of resources (Docherty *et al.*, 1996).” Another possibility they discuss is “the fact that CO₂ acts as a plant fertilizer” and, as a result, “elevated CO₂ ameliorates plant stress compared with ambient levels of CO₂,” which is one of the well-documented biological benefits of atmospheric CO₂ enrichment (Idso and Idso, 1994).

With respect to the ancillary finding of CO₂-induced increases in tannin concentrations in the leaves of both oaks (a mean increase of approximately 35% for *Q. myrtifolia* and 43% for *Q. geminata*), it should be noted this phenomenon may provide protection against herbivores, and part of that protection may be associated with the observed CO₂-induced reductions in the amount and degree of asymmetry in the leaves of the CO₂-enriched trees. Consistent with this hypothesis, for example, Stiling *et al.* (1999, 2003) found higher abundances of leaf miners in the leaves of the trees in the ambient CO₂ chambers, where asymmetric leaves were more abundant, while in the more recent study it was determined leaf miners attacked asymmetric leaves more frequently than would be expected by chance alone in both CO₂ treatments.

In further support of this CO₂-induced benefit, Cornelissen and Stiling (2005) evaluated patterns of asymmetry in 40 leaves from each of 30 trees of each of two species of oak—sand live oak (*Quercus geminata*) and turkey oak (*Q. laevis*)—at the University of South Florida Botanical Garden in Tampa, Florida (USA), well before any herbivores had begun to attack the trees that growing season. Thereafter, patterns of leaf asymmetry, leaf quality, and herbivory were examined for 30 individual trees of each of the two oak species from March to October of the same year.

These “before and after” measurements clearly indicated differential herbivory patterns neither caused nor affected patterns of leaf FA. However, the two scientists suggest “herbivores may use asymmetry as a cue to plant quality and suitable oviposition sites,” as plants with a higher percentage of asymmetric leaves were attacked more frequently by various leaf miners, as were leaves on the same

Plant Characteristics

plant that were more asymmetric. Cornelissen and Stiling report, “asymmetric leaves of both plant species exhibited better nutritional quality for herbivores than symmetric leaves,” with asymmetric leaves possessing “significantly lower concentrations of tannins [-22% for *Q. geminata* and -36% for *Q. laevis*] and higher nitrogen content [+8% for both species].”

Kaligarić *et al.* (2008) measured the degree of FA in “undamaged (not grazed, not visibly attacked by herbivores or pathogens) fully developed leaves” of the Mediterranean shrub *Myrtus communis* L. growing along an atmospheric CO₂ gradient (570, 530, 490, 450, 410, and 370 ppm) moving away from a natural CO₂ spring “I Borboi” near Lajatico (Pisa, Tuscany, Italy) at distances of 2, 18, 34, 50, 66, and 82 m, respectively, from the CO₂ source. They found “a significant and negative correlation between CO₂ concentration and leaf FA,” such that “with increased CO₂ concentration the leaf FA decreased.” This result, they write, “confirms what was obtained by Cornelissen *et al.* (2004) on *Quercus myrtifolia* and *Quercus geminata* (in a short-term experiment).” In addition, they note, “*Myrtus communis*, grown under elevated CO₂ concentration at ‘I Borboi,’ showed a reduction in xylem embolism and an increase in hydraulic efficiency (Tognetti *et al.*, 2001),” stating “improved water relations could represent a good explanation for the observed reduction in leaf FA [as the air’s CO₂ content increased].”

Kaligarić *et al.* suggest “adaptation and selection could explain the tendency towards decreased leaf FA in plants from the CO₂ spring relative to ambient conditions,” since “the more symmetrical leaves under long-term elevated CO₂ concentration were more developmentally stable in these conditions.”

Consequently, and in light of the results discussed above, a reduction in leaf FA can be added to the ever-growing number of benefits plants likely will experience as the atmosphere’s CO₂ concentration continues to rise.

References

Cornelissen, T. and Stiling, P. 2005. Perfect is best: low leaf fluctuating asymmetry reduces herbivory by leaf miners. *Oecologia* **142**: 46–56.

Cornelissen, T., Stiling, P., and Drake, B. 2004. Elevated CO₂ decreases leaf fluctuating asymmetry and herbivory by leaf miners on two oak species. *Global Change Biology* **10**: 27–36.

Docherty, M., Hurst, D.K., Holopainen, J.K., Whittaker,

J.B., Lea, P.J., and Watt, A.D. 1996. Carbon dioxide-induced changes in beech foliage cause female beech weevil larvae to feed in a compensatory manner. *Global Change Biology* **2**: 335–341.

Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: a review of the past 10 years’ research. *Agricultural and Forest Meteorology* **69**: 153–203.

Kaligarić, M., Tognetti, R., Janzekovic, F., and Raschi, A. 2008. Leaf fluctuating asymmetry of *Myrtus communis* L., affected by increases in atmospheric CO₂ concentration: Evidence from a natural CO₂ spring. *Polish Journal of Environmental Studies* **17**: 503–508.

Martel, J., Lempa, K., and Haukioja, E. 1999. Effects of stress and rapid growth on fluctuating asymmetry and insect damage in birch leaves. *Oikos* **86**: 208–216.

Moller, A.P. and Shykoff, P. 1999. Morphological developmental stability in plants: patterns and causes. *International Journal of Plant Sciences* **160**: S135–S146.

Moller, A.P. and Swaddle, J.P. 1997. *Asymmetry, Developmental Stability and Evolution*. Oxford University Press, Oxford, UK.

Stiling, P., Moon, D.C., Hunter, M.D., Colson, J., Rossi, A.M., Hymus, G.J., and Drake, B.G. 2003. Elevated CO₂ lowers relative and absolute herbivore density across all species of a scrub-oak forest. *Oecologia* **134**: 82–87.

Stiling, P., Rossi, A.M., Hungate, B., Dijkstra, P., Hinkle, C.R., Knot III, W.M., and Drake, B. 1999. Decreased leaf-miner abundance in elevated CO₂: Reduced leaf quality and increased parasitoid attack. *Ecological Applications* **9**: 240–244.

Tognetti, R., Longobucco, A., Raschi, A., and Jones, M.B. 2001. Stem hydraulic properties and xylem vulnerability to embolism in three co-occurring Mediterranean shrubs at a natural CO₂ spring. *Australian Journal of Plant Physiology* **28**: 257–268.

2.7 Hormones

- Atmospheric CO₂ enrichment enhances plant growth, development, and ultimate yield (in the case of agricultural crops) by increasing the concentrations of plant hormones that stimulate cell division, cell elongation, and protein synthesis.

Investigating the effects of atmospheric CO₂ enrichment on plant hormones, Teng *et al.* (2006) grew well-watered and -fertilized thale cress (*Arabidopsis thaliana* (L.) Heynh.) plants from seed

to commencement of bolting in pots within controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 370 or 700 ppm, measuring several plant properties and processes. The elevated CO₂ increased the biomass production of the plants by 29% and leaf total nonstructural carbohydrates by 76%. With respect to plant hormones, it “significantly increased the IAA [indole-3-acetic acid, by 13.7%], GA3 [gibberellic acid, by 55.4%], ZR [zeatin riboside, by 15.6%], DHZR [dihydrozeatin riboside, by 55.9%] and iPA [isopentenyladenosine, by 74.6%] contents of leaves, but ... significantly reduced the ABA [abscisic acid, by 15.2%] content.”

The six Chinese researchers conclude by noting plant hormones “can enhance plant growth and development by stimulating cell division, cell elongation and protein synthesis (Yong *et al.*, 2000), whereas ABA is considered an inhibitor of leaf growth (Zhang and Davies, 1990).” In addition, they note, “plant hormone metabolism is dependent on the supply of carbohydrates (Taiz and Zeiger, 1998).” They conclude, “higher carbohydrate production,” such as that induced by atmospheric CO₂ enrichment, “may result in higher hormone concentrations, which in turn may enhance plant growth.” That phenomenon also was observed by Jitla *et al.* (1997) and Li *et al.* (2002), with the latter reporting elevated CO₂ increased the concentrations of several plant hormones in leaf and aerial root tips of an epiphytic CAM orchid by as much as 21-fold.

In another experiment, Li *et al.* (2009) grew six-year-old *Ginkgo biloba* tree saplings in pots containing fertile soil out-of-doors in open-top chambers maintained at either 350 or 700 ppm CO₂ at the Shenyang Arboretum of the Chinese Academy of Science in Shenyang, Liaoning Province (China) from 1 June to 30 September. In addition to measuring the growth of the trees’ terminal shoots over this period, they also measured leaf concentrations of the endogenous plant-growth regulator indole-3-acetic acid (IAA). After 40 days’ exposure to elevated CO₂, the IAA concentration in the plants’ leaves was increased significantly relative to that of plants in the control treatment, and maximum IAA enhancement was observed 100 days after exposure, when leaf concentrations of IAA were fully 90% greater in the elevated CO₂ treatment. The growth increment of ginkgo terminal shoots in the high CO₂ chambers was increased by 44% from 20 days to 90 days of exposure to the elevated CO₂ conditions.

Jiang *et al.* (2012) write, “brassinosteroids (BRs) are a family of over 40 naturally occurring plant

steroid hormones that are ubiquitously distributed in the plant kingdom,” citing Clouse and Sasse (1998), Bishop and Koncz (2002), Krishna (2003), and Montoya *et al.* (2005). They report, “BRs play prominent roles in various physiological processes including the induction of a broad spectrum of cellular responses, such as stem elongation, pollen tube growth, xylem differentiation, leaf epinasty, root inhibition, induction of ethylene biosynthesis, proton pump activation, regulation of gene expression and photosynthesis, and adaptive responses to environmental stress,” citing Clouse and Sasse (1998), Dhaubhadel *et al.* (1999), Khripach *et al.* (2000), Krishna (2003), and Yu *et al.* (2004). They also note, “as potent plant growth regulators, BRs are now widely used to enhance plant growth and yield of important agricultural crops,” citing Khripach *et al.* (2000) and Divi and Krishna (2009).

The six scientists conducted an experiment to determine the effects of increased atmospheric CO₂ on such of these plant steroid hormones as are found in young cucumber plants, growing them at atmospheric CO₂ concentrations of either 380 (ambient) or 760 (enriched) ppm, and with or without being sprayed with a solution of brassinosteroids (0.1 μM 24-epibrassinolide).

Jiang *et al.* determined their doubling of the atmosphere’s CO₂ concentration resulted in a 44.1% increase in CO₂ assimilation rate. They state the BR treatment “also significantly increased CO₂ assimilation under ambient atmospheric CO₂ conditions” and “the increase was close to that by CO₂ enrichment.” Most interesting, they found the combined treatment of “plants with BR application under CO₂-enriched conditions showed the highest CO₂ assimilation rate, which was increased by 77.2% relative to the control.” Likewise, they found “an elevation in the atmospheric CO₂ level from 380 to 760 ppm resulted in 20.5% and 16.0% increases in leaf area and shoot biomass accumulation, respectively,” and the plants that received the BR application “exhibited 22.6% and 20.6% increases in leaf area and shoot biomass accumulation, respectively.” The combined treatment of “CO₂ enrichment and BR application further improved the plant growth, resulting in 49.0% and 40.2% increases in leaf area and shoot biomass, relative to that of the control, respectively.”

References

Bishop, G.J. and Koncz, C. 2002. Brassinosteroids and

Plant Characteristics

plant steroid hormone signaling. *The Plant Cell* **14**: S97–S110.

Clouse, S.D. and Sasse, J.M. 1998. Brassinosteroids: essential regulators of plant growth and development. *Annual Review of Plant Physiology and Plant Molecular Biology* **49**: 427–451.

Dhaubhadel, S., Chaudhary, S., Dobinson, K.F., and Krishna, P. 1999. Treatment with 24-epibrassinolide, a brassinosteroid, increases the basic thermotolerance of *Brassica napus* and tomato seedlings. *Plant Molecular Biology* **40**: 333–342.

Divi, U.K. and Krishna, P. 2009. Brassinosteroid: a biotechnological target for enhancing corn yield and stress tolerance. *New Biotechnology* **26**: 131–136.

Jiang, Y.-P., Cheng, F., Zhou, Y.-H., Xia, X.-J., Shi, K., and Yu, J.-Q. 2012. Interactive effects of CO₂ enrichment and brassinosteroid on CO₂ assimilation and photosynthetic electron transport in *Cucumis sativus*. *Environmental and Experimental Botany* **75**: 98–106.

Jitla, D.S., Rogers, G.S., Seneweera, S.P., Basra, A.S., Oldfield, R.J., and Conroy, J.P. 1997. Accelerated early growth of rice at elevated CO₂: is it related to developmental changes in the shoot apex? *Plant Physiology* **115**: 15–22.

Khripach, V., Zhabinskii, V., and De Groot, A. 2000. Twenty years of Brassinosteroids: steroidal plant hormones warrant better crops for the XXI century. *Annals of Botany* **86**: 441–447.

Krishna, P. 2003. Brassinosteroid-mediated stress responses. *Journal of Plant Growth Regulators* **22**: 289–297.

Li, C.R., Gan, I.J., Xia, K., Zhou, X., and Hew, C.S. 2002. Responses of carboxylating enzymes, sucrose metabolizing enzymes and plant hormones in a tropical epiphytic CAM orchid to CO₂ enrichment. *Plant, Cell and Environment* **25**: 369–377.

Li, X.-M., He, X.-Y., Zhang, L.-H., Chen, W., and Chen, Q. 2009. Influence of elevated CO₂ and O₃ on IAA, IAA oxidase and peroxidase in the leaves of ginkgo trees. *Biologia Plantarum* **53**: 339–342.

Montoya, T., Normura, T., Yokota, T., Farrar, K., Harrison, K., Jones, J.G.D., Kaneta, T., Kamiya, W., Szekeres, M., and Bishop, G.R. 2005. Patterns of dwarf expression and brassinosteroid accumulation in tomato reveal the importance of brassinosteroid synthesis during fruit development. *Plant Journal* **42**: 262–269.

Taiz, L. and Zeiger, E. 1998. *Plant Physiology*. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Teng, N., Wang, J., Chen, T., Wu, X., Wang, Y., and Lin, J. 2006. Elevated CO₂ induces physiological, biochemical

and structural changes in leaves of *Arabidopsis thaliana*. *New Phytologist* **172**: 92–103

Yong, J.W.H., Wong, S.C., Letham, D.S., Hocart, C.H., and Farquhar, G.D. 2000. Effects of elevated CO₂ and nitrogen nutrition on cytokinins in the xylem sap and leaves of cotton. *Plant Physiology* **124**: 769–779.

Yu, J.Q., Huang, L.F., Hu, W.H., Zhou, Y.H., Mao, W.H., Ye, S.F., and Nogués, S. 2004. A role for brassinosteroids in the regulation of photosynthesis in *Cucumis sativus*. *Journal of Experimental Botany* **55**: 1135–1143.

Zhang, J. and Davies, W.J. 1990. Changes in the concentration of ABA in xylem sap as a function of changing soil-water status can account for changes in leaf conductance and growth. *Plant, Cell and Environment* **13**: 277–285.

2.8 Glomalin

- Atmospheric CO₂ enrichment increases the production of glomalin, a protein created by fungi living in symbiotic association with the roots of 80% of the planet's vascular plants, which is being released to almost every soil in the world in ever-greater quantities with the passage of time, where it is having a positive impact on the biosphere.

In a multifaceted research program carried out at experimental sites in northern and southern California, USA, Rillig *et al.* (1999) studied belowground ecosystem responses to elevated atmospheric CO₂ concentrations over a period of several years, focusing their attention on arbuscular mycorrhizal fungi (AMF) that form symbiotic associations with plant roots. In addition, they measured soil concentrations of an AMF-produced glycoprotein called glomalin and evaluated its response to elevated CO₂. They then studied the impact of glomalin on the formation of small soil aggregates and their subsequent stability.

The degree of soil aggregation and the stability of soil aggregates across many different soil types is closely related to the amount of glomalin in the soil. Rillig *et al.* wanted to see if the aboveground benefits of atmospheric CO₂ enrichment would trickle down, so to speak, from plant leaves to plant roots to symbiotic soil fungi to glomalin production to soil aggregate formation and, ultimately, to an enhanced stability of soil aggregates in the presence of water.

The researchers found the amount of fungal-produced glomalin in the soils of the CO₂-enriched treatments in all three of the ecosystems they studied

was greater than that observed in the soils of corresponding ambient CO₂ treatments. They also observed increases in the mass of small soil aggregates in the treatments exposed to elevated CO₂, and the stability of the small soil aggregates in the CO₂-enriched treatments was greater than the stability of the aggregates in the ambient CO₂ treatments. And in one of their studies, where six CO₂ concentrations ranging from 250 to 750 ppm were imposed as treatments, they found “the proportion of soil mass in aggregates of 0.25–1 mm showed a linear increase along the CO₂ gradient,” and “glomalin concentrations followed a pattern similar to that of the small aggregate size class,” indicating increasing soil structure benefits with increasing concentrations of atmospheric CO₂.

In a subsequent study conducted in New Zealand, Rillig *et al.* (2000) examined several characteristics of AMF associated with the roots of plants that had been growing for at least 20 years along a natural CO₂ gradient near a CO₂-emitting spring. They found the elevated CO₂ significantly increased percent of root colonization by AMF in a linear fashion—and nearly fourfold—in going from 370 to 670 ppm. In addition, fungal hyphal length experienced a linear increase of more than threefold along the same CO₂ gradient, and total soil glomalin experienced a linear increase of approximately fivefold.

Just as more and longer roots help plants hold soil together and prevent its erosion, so too do more and longer fungal hyphae protect soil from disruption and dispersion. In addition, fungal-produced glomalin acts like a biological glue, helping to bind tiny particles of soil into small aggregates that are much more difficult to break down and blow or wash away. To have soil glomalin concentrations increase fivefold as a consequence of less than a doubling of the air’s CO₂ content is an astounding benefit.

Ross *et al.* (2000) measured soil carbon (C) and nitrogen (N) contents in areas exposed to atmospheric CO₂ concentrations on the order of 440 to 460 ppm and other areas exposed to concentrations on the order of 510 to 900 ppm, near a natural CO₂ vent in New Zealand. Their work bears on the question whether CO₂-induced increases in soil-stabilizing fungal activities might lead to increases in soil carbon sequestration.

They found several decades of differential atmospheric CO₂ exposure had increased soil organic C and total N contents by approximately 24% each, and it had increased microbial C and N contents by more than 100% each. Hence, the scientists write, “storage of C and N can increase under prolonged

exposure to elevated CO₂.” In addition, they conclude increased storage of soil organic matter can occur “even when soil C concentrations are already high,” as they were in the situation they investigated. Consequently, not only will the capacity of soils to store carbon increase because of the increasing aerial fertilization effect of atmospheric CO₂ enrichment—which enhances plant growth and results in more carbon being transferred to the soil—increasingly active soil fungi will help to keep ever-greater portions of that carbon better preserved in increasingly more stable soils.

Augmented soil carbon sequestration is but the beginning of benefits that can be expected from CO₂-enhanced AMF growth and glomalin production. Rillig *et al.* (2001) report the results of a FACE study of sorghum they conducted near Phoenix, Arizona (USA), where they found an approximate 50% increase in the air’s CO₂ content increased fungal hyphae lengths by 120% and 240% in wet and dry irrigation treatments, respectively, with the mass of water-stable soil aggregates increasing by 40% and 20% in the same respective treatments. They note, “soil structure and water-stable aggregation are crucial for facilitating water infiltration, soil-borne aspects of biogeochemical cycling processes, success of sustainable agriculture, and for providing resistance against erosional loss of soil (Oades, 1984; Elliott and Coleman, 1988; Van Veen and Kuikman, 1990; Bethlenfalvay and Lindermann, 1992; Daily, 1995; Arshad *et al.*, 1996; Coleman, 1996; Jastrow and Miller, 1997; Young *et al.*, 1998).”

In addition, Gonzalez-Chavez *et al.* (2004) found “glomalin participates in the sequestration of different PTEs [potentially toxic elements],” “the glomalin pool in the soil may have a potential to sequester PTEs, not only by the colonized roots, but also by the hyphae and through deposition of glomalin in soil,” and “this glycoprotein may be stabilizing PTEs, reducing PTE availability and decreasing the toxicity risk to other soil microorganisms and plants.” The authors note “glomalin is ... copiously produced by all AMF tested to date (Wright *et al.*, 1996, 1998; Nichols, 2003),” “AMF colonize 80% of vascular plant species (Trappe, 1987),” and AMF “are found worldwide in almost every soil.”

In light of these observations, it should be evident the ongoing rise in the air’s CO₂ content must be having a tremendous positive impact on the biosphere via a suite of mechanisms linked to a fungal-produced protein that only a couple decades ago was largely unknown—even to most plant and soil scientists—and similarly unappreciated.

References

- Arshad, M.A., Lowery, B., and Grossman, B. 1996. Physical tests for monitoring soil quality. In: *Methods for Assessing Soil Quality*, SSSA Special Publication 49. Soil Science Society of America, Madison, Wisconsin, USA, pp. 123–141.
- Bethlenfalvay, G.J. and Linderman, R.G. 1992. *Mycorrhizae in Sustainable Agriculture*. ASA Special Publication 54. American Society of Agronomy, Madison, Wisconsin, USA.
- Coleman, D.C. 1996. *Fundamentals of Soil Ecology*. Academic Press, San Diego, California, USA.
- Daily, G.C. 1995. Restoring value to the world's degraded lands. *Science* **269**: 350–354.
- Elliott, E.T. and Coleman, D.C. 1988. Let the soil work for us. *Ecological Bulletin* **39**: 23–32.
- Gonzalez-Chavez, M.C., Carrillo-Gonzalez, R., Wright, S.F., and Nichols, K.A. 2004. The role of glomalin, a protein produced by arbuscular mycorrhizal fungi, in sequestering potentially toxic elements. *Environmental Pollution* **130**: 317–323.
- Jastrow, J.D. and Miller, R.M. 1997. Soil aggregate stabilization and carbon sequestration: feedbacks through organomineral associations. In: Lal, R. *et al.* (Eds.) *Soil Processes and the Carbon Cycle*. CRC Press, Boca Raton, Florida, USA, pp. 207–223.
- Nichols, K. 2003. *Characterization of Glomalin—A Glycoprotein Produced by Arbuscular Mycorrhizal Fungi*. PhD Dissertation, University of Maryland, College Park, Maryland, USA.
- Oades, J.M. 1984. Soil organic matter and structural stability: mechanisms and implications for management. *Plant and Soil* **76**: 319–337.
- Rillig, M.C., Hernandez, G.Y., and Newton, P.C.D. 2000. Arbuscular mycorrhizae respond to elevated atmospheric CO₂ after long-term exposure: evidence from a CO₂ spring in New Zealand supports the resource balance model. *Ecology Letters* **3**: 475–478.
- Rillig, M.C., Wright, S.F., Allen, M.F., and Field, C.B. 1999. Rise in carbon dioxide changes soil structure. *Nature* **400**: 628.
- Rillig, M.C., Wright, S.F., Kimball, B.A., Pinter, P.J., Wall, G.W., Ottman, M.J., and Leavitt, S.W. 2001. Elevated carbon dioxide and irrigation effects on water stable aggregates in a *Sorghum* field: a possible role for arbuscular mycorrhizal fungi. *Global Change Biology* **7**: 333–337.
- Ross, D.J., Tate, K.R., Newton, P.C.D., Wilde, R.H., and Clark, H. 2000. Carbon and nitrogen pools and mineralization in a grassland gley soil under elevated carbon dioxide at a natural CO₂ spring. *Global Change Biology* **6**: 779–790.
- Trappe, J.M. 1987. Phylogenetic and ecological aspects of mycotrophy in the angiosperms from an evolutionary standpoint. In: Safir, G.R. (Ed.) *Ecophysiology of VA Mycorrhizal Plants*. CRC Press, Boca Raton, Florida, USA, pp. 5–25.
- Van Veen, J.A. and Kuikman, P.J. 1990. Soil structural aspects of decomposition of organic matter by micro-organisms. *Biogeochemistry* **11**: 213–233.
- Wright, S.F., Franke-Snyder, M., Morton, J.B., and Upadhyaya, A. 1996. Time-course study and partial characterization of a protein on hyphae of arbuscular mycorrhizal fungi during active colonization of roots. *Plant and Soil* **181**: 193–203.
- Wright, S.F., Upadhyaya, A., and Buyer, J.S. 1998. Comparison of N-linked oligosaccharides of glomalin from arbuscular mycorrhizal fungi and soils by capillary electrophoresis. *Soil Biology and Biochemistry* **30**: 1853–1857.
- Young, I.M., Blanchart, E., and Chenu, C., *et al.* 1998. The interaction of soil biota and soil structure under global change. *Global Change Biology* **4**: 703–712.

2.9 Isoprene

A number of experimental findings indicate the ongoing rise in the air's CO₂ content likely will lead to significant reductions in the air's concentration of isoprene, which is responsible for the production of vast amounts of tropospheric ozone, thereby helping to reduce the atmospheric presence of the latter noxious trace gas. Other research suggests a CO₂-induced reduction in plant isoprene emissions will result in greater concentrations of cloud condensation nuclei, which act as a negative feedback to atmospheric warming.

The influence of atmospheric CO₂ on plant isoprene emissions is discussed in Section 2.5.2.2.1 of the Forcings and Feedbacks chapter of *Climate Change Reconsidered II: Physical Science* (Idso *et al.*, 2013).

Reference

- Idso, C.D., Carter, R.M., and Singer, S.F. 2013. (Eds.) *Climate Change Reconsidered II: Physical Science*. Chicago, IL: The Heartland Institute.

2.10 Leaves

Nearly all crops respond to increases in the air's CO₂ content by displaying enhanced rates of photosynthesis and biomass production. The subsections below examine some of the other changes they often experience when exposed to elevated levels of atmospheric CO₂—namely, various changes in leaf characteristics.

2.10.1 Agricultural Species

- Increasing atmospheric CO₂ concentrations likely will affect many leaf characteristics of agricultural plants, with the majority of the changes leading to higher rates and efficiencies of photosynthesis and growth, with the ultimate result that agricultural yields likely will rise as the air's CO₂ content continues to rise.

As the air's CO₂ concentration rises, plants commonly reduce the concentration of the nitrogen-rich photosynthetic enzyme rubisco, which is normally present in their leaves in excess amounts at ambient atmospheric CO₂ concentrations. Consequently, elevated CO₂ exposure frequently results in reduced foliar nitrogen concentrations, which allows excess nitrogen in leaves to be mobilized away from the photosynthetic apparatus and devoted to processes more limiting to growth. In the study of Monje and Bugbee (1998), for example, a near-900-ppm increase in the air's CO₂ concentration reduced leaf nitrogen contents in wheat by 28%. Similar results were obtained for soybeans grown at twice-ambient CO₂ concentrations (Sims *et al.*, 1998); it is thus quite likely many agricultural species will exhibit reductions in foliar nitrogen content in response to atmospheric CO₂ enrichment.

In addition to nitrogen, elevated CO₂ also can mobilize other limiting resources away from a plant's photosynthetic machinery and direct them into various plant parts important to growth and development. Watling *et al.* (2000), for example, found a doubling of the air's CO₂ content reduced the thickness of specialized bundle sheath cells in sorghum by approximately 50%, which freed up important resources that were sent to other parts of the plant for utilization, as indicated by a 36% enhancement in total plant biomass.

Elevated CO₂ also may impact leaf concentrations of chlorophylls, important light-absorbing pigments involved in the photosynthetic process. In the study of Sgherri *et al.* (1998), for example, water-stressed

alfalfa displayed a 30% reduction in leaf chlorophyll content, but water-stressed plants exposed to 600 ppm CO₂ exhibited only a 6% reduction. In potato, on the other hand, Sicher and Bunce (1999) found no change in leaf chlorophyll content when exposing plants to twice-ambient levels of atmospheric CO₂, nor did Monje and Bugbee (1998) in their previously mentioned study on wheat.

Excess carbohydrates resulting from enhanced photosynthetic rates often are used to increase leaf growth and development. As an example, Reddy *et al.* (1998) reported cotton plants grown at 700 ppm CO₂ displayed individual leaf areas 20% greater than those of the leaves of ambiently grown control plants. Similarly, Masle (2000) noted a 600-ppm increase in atmospheric CO₂ concentration increased individual leaf size in wheat plants by increasing the number of photosynthetic mesophyll cell layers, as well as overall leaf thickness. In a related study on sunflower, however, Sims *et al.* (1999) did not report an increase in leaf size or thickness, but they documented a CO₂-induced shift in the distribution of leaf area that concentrated 30 to 40% more of it in the upper layer of the plant canopy, where the CO₂-induced photosynthetic stimulation was greatest.

Sometimes, excess carbohydrates are used to enhance the biosynthesis of secondary carbon compounds in leaves. Estiarte *et al.* (1999), for example, found leaves of spring wheat grown at 550 ppm CO₂ displayed 14% higher total flavonoid concentrations than leaves of plants grown at 370 ppm CO₂. This observation is important because flavonoids are generally characterized as having anti-herbivory properties. Thus, less pest-induced yield losses in this important grain crop may occur in future climates characterized by elevated atmospheric CO₂ concentrations.

Increasing atmospheric CO₂ concentrations likely will affect many leaf characteristics of agricultural plants. The majority of these changes likely will lead to greater rates and higher efficiencies of photosynthesis and growth. As a result, agricultural yields likely will rise in the future, resulting in part from changes in foliar properties mediated by the ongoing rise in the air's CO₂ content.

References

- Estiarte, M., Peñuelas, J., Kimball, B.A., Hendrix, D.L., Pinter Jr., P.J., Wall, G.W., LaMorte, R.L., and Hunsaker, D.J. 1999. Free-air CO₂ enrichment of wheat: leaf flavonoid concentration throughout the growth cycle. *Physiologia Plantarum* **105**: 423–433.

Plant Characteristics

Masle, J. 2000. The effects of elevated CO₂ concentrations on cell division rates, growth patterns, and blade anatomy in young wheat plants are modulated by factors related to leaf position, vernalization, and genotype. *Plant Physiology* **122**: 1399–1415.

Monje, O. and Bugbee, B. 1998. Adaptation to high CO₂ concentration in an optimal environment: radiation capture, canopy quantum yield and carbon use efficiency. *Plant, Cell and Environment* **21**: 315–324.

Reddy, K.R., Robana, R.R., Hodges, H.F., Liu, X.J., and McKinion, J.M. 1998. Interactions of CO₂ enrichment and temperature on cotton growth and leaf characteristics. *Environmental and Experimental Botany* **39**: 117–129.

Sgherri, C.L.M., Quartacci, M.F., Menconi, M., Raschi, A., and Navari-Izzo, F. 1998. Interactions between drought and elevated CO₂ on alfalfa plants. *Journal of Plant Physiology* **152**: 118–124.

Sicher, R.C. and Bunce, J.A. 1999. Photosynthetic enhancement and conductance to water vapor of field-grown *Solanum tuberosum* (L.) in response to CO₂ enrichment. *Photosynthesis Research* **62**: 155–163.

Sims, D.A., Cheng, W., Luo, Y., and Seeman, J.R. 1999. Photosynthetic acclimation to elevated CO₂ in a sunflower canopy. *Journal of Experimental Botany* **50**: 645–653.

Sims, D.A., Luo, Y., and Seeman, J.R. 1998. Comparison of photosynthetic acclimation to elevated CO₂ and limited nitrogen supply in soybean. *Plant, Cell and Environment* **21**: 945–952.

Watling, J.R., Press, M.C., and Quick, W.P. 2000. Elevated CO₂ induces biochemical and ultrastructural changes in leaves of the C₄ cereal sorghum. *Plant Physiology* **123**: 1143–1152.

2.10.2 Trees

- The leaves of nearly all woody species exposed to increases in the air's CO₂ content display enhanced rates of photosynthesis, as well as a number of other changes in leaf characteristics that help promote increased resistance to attacks by herbivores and pathogens.

Norby *et al.* (2000) found a 300-ppm increase in the air's CO₂ concentration reduced the nitrogen content in the leaves of red and sugar maple trees by 19 and 25%, respectively, and Rey and Jarvis (1998) found young silver birch trees exposed to twice-ambient levels of atmospheric CO₂ displayed leaf nitrogen contents 13% below those observed in leaves of ambiently growing trees. This phenomenon also has

been noticed in the needles of conifers. Gielen *et al.* (2000), for example, documented a 33% reduction in the needle nitrogen content of young Scots pines growing at 750 ppm CO₂ compared to that of control trees growing at 350 ppm CO₂.

The nitrogen thus given up by the photosynthetic machinery of both broad-leaved and coniferous trees typically is used to further enhance the overall biomass production of the trees, including roots, trunks, branches, and still more leaves.

Elevated CO₂ also can mobilize other limiting resources away from the photosynthetic process for input into still other processes important to tree growth and development. Ormrod *et al.* (1999), for example, found a 180-ppm increase in the air's CO₂ content caused 19 and 25% reductions in the chlorophyll *a* and *b* concentrations of Douglas fir needles, respectively. Similar results were reported in young Scots pines, which exhibited a 26% reduction in total needle chlorophyll concentration in response to a 350-ppm increase in the CO₂ content of the air (Gielen *et al.*, 2000). However, Carter *et al.* (2000) noted elevated CO₂ (+300 ppm) had no effect on leaf chlorophyll concentrations in sugar maple.

Excess carbohydrates resulting from CO₂-enhanced photosynthesis often are used close to their site of production to increase leaf growth. In reviewing the results of several peer-reviewed papers related to this topic, Taylor *et al.* (2001) conclude elevated CO₂ consistently enhanced leaf extension rates in poplar species, which positively correlates with increased wood production. Similarly, Ferris *et al.* (2001) report a 200-ppm increase in the air's CO₂ concentration boosted leaf area in three poplar species by approximately 40%. In addition, a doubling of the atmospheric CO₂ concentration enhanced leaf size in a native British tree species (*Alnus glutinosa*) by 17% (Poole *et al.*, 2000). In all of these cases, it is likely CO₂-induced increases in leaf turgor pressure (Tognetti *et al.*, 2000) contributed to the CO₂-induced enhancements in leaf growth, as mediated through enhanced cell division and elongation.

Sometimes, excess carbohydrates are used to enhance the biosynthesis of secondary carbon compounds within leaves, which often results in greater specific leaf areas (Cornelissen *et al.*, 1999) and defensive resistance to pathogens and herbivores. Hattenschwiler *et al.* (1999) found a 280-ppm increase in the air's CO₂ concentration significantly increased needle concentrations of tannins and phenolics in spruce trees. Similarly, a 350-ppm increase in the CO₂ content of the air enhanced total phenolics in needles of loblolly pine by 21%

(Gebauer *et al.*, 1998). Leaves of various Mediterranean forest species grown at 710 ppm CO₂ displayed 18% greater lignin concentrations than leaves from species grown at 350 ppm CO₂ (De Angelis *et al.*, 2000). However, Heyworth *et al.* (1998) did not observe any significant effects of elevated CO₂ on tannin concentrations in needles of Scots pine exposed to 700 ppm CO₂, nor did King *et al.* (2001) for aspen leaves exposed to the same atmospheric CO₂ concentration. And Schaffer *et al.* (1997) found twice-ambient levels of atmospheric CO₂ stimulated the production of foliar carbon compounds in mango trees so dramatically that the concentrations of several leaf minerals fell due to this “dilution effect.”

Under certain conditions, excess carbohydrates also are used to enhance various leaf anatomical features. Paoletti *et al.* (1998), for example, report white oak trees fumigated with air containing 750 ppm CO₂ displayed leaf cuticles three times thicker than those of leaves on trees grown in air containing 350 ppm CO₂. Lin *et al.* (2001) report this same elevated CO₂ concentration enhanced needle thickness in young Scots pines by increasing the area occupied by photosynthetic mesophyll tissue. Such increases in leaf and cuticle thickness can increase resistance to herbivory and pathogenic attack, much as increased concentrations of secondary carbon compounds do.

It would appear the current upward trend in atmospheric CO₂ concentration will affect numerous leaf characteristics of woody plants. The available data suggest the resulting changes likely will lead to greater and more efficient photosynthesis and growth rates, together with increased leaf resistance to herbivory and pathogen attack. Thus, tree productivity likely will continue to increase in the future due to changes in foliar properties driven by the ongoing rise in the air’s CO₂ content.

References

Carter, G.A., Bahadur, R., and Norby, R.J. 2000. Effects of elevated atmospheric CO₂ and temperature on leaf optical properties in *Acer saccharum*. *Environmental and Experimental Botany* **43**: 267–273.

Cornelissen, J.H.C., Carnelli, A.L., and Callaghan, T.V. 1999. Generalities in the growth, allocation and leaf quality responses to elevated CO₂ in eight woody species. *New Phytologist* **141**: 401–409.

De Angelis, P., Chigwerewe, K.S., and Mugnozza, G.E.S. 2000. Litter quality and decomposition in a CO₂-enriched

Mediterranean forest ecosystem. *Plant and Soil* **224**: 31–41.

Ferris, R., Sabatti, M., Miglietta, F., Mills, R.F., and Taylor, G. 2001. Leaf area is stimulated in *Populus* by free air CO₂ enrichment (POPFACE), through increased cell expansion and production. *Plant, Cell and Environment* **24**: 305–315.

Gebauer, R.L.E., Strain, B.R., and Reynolds, J.F. 1998. The effect of elevated CO₂ and N availability on tissue concentrations and whole plant pools of carbon-based secondary compounds in loblolly pine (*Pinus taeda*). *Oecologia* **113**: 29–36.

Gielen, B., Jach, M.E., and Ceulemans, R. 2000. Effects of season, needle age and elevated atmospheric CO₂ on chlorophyll fluorescence parameters and needle nitrogen concentration in (*Pinus sylvestris* L.). *Photosynthetica* **38**: 13–21.

Hattenschwiler, S. and Schafellner, C. 1999. Opposing effects of elevated CO₂ and N deposition on *Lymantria monacha* larvae feeding on spruce trees. *Oecologia* **118**: 210–217.

Heyworth, C.J., Iason, G.R., Temperton, V., Jarvis, P.G., and Duncan, A.J. 1998. The effect of elevated CO₂ concentration and nutrient supply on carbon-based plant secondary metabolites in *Pinus sylvestris* L. *Oecologia* **115**: 344–350.

King, J.S., Pregitzer, K.S., Zak, D.R., Kubiske, M.E., Ashby, J.A., and Holmes, W.E. 2001. Chemistry and decomposition of litter from *Populus tremuloides* Michaux grown at elevated atmospheric CO₂ and varying N availability. *Global Change Biology* **7**: 65–74.

Lin, J., Jach, M.E., and Ceulemans, R. 2001. Stomatal density and needle anatomy of Scots pine (*Pinus sylvestris*) are affected by elevated CO₂. *New Phytologist* **150**: 665–674.

Norby, R.J., Long, T.M., Hartz-Rubin, J.S., and O’Neill, E.G. 2000. Nitrogen resorption in senescing tree leaves in a warmer, CO₂-enriched atmosphere. *Plant and Soil* **224**: 15–29.

Ormrod, D.P., Lesser, V.M., Olszyk, D.M., and Tingey, D.T. 1999. Elevated temperature and carbon dioxide affect chlorophylls and carotenoids in Douglas-fir seedlings. *International Journal of Plant Science* **160**: 529–534.

Paoletti, E., Nourrisson, G., Garrec, J.P., and Raschi, A. 1998. Modifications of the leaf surface structures of *Quercus ilex* L. in open, naturally CO₂-enriched environments. *Plant, Cell and Environment* **21**: 1071–1075.

Poole, I., Lawson, T., Weyers, J.D.B., and Raven, J.A. 2000. Effect of elevated CO₂ on the stomatal distribution

and leaf physiology of *Alnus glutinosa*. *New Phytologist* **145**: 511–521.

Rey, A. and Jarvis, P.G. 1998. Long-term photosynthetic acclimation to increased atmospheric CO₂ concentration in young birch (*Betula pendula*) trees. *Tree Physiology* **18**: 441–450.

Schaffer, B., Whiley, A.W., Searle, C., and Nissen, R.J. 1997. Leaf gas exchange, dry matter partitioning, and mineral element concentrations in mango as influenced by elevated atmospheric carbon dioxide and root restriction. *Journal of the American Society of Horticultural Science* **122**: 849–855.

Taylor, G., Ceulemans, R., Ferris, R., Gardner, S.D.L., and Shao, B.Y. 2001. Increased leaf area expansion of hybrid poplar in elevated CO₂. From controlled environments to open-top chambers and to FACE. *Environmental Pollution* **115**: 463–472.

Tognetti, R., Rashi, A., and Jones, M.B. 2000. Seasonal patterns of tissue water relations in three Mediterranean shrubs co-occurring at a natural CO₂ spring. *Plant, Cell and Environment* **23**: 1341–1351.

2.10.3 Other

- The ongoing rise in the air's CO₂ content will alter many physical and physiological leaf characteristics of Earth's plants; some of these changes will lead to more efficient plant growth, including the production of important secondary carbon compounds possessing high potential for combating a number of human maladies.

Nearly all plants respond to increases in the air's CO₂ content by displaying enhanced rates of photosynthesis and biomass production. Simultaneously, plants often exhibit changes in leaf characteristics. This review summarizes some of the CO₂-induced leaf responses observed in non-agricultural and non-woody species.

When the air's CO₂ concentration is experimentally increased, plants commonly reduce their foliar concentrations of the nitrogen-rich photosynthetic enzyme rubisco. Consequently, exposure to elevated CO₂ concentrations frequently results in lowered foliar nitrogen concentrations. This adjustment allows excess nitrogen to be mobilized away from the photosynthetic process and into processes more limiting to growth.

Schappi and Korner (1997), for example, note two species common to the Swiss Alps displayed reduced foliar nitrogen concentrations in response to

atmospheric CO₂ enrichment. However, Goverde *et al.* (1999) found no change in the leaf nitrogen contents of *Lotus corniculatus* plants exposed to twice-ambient atmospheric CO₂ concentrations, nor did David *et al.* (2001) in leaves of *Medicago* and *Trifolium* species. In the latter study, the authors report a CO₂-induced increase in leaf nitrogen content for a certain *Galactites* species. Nevertheless, in a review of 67 published experimental observations made on several dozen species, Norby *et al.* (2001) conclude a doubling of the air's CO₂ concentration reduced leaf nitrogen content by, on average, approximately 7%.

At the other end of the spectrum of leaf responses to atmospheric CO₂ enrichment, excess carbohydrates resulting from CO₂-induced increases in photosynthetic rates often are used to enhance the biosynthesis of secondary carbon compounds. Norby *et al.* (2001), for example, analyzed 46 published experimental observations and determined a doubling of the atmospheric CO₂ content increased leaf lignin concentrations in a number of species by an average of 6.5%. Leaf chlorophyll contents also have been reported to increase in young orchid plantlets exposed to elevated CO₂ concentrations (Gouk *et al.*, 1999). Also, Goverde *et al.* (1999) observed elevated CO₂ concentrations increased leaf tannin concentrations in *Lotus corniculatus*, although Kerslake *et al.* (1998) could not discern any CO₂ effect on foliar phenolic concentrations in *Calluna vulgaris*.

Idso and Idso (2001) note a near-tripling of the air's CO₂ content enhanced the concentration of the heart-helping compound digoxin in the woolly foxglove by about 12%, and a 75% increase in the air's CO₂ content produced 6 to 28% increases in the concentrations of five substances produced by spider lilies that have proven effective in treating a number of human cancers and viral diseases.

The ongoing rise in the air's CO₂ concentration will alter many physical and physiological leaf characteristics of Earth's plants. The data suggest the resulting changes will lead to more efficient plant growth and increase the production of secondary carbon compounds, some of which have high potential for combating human diseases. Thus, the increasing CO₂ content of the air may indirectly—but significantly—improve the quality of human life.

References

David, J.-F., Malet, N., Couteaux, M.-M., and Roy, J. 2001. Feeding rates of the woodlouse *Armadillidium*

vulgare on herb litters produced at two levels of atmospheric CO₂. *Oecologia* **127**: 343–349.

Gouk, S.S., He, J., and Hew, C.S. 1999. Changes in photosynthetic capability and carbohydrate production in an epiphytic CAM orchid plantlet exposed to super-elevated CO₂. *Environmental and Experimental Botany* **41**: 219–230.

Goverde, M., Bazin, A., Shykoff, J.A., and Erhardt, A. 1999. Influence of leaf chemistry of *Lotus corniculatus* (Fabaceae) on larval development of *Polyommatus icarus* (Lepidoptera, Lycaenidae): effects of elevated CO₂ and plant genotype. *Functional Ecology* **13**: 801–810.

Idso, S.B. and Idso, K.E. 2001. Effects of atmospheric CO₂ enrichment on plant constituents related to animal and human health. *Environmental and Experimental Botany* **45**: 179–199.

Kerslake, J.E., Woodin, S.J., and Hartley, S.E. 1998. Effects of carbon dioxide and nitrogen enrichment on a plant-insect interaction: the quality of *Calluna vulgaris* as a host for *Operophtera brumata*. *New Phytologist* **140**: 43–53.

Norby, R.J., Cotrufo, M.F., Ineson, P., O'Neill, E.G., and Canadell, J.G. 2001. Elevated CO₂, litter chemistry, and decomposition: a synthesis. *Oecologia* **127**: 153–165.

Schappi, B. and Korner, C. 1997. *In situ* effects of elevated CO₂ on the carbon and nitrogen status of alpine plants. *Functional Ecology* **11**: 290–299.

2.11 Lignin

- Atmospheric CO₂ enrichment stimulates photosynthesis in nearly all plants, enabling them to produce more nonstructural carbohydrates that can be used to create important carbon-based secondary compounds, one of which is lignin.

Lignin is important because it tends to inhibit the biodegradation of organic materials. Some studies suggest plant lignin concentrations tend to decline in response to increases in the air's CO₂ concentration. In one such study—a five-year open-top chamber experiment—Cotrufo and Ineson (2000) found a doubling of the air's CO₂ concentration decreased lignin concentrations in twigs of beech seedlings by approximately 12%. Nevertheless, after 42 months of incubation in native forest soils, the decomposition rate of the CO₂-enriched twigs was still 5% less than that of the twigs grown in ambient air. Likewise, in an open-top chamber study of an agricultural crop (tall fescue), Newman *et al.* (2003) found doubling the air's CO₂ content reduced forage lignin concentration

by 14%.

At the other end of the spectrum, a larger number of experiments has revealed CO₂-induced increases in plant lignin concentrations. With the CO₂-induced production of more lignin in plant tissues, the ongoing rise in the air's CO₂ content could lead to enhanced carbon sequestration in the world's soils, because plant-produced organic matter supplied to soils would be more resistant to decomposition; the end result of this phenomenon would be a slowing of the rate-of-rise of the atmosphere's CO₂ concentration, which could reduce the magnitude of CO₂-induced global warming.

In a two-year study of ash and sycamore seedlings grown in closed-top chambers (solar domes) at CO₂ concentrations of either 350 ppm (ambient) or 600 ppm (enriched), Cotrufo *et al.* (1998) observed greater concentrations of lignin in the litter produced by both species, and after one year of incubating the litter from the two CO₂ treatments in bags placed within a forest soil, the bags containing the litter produced by the CO₂-enriched trees of both species had about 30% more dry mass remaining in them than did the bags containing the litter produced by the ambient-treatment trees. In addition, woodlouse arthropods consumed 16% less litter in the CO₂-enriched chambers than in the ambient-treatment chambers.

Higher plant lignin concentrations also were observed in oak seedlings growing in doubled-CO₂ air (700 ppm as opposed to 350 ppm) in the controlled-environment greenhouse study of Staudt *et al.* (2001), as well as in trembling aspen seedlings growing in doubled-CO₂ air in the open-top chamber study of Tuchman *et al.* (2003). And in an open-top chamber study of a 30-year-old mixed-stand of various Mediterranean forest species growing near the coast of central Italy, De Angelis *et al.* (2000) determined doubled-CO₂ air increased leaf-litter lignin concentrations by 18%, which was accompanied by an 8% reduction in the initial loss of mass from the decomposing CO₂-enriched litter and a 4% reduction one year later.

Booker *et al.* (2000) observed higher lignin concentrations in the roots of CO₂-enriched cotton, a perennial woody plant, as did Booker *et al.* (2005) in CO₂-enriched soybean, an annual herbaceous plant. They conclude, “one result of increased residue production and higher levels of recalcitrant material such as lignin being added to the soil is that soil carbon sequestration should increase, a response anticipated to occur with increasing concentrations of atmospheric CO₂.”

Plant Characteristics

More often than not, however, experiments of this type have found no significant changes in the tissue lignin concentrations of plants grown in CO₂-enriched air. Studies in this category include the work of Hirschel *et al.* (1997) dealing with plants growing in an alpine grassland, a lowland calcareous grassland, and a lowland, wet, tropical rainforest; Booker and Maier (2001) and Finzi and Schlesinger (2002) dealing with loblolly pine trees; Peñuelas *et al.* (2002) investigating three species of shrub in Pisa, Italy; and Billings *et al.* (2003) dealing with four species of shrub in the Mojave Desert, Nevada, USA.

Norby *et al.* (2001) conducted a meta-analytic review that considered this issue from a number of different perspectives. Based on 46 experimental observations, they determined elevated atmospheric CO₂ concentrations increased leaf-litter lignin concentrations by an average of 6.5%. These increases in lignin content occurred only in woody species. Leaf-litter lignin concentrations were not affected by elevated CO₂ when plants were grown in open-top chambers, FACE plots, or in the proximity of CO₂-emitting springs. In analyzing 101 observations, Norby *et al.* found elevated CO₂ had no consistent effect on leaf litter decomposition rate in any experimental setting.

Almost all of the studies conducted to date on woody species, where there is some evidence of an increase in leaf-litter lignin concentration (and there thus remains a possibility of CO₂-enhanced carbon sequestration), have been of short duration compared to the lifespans of various forest components. The long-term consequences of modest CO₂-induced increases in woody-plant lignin concentrations for soil carbon sequestration will not be known until several experiments of much longer duration than any conducted so far have been conducted. Nevertheless, as Booker *et al.* (2005) remind us, because there is also considerably more litter produced by almost all plants in CO₂-enriched air, soil carbon sequestration should continue to increase as the air's CO₂ content continues to rise.

References

Billings, S.A., Zitzer, S.F., Weatherly, H., Schaeffer, S.M., Charlet, T., Arnone III, J.A., and Evans, R.D. 2003. Effects of elevated carbon dioxide on green leaf tissue and leaf litter quality in an intact Mojave Desert ecosystem. *Global Change Biology* **9**: 729–735.

Booker, F.L. and Maier, C.A. 2001. Atmospheric carbon dioxide, irrigation, and fertilization effects on phenolic and

nitrogen concentrations in loblolly pine (*Pinus taeda*) needles. *Tree Physiology* **21**: 609–616.

Booker, F.L., Prior, S.A., Torbert, H.A., Fiscus, E.L., Pursley, W.A., and Hu, S. 2005. Decomposition of soybean grown under elevated concentrations of CO₂ and O₃. *Global Change Biology* **11**: 685–698.

Booker, F.L., Shafer, S.R., Wei, C.-M., and Horton, S.J. 2000. Carbon dioxide enrichment and nitrogen fertilization effects on cotton (*Gossypium hirsutum* L.) plant residue chemistry and decomposition. *Plant and Soil* **220**: 89–98.

Cotrufo, M.F., Briones, M.J.I., and Ineson, P. 1998. Elevated CO₂ affects field decomposition rate and palatability of tree leaf litter: importance of changes in substrate quality. *Soil Biology and Biochemistry* **30**: 1565–1571.

Cotrufo, M.F. and Ineson, P. 2000. Does elevated atmospheric CO₂ concentration affect wood decomposition? *Plant and Soil* **224**: 51–57.

De Angelis, P., Chigwerewe, K.S., and Mugnozza, G.E.S. 2000. Litter quality and decomposition in a CO₂-enriched Mediterranean forest ecosystem. *Plant and Soil* **224**: 31–41.

Finzi, A.C. and Schlesinger, W.H. 2002. Species control variation in litter decomposition in a pine forest exposed to elevated CO₂. *Global Change Biology* **8**: 1217–1229.

Hirschel, G., Korner, C., and Arnone III, J.A. 1997. Will rising atmospheric CO₂ affect leaf litter quality and in situ decomposition rates in native plant communities? *Oecologia* **110**: 387–392.

Newman, J.A., Abner, M.L., Dado, R.G., Gibson, D.J., Brookings, A., and Parsons, A.J. 2003. Effects of elevated CO₂, nitrogen and fungal endophyte-infection on tall fescue: growth, photosynthesis, chemical composition and digestibility. *Global Change Biology* **9**: 425–437.

Norby, R.J., Cotrufo, M.F., Ineson, P., O'Neill, E.G., and Canadell, J.G. 2001. Elevated CO₂, litter chemistry, and decomposition: a synthesis. *Oecologia* **127**: 153–165.

Peñuelas, J., Castells, E., Joffre, R., and Tognetti, R. 2002. Carbon-based secondary and structural compounds in Mediterranean shrubs growing near a natural CO₂ spring. *Global Change Biology* **8**: 281–288.

Staudt, M., Joffre, R., Rambal, S., and Kesselmeier, J. 2001. Effect of elevated CO₂ on monoterpene emission of young *Quercus ilex* trees and its relation to structural and ecophysiological parameters. *Tree Physiology* **21**: 437–445.

Tuchman, N.C., Wahtera, K.A., Wetzel, R.G., and Teeri, J.A. 2003. Elevated atmospheric CO₂ alters leaf litter quality for stream ecosystems: an *in situ* leaf decomposition study. *Hydrobiologia* **495**: 203–211.

2.12 Lipids

- The highly positive effects of atmospheric CO₂ enrichment on lipid concentrations and characteristics in various terrestrial and aquatic plants portend benefits for both the managed and unmanaged components of Earth's biosphere as the air's CO₂ content continues to climb.

Lipids are hydrophobic molecules consisting mainly of fats, oils, and waxes that possess long non-polar hydrocarbon groups arranged in chains commonly called fatty acid chains, one type of which (phospholipids) is a major component of plant and animal membranes. They are extremely important to the well-being of nearly all living organisms.

Seeking to discover how lipids are affected by elevated concentrations of atmospheric CO₂, Sgherri *et al.* (1998) grew alfalfa in open-top chambers at ambient (340 ppm) and enriched (600 ppm) CO₂ concentrations for 25 days. They then withheld water from the plants for five additional days. They found the plants grown at the elevated CO₂ concentration maintained greater leaf lipid to protein ratios, especially under conditions of water stress. In addition, leaf lipid contents of the plants grown in the CO₂-enriched air were 22 and 83% greater than those of the plants grown in ambient air for periods of ample and insufficient soil moisture, respectively. Also, the degrees of unsaturation of two of the most important lipids of the thylakoid membranes (which are found within chloroplasts and contain chlorophyll, other pigments that absorb sunlight, and specialized protein complexes that convert sunlight into usable cellular energy during photosynthesis) were approximately 20 and 37% greater in the high-compared to the low-CO₂ treatments during times of adequate and inadequate soil moisture, respectively.

Sgherri *et al.* suggest the greater lipid contents observed in CO₂-enriched air and their increased degree of unsaturation may allow thylakoid membranes to maintain a more fluid and stable environment, critical during periods of water stress in enabling plants to continue photosynthetic carbon uptake. Some researchers have suggested adaptive plant responses such as these may allow plants to better cope with *any* altered environmental condition that produces stress.

With greater amounts of CO₂ in the atmosphere, the resulting greater lipid contents of thylakoid membranes plus their greater degree of unsaturation may provide greater membrane stability and integrity, thereby allowing proper functioning in times of drought or other adverse environmental conditions. In

some cases, these CO₂-induced adaptations may mean the difference between a plant's living or dying.

Consider, for example, the stress of exposure to overly cold temperatures that often leads to chilling injury in plants and the role played by membrane lipid unsaturation in alleviating those injuries.

Hugly and Somerville (1992) worked with wild-type *Arabidopsis thaliana* and two mutants of the species that were deficient in thylakoid lipid unsaturation. They found "chloroplast membrane lipid polyunsaturation contributes to the low-temperature fitness of the organism," and that it is required for some aspect of chloroplast biogenesis. When lipid polyunsaturation was low, for example, they observed what they called "dramatic reductions in chloroplast size, membrane content, and organization in developing leaves." They found a positive correlation "between the severity of chlorosis in the two mutants at low temperatures and the degree of reduction in polyunsaturated chloroplast lipid composition."

Kodama *et al.* (1994) demonstrate the low-temperature-induced suppression of leaf growth and concomitant induction of chlorosis observed in wild-type plants is much less evident in transgenic plants containing a gene that allows for greater expression of unsaturation in the fatty acids of leaf lipids. They conclude substantially unsaturated fatty acids "are undoubtedly an important factor contributing to cold tolerance."

Moon *et al.* (1995) found heightened unsaturation of the membrane lipids of chloroplasts stabilized the photosynthetic machinery of transgenic tobacco plants against low-temperature photo-inhibition "by accelerating the recovery of the photosystem II protein complex." Kodama *et al.* (1995), also working with transgenic tobacco plants, showed increased fatty acid desaturation is one of the prerequisites for normal leaf development at low, nonfreezing temperatures. Ishizaki-Nishizawa *et al.* (1996) found transgenic tobacco plants with a reduced level of saturated fatty acids in most membrane lipids "exhibited a significant increase in chilling resistance."

These observations are laden with significance for Earth's agro-ecosystems, since many economically important crops, such as rice, maize, and soybeans, are classified as chilling-sensitive: they experience injury or death at temperatures between 0 and 15°C (Lyons, 1973). If atmospheric CO₂ enrichment enhances their production of thylakoid lipids and their degree of unsaturation, as it does in alfalfa, a continuation of the ongoing rise in the air's CO₂

content could increase the abilities of these agricultural species to withstand periodic exposure to debilitating low temperatures; this phenomenon could provide the extra boost to food production that will be needed to sustain the planet's increasing numbers in the future (Tilman *et al.*, 2001).

Hussain *et al.* (2001) collected and analyzed seeds from loblolly pine trees exposed to atmospheric CO₂ concentrations of either 350 or 560 ppm since 1996 in the Duke Forest FACE study. The seeds collected from the CO₂-enriched trees were 90% heavier than seeds collected from the trees growing in ambient air, and their mean lipid content was 265% greater. The germination success of seeds developed under CO₂-enriched conditions was more than three times greater than that of the seeds from the ambient-air treatment, regardless of germination CO₂ concentration. In addition, seeds from the CO₂-enriched trees germinated approximately five days earlier, regardless of germination CO₂ concentration, and the seedlings derived from the seeds collected from the CO₂-enriched trees displayed significantly greater root lengths and needle numbers than those derived from seeds collected from the ambient-treatment trees.

Schwanz and Polle (1998) evaluated the degree of lipid peroxidation in leaves of mature holm and white oak trees that had been growing in the vicinity of natural CO₂ springs in central Italy for close to half a century. They found the trees growing in close proximity to the CO₂-emitting springs often exhibited lipid peroxidation reductions, which indicate less intrinsic oxidative stress and the presence of fewer internal harmful oxidants.

Yu *et al.* (2004) grew the marine microalgae *Platymonas subcordiformis* in the laboratory at ambient levels of atmospheric CO₂ concentration and UV-B radiation flux density, as well as at elevated levels of 5,000 ppm CO₂ and the UV-B radiation flux anticipated to result from a 25% stratospheric ozone depletion under clear sky conditions in summer. They report the elevated UV-B treatment by itself significantly increased the production of the toxic superoxide anion and hydrogen peroxide, as well as malonyldialdehyde, an end product of lipid peroxidation. Elevated CO₂ by itself did just the opposite. In the treatment consisting of elevated UV-B and elevated CO₂, the concentrations of these three substances were all lower than those observed in the elevated UV-B and ambient CO₂ treatment. Yu *et al.* conclude, "CO₂ enrichment could reduce oxidative stress of reactive oxygen species to *P. subcordiformis*, and reduce the lipid peroxidation damage of UV-B to

P. subcordiformis."

An interesting aspect of these findings is what they imply about coral bleaching. In the introduction to their review of this important subject, Smith *et al.* (2005) report, "photoinhibition of photosynthesis and photodamage to photosystem II of the zooxanthellae, with the consequent increase in the production of damaging reactive oxygen species (ROS), have been implicated as the cause of thermal bleaching (Brown, 1997; Fitt *et al.*, 2001; Lesser, 2004; Tchernov *et al.*, 2004)." At the end of their review, they report the "thermal bleaching of many corals is ultimately the result of the destruction of photosynthetic pigments by ROS," and the production by the zooxanthellae of one particular ROS, hydrogen peroxide, "may be a signal that triggers a response in the host cell to eject the zooxanthellae or shed the host cell from the coral." Combining these observations with the finding of Yu *et al.* that CO₂ enrichment counters the production of hydrogen peroxide, it follows that some degree of atmospheric CO₂ enrichment should likewise cause host cells to not eject their zooxanthellae.

Goverde *et al.*, 2002) examined the impact of atmospheric CO₂ enrichment on lipid concentrations in the body of an animal, specifically, the satyrid butterfly (*Coenonympha pamphilus*), larvae of which were raised in semi-natural, undisturbed calcareous grassland plots exposed to atmospheric CO₂ concentrations of 370 and 600 ppm for five growing seasons. Among other things, this work revealed the elevated atmospheric CO₂ concentration increased lipid concentrations in the bodies of adult male butterflies by nearly 14%. Since these compounds are used as energy resources in these and other butterflies, this animal species—and perhaps others—likely will exhibit positive responses to future increases in the air's CO₂ concentration.

References

- Brown, B.E. 1997. Coral bleaching: causes and consequences. *Coral Reefs* **16**: S129–S138.
- Fitt, W.K., Brown, B.E., and Warner, M.E., *et al.* 2001. Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* **20**: 51–65.
- Goverde, M., Erhardt, A., and Niklaus, P.A. 2002. *In situ* development of a satyrid butterfly on calcareous grassland exposed to elevated carbon dioxide. *Ecology* **83**: 1399–1411.

Hugly, S. and Somerville, C. 1992. A role for membrane lipid polyunsaturation in chloroplast biogenesis at low temperature. *Plant Physiology* **99**: 197–202.

Hussain, M., Kubiske, M.E., and Connor, K.F. 2001. Germination of CO₂-enriched *Pinus taeda* L. seeds and subsequent seedling growth responses to CO₂ enrichment. *Functional Ecology* **15**: 344–350.

Ishizaki-Nishizawa, O., Fujii, T., Azuma, M., Sekiguchi, K., Murata, N., Ohtani, T., and Toguri T. 1996. Low-temperature resistance of higher plants is significantly enhanced by a nonspecific cyanobacterial desaturase. *Nature Biotechnology* **14**: 1003–1006.

Kodama, H., Hamada, T., Horiguchi, G., Nishimura, M., and Iba, K. 1994. Genetic enhancement of cold tolerance by expression of a gene for chloroplast w-3 fatty acid desaturase in transgenic tobacco. *Plant Physiology* **105**: 601–605.

Kodama, H., Horiguchi, G., Nishiuchi, T., Nishimura, M., and Iba, K. 1995. Fatty acid desaturation during chilling acclimation is one of the factors involved in conferring low-temperature tolerance to young tobacco leaves. *Plant Physiology* **107**: 1177–1185.

Lesser, M.P. 2004. Experimental biology of coral reef systems. *Journal of Experimental Marine Biology and Ecology* **300**: 217–252.

Lyons, J.M. 1973. Chilling injury in plants. *Annual Review of Plant Physiology* **24**: 445–466.

Moon, B.Y., Higashi, S.-I., Gombos, Z., and Murata, N. 1995. Unsaturation of the membrane lipids of chloroplasts stabilizes the photosynthetic machinery against low-temperature photoinhibition in transgenic tobacco plants. *Proceedings of the National Academy of Sciences, USA* **92**: 6219–6223.

Schwanz, P. and Polle, A. 1998. Antioxidative systems, pigment and protein contents in leaves of adult mediterranean oak species (*Quercus pubescens* and *Q. ilex*) with lifetime exposure to elevated CO₂. *New Phytologist* **140**: 411–423.

Sgherri, C.L.M., Quartacci, M.F., Menconi, M., Raschi, A., and Navari-Izzo, F. 1998. Interactions between drought and elevated CO₂ on alfalfa plants. *Journal of Plant Physiology* **152**: 118–124.

Smith, D.J., Suggett, D.J., and Baker, N.R. 2005. Is photoinhibition of zooxanthellae photosynthesis the primary cause of thermal bleaching in corals? *Global Change Biology* **11**: 1–11.

Tchernov, D., Gorbunov, M.Y., de Vargas, C., Yadav, S.N., Milligan, A.J., Hagglblom, M., and Falkowski, P.G. 2004. Membrane lipids of symbiotic algae are diagnostic of sensitivity to thermal bleaching in corals. *Proceedings of*

the National Academy of Sciences USA **101**: 13,531–13,535.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., and Swackhamer, D. 2001. Forecasting agriculturally driven global environmental change. *Science* **292**: 281–284.

Yu, J., Tang, X.-X., Zhang, P.-Y., Tian, J.-Y., and Cai, H.-J. 2004. Effects of CO₂ enrichment on photosynthesis, lipid peroxidation and activities of antioxidative enzymes of *Platymonas subcordiformis* subjected to UV-B radiation stress. *Acta Botanica Sinica* **46**: 682–690.

2.13 Low Temperature

- The stresses of low temperature have been shown to be both alleviated and enhanced in plants growing under elevated CO₂ concentrations. It appears far more plants are benefiting from such stress alleviation than are experiencing stress augmentation.

Loik *et al.* (2000) grew three *Yucca* species (*brevifolia*, *schidigera*, and *whipplei*) in pots placed in glasshouses maintained at atmospheric CO₂ concentrations of 360 and 700 ppm and day/night air temperatures of 40/24°C for seven months, after which some of the plants were subjected to a two-week day/night air temperature treatment of 20/5°C. In addition, leaves from each *Yucca* species were removed and placed in a freezer cooled at a rate of 3°C per hour until a minimum temperature of -15°C was reached. These manipulations indicated elevated CO₂ lowered the air temperature at which 50% low-temperature-induced cell mortality occurred by 1.6, 1.4, and 0.8°C in *brevifolia*, *schidigera*, and *whipplei*, respectively. On the basis of the result obtained for *Y. brevifolia*, Dole *et al.* (2003) estimate “the increase in freezing tolerance caused by doubled CO₂ would increase the potential habitat of this species by 14%.”

Obrist *et al.* (2001) observed just the opposite response. In an open-top chamber study of a temperate grass ecosystem growing on a nutrient-poor calcareous soil in northwest Switzerland, portions of which had been exposed to atmospheric CO₂ concentrations of 360 and 600 ppm for six years, they found the average temperature at which 50% low-temperature-induced leaf mortality occurred in five prominent species rose by an average of 0.7°C in response to the extra 240 ppm of CO₂ employed in their experiment.

Most relevant investigations, however, have

Plant Characteristics

produced evidence of positive CO₂ effects on plants' low-temperature tolerance. Sigurdsson (2001), for example, grew black cottonwood seedlings near Gunnarsholt, Iceland within closed-top chambers maintained at ambient and twice-ambient atmospheric CO₂ concentrations for three years, finding elevated CO₂ tended to hasten the end of the growing season. This effect was interpreted as enabling the seedlings to better avoid the severe cold-induced dieback of newly produced tissues that often occurs with the approach of winter in this region. Likewise, Wayne *et al.* (1998) found yellow birch seedlings grown at an atmospheric CO₂ concentration of 800 ppm exhibited greater dormant bud survivorship at low air temperatures than did seedlings grown at 400 ppm CO₂.

Schwanz and Polle (2001) investigated the effects of elevated CO₂ on chilling stress in micropropagated hybrid poplar clones that were subsequently potted and transferred to growth chambers maintained at either ambient (360 ppm) or elevated (700 ppm) CO₂ for three months. They found "photosynthesis was less diminished and electrolyte leakage was lower in stressed leaves from poplar trees grown under elevated CO₂ as compared with those from ambient CO₂." Although severe chilling caused pigment and protein degradation in all stressed leaves, the damage was expressed to a lower extent in leaves from the elevated CO₂ treatment. This CO₂-induced chilling protection was accompanied by a rapid induction of superoxide dismutase activity and by slightly higher stabilities of other antioxidative enzymes.

Sgherri *et al.* (1998) report raising the air's CO₂ concentration from 340 to 600 ppm increased lipid concentrations in alfalfa thylakoid membranes while inducing a higher degree of unsaturation in the most prominent of those lipids. Under well-watered conditions, for example, the 76% increase in atmospheric CO₂ enhanced overall thylakoid lipid concentration by about 25%, while it increased the degree of unsaturation of the two main lipids by approximately 17% and 24%. Under conditions of water stress, these responses were even greater, as thylakoid lipid concentration rose by approximately 92%, and the degree of unsaturation of the two main lipids rose by about 22% and 53%.

What these observations have to do with a plant's susceptibility to chilling injury is evident from a number of studies conducted over the past decade. For example, Hugly and Somerville (1992) studied wild-type *Arabidopsis thaliana* and two mutants deficient in thylakoid lipid unsaturation, finding "chloroplast membrane lipid polyunsaturation

contributes to the low-temperature fitness of the organism" and it "is required for some aspect of chloroplast biogenesis." When lipid polyunsaturation was low, they observed "dramatic reductions in chloroplast size, membrane content, and organization in developing leaves." They found a positive correlation "between the severity of chlorosis in the two mutants at low temperatures and the degree of reduction in polyunsaturated chloroplast lipid composition."

Kodama *et al.* (1994) demonstrate the low-temperature-induced suppression of leaf growth and concomitant induction of chlorosis observed in wild-type tobacco plants is much less evident in transgenic plants containing a gene that allows for greater expression of unsaturation in the fatty acids of leaf lipids. They conclude substantially unsaturated fatty acids "are undoubtedly an important factor contributing to cold tolerance."

Moon *et al.* (1995) found heightened unsaturation of the membrane lipids of chloroplasts stabilized the photosynthetic machinery of transgenic tobacco plants against low-temperature photoinhibition "by accelerating the recovery of the photosystem II protein complex." Likewise, Kodama *et al.* (1995), also working with transgenic tobacco plants, showed increased fatty acid desaturation is one of the prerequisites for normal leaf development at low, nonfreezing temperatures. Ishizaki-Nishizawa *et al.* (1996) demonstrate transgenic tobacco plants with a reduced level of saturated fatty acids in most membrane lipids "exhibited a significant increase in chilling resistance."

Many economically important crops, such as rice, maize, and soybeans, are classified as chilling-sensitive—they experience injury or death at temperatures between 0 and 15°C (Lyons, 1973). If atmospheric CO₂ enrichment enhances their production and degree-of-unsaturation of thylakoid lipids, as it does in alfalfa, a continuation of the ongoing rise in the air's CO₂ content could increase the abilities of these critically important agricultural species to withstand periodic exposure to debilitating low temperatures, and this could provide the extra boost in food production that will be needed to sustain the planet's increasing numbers in the years and decades ahead.

Earth's natural ecosystems also would benefit from a CO₂-induced increase in thylakoid lipids containing more-highly-unsaturated fatty acids. Many plants of tropical origin, for example, suffer cold damage when temperatures fall below 20°C (Graham and Patterson, 1982). With improved lipid charac-

teristics provided by the ongoing rise in the air's CO₂ content, such plants would be able to expand their ranges both poleward and upward in a higher-CO₂ world.

Baczek-Kwinta and Koscielniak (2003) grew two hybrid maize (*Zea mays* L.) genotypes—KOC 9431 (chill-resistant) and K103xK85 (chill-sensitive)—from seed in air of either ambient (350 ppm) or elevated (700 ppm) CO₂ concentration (AC or EC, respectively), after which the plants were exposed to air of 7°C for 11 days and then recovered in ambient air of 20°C for one day. Throughout this period, physiological and biochemical parameters were measured on the plants' third fully expanded leaves.

Under such conditions, Baczek-Kwinta and Koscielniak report, "EC inhibited chill-induced depression of net photosynthetic rate (PN), especially in leaves of chill-resistant genotype KOC 9431." This phenomenon "was distinct not only during chilling, but also during the recovery of plants at 20°C." They note, "seedlings subjected to EC showed 4-fold higher PN when compared to AC plants." They also determined "EC diminished the rate of superoxide radical formation in leaves in comparison to the AC control." In addition, "electrolyte leakage from the [leaf membrane] tissue, a parameter reflecting membrane injury, was significantly lower in samples of plants subjected to EC than AC." Finally, they report enrichment of air with CO₂ successfully inhibited the decrease in the maximal quantum efficiency of photosystem 2, both after chilling and during the one-day recovery period. Taking all these positive effects of elevated CO₂ together, the authors conclude, "the increase in atmospheric CO₂ concentration seems to be one of the protective factors for maize grown in cold temperate regions."

Melkonian *et al.* (2004) grew well-watered and fertilized mature bean plants (*Phaseolus vulgaris* L., cv. Bush Blue Lake 274) in CO₂-controlled growth chambers maintained at concentrations of either 350 or 700 ppm at 25/18°C day/night temperatures. The plants then received 24 hours of chilling at 6.5°C (8 hours light, 10 hours dark, 6 hours light), after which there was a 24-hour recovery period under pre-chill growing conditions, followed by a second 24 hours of chilling and a 48-hour recovery period consisting of pre-chill conditions. Throughout this time, net photosynthesis measurements were made two to three hours before and after each shift in temperature.

According to the authors, prior to chilling, net photosynthesis was approximately 20% higher at elevated compared to ambient CO₂. During chilling, plants of both treatments exhibited near-identical

much-reduced values. Subsequently, however, and "consistent with previous research [Boese *et al.*, 1997] on this cultivar," in the words of Melkonian *et al.*, "post-chilling recovery was more rapid at elevated compared to ambient CO₂."

Alam *et al.* (2005) grew eight-month-old saplings of two clones (PB 235 and RRII 105) of *Hevea brasiliensis*, a tree species indigenous to humid tropical climates, in 0.75-m³ polybags filled with garden soil during the two coldest months of the year in warm and cool regions of peninsular India having mean minimum temperatures of 22.0 and 10.0°C, respectively, while they measured a number of photosynthetic properties of the trees' leaves. The authors report, "irrespective of the differences in growth environment, higher CO₂ in the ambient air during measurements improved the photochemical efficiency of the plants as reflected in higher net photosynthetic rate, effective photosystem 2 quantum efficiency, and photochemical quenching." The Indian scientists conclude their results imply "inhibition in photochemical efficiency due to sub-optimal temperatures could be improved considerably with higher CO₂ concentration by making more CO₂ available to photosynthesis."

Kostiainen *et al.* (2006) studied the effects of elevated carbon dioxide (CO₂) and ozone (O₃) on various wood properties of two initially seven-year-old fast-growing silver birch (*Betula pendula* Roth) clones grown out-of-doors at Suonenjoki, Finland for three additional years in open-top chambers maintained at ambient and 1.9x ambient CO₂ concentrations in combination with ambient and 1.5x ambient O₃ concentrations. The Finnish researchers note "the concentration of nonstructural carbohydrates (starch and soluble sugars) in tree tissues is considered a measure of carbon shortage or surplus for growth (Korner, 2003)." Hence, they say "starch accumulation observed under elevated CO₂ in this study indicates a surplus of carbohydrates produced by enhanced photosynthesis of the same trees (Riikonen *et al.*, 2004)." In addition, they report, "during winter, starch reserves in the stem are gradually transformed to soluble carbohydrates involved in freezing tolerance (Bertrand *et al.*, 1999; Piispanen and Saranpaa, 2001), so the increase in starch concentration may improve acclimation in winter."

Bigras and Bertrand (2006) grew well-watered and fertilized black spruce (*Picea mariana* Mill. BSP) plants from seed in containers filled with a 3:1 mixture of peat:vermiculite in mini-greenhouses located within a larger greenhouse where they were

Plant Characteristics

exposed—at ambient and elevated (370 and 710 ppm) concentrations of atmospheric CO₂)—to environmental conditions that simulated “a growth period (Summer, April 17–September 15) followed by hardening (Fall, September 16–November 5; Winter, November 6–February 5) and dehardening (Spring, February 6–February 28).” During these periods numerous plant properties and physiological processes were measured.

In October, during the process of hardening, Bigras and Bertrand found “bud set began earlier in elevated CO₂ than in ambient CO₂” and “an increase in seedling cold tolerance in early fall was related to early bud set in elevated CO₂.” In addition, their results “showed reductions in dark respiration and light compensation point during cold acclimation and de-acclimation can contribute to increased productivity in elevated CO₂.” They “observed an increase in light-saturated photosynthetic rate in response to elevated CO₂ during the growth, hardening and de-hardening periods” which “varied seasonally between 12 and 50%.” The net result of these and other CO₂-induced plant benefits was a 38% increase in total plant mass at the end of the growing season that slowly declined to a value of 18% at the end of the winter.

Bertrand *et al.* (2007) grew well-watered and fertilized alfalfa (*Medicago sativa* L.) plants which they inoculated with one of two strains (either A2 or NRG34) of the nitrogen-fixing symbiont *Sinorhizobium meliloti* from seed in 12.5-cm-diameter pots filled with non-sterile topsoil within controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 400 or 800 ppm for two months under optimal light (600 $\mu\text{mol}/\text{m}^2/\text{s}$ for 16 hours per day) and day/night temperatures of 22/17°C and for two final weeks at a reduced light level of 200 $\mu\text{mol}/\text{m}^2/\text{s}$ for 8 hours per day and a cold day/night temperature regime of 5/2°C. Over this time they periodically measured plant physiological functions and characteristics.

At the end of the experiment, the researchers determined the total biomass of the plants in the elevated CO₂ treatment was approximately 33% greater than that of the plants in the control treatment when infected with the A2 strain of *S. meliloti*, but about 36% greater when infected with the NRG34 strain. Plants in the 800 ppm CO₂ treatment were found to be less freezing-tolerant than those in the 400 ppm treatment, and the plants inoculated with the NRG34 strain were determined to be less freezing-tolerant than those inoculated with the A2 strain.

Providing some comparative background for their

freezing tolerance results, Bertrand *et al.* write, “CO₂ enrichment led to more severe frost damage in leaves of *Eucalyptus pauciflora* (Barker *et al.*, 2005) and *Ginkgo biloba* (Terry *et al.*, 2000), and in a native temperate grassland (Obrist *et al.*, 2001), whereas it increased frost resistance of *Betula allaghamensis* (Wayne *et al.*, 1998) and *Picea mariana* (Bigras and Bertrand, 2006) but had no effect on freezing tolerance of *Picea abies* (Dalen *et al.*, 2001).” This suggests there may not be a single freezing tolerance response to atmospheric CO₂ enrichment that is typical of plants in general. However, because their results suggest “it is possible to select or identify rhizobial strains to improve alfalfa performance under high CO₂,” Bertrand *et al.* conclude the “freezing tolerance as well as the expression of key overwintering genes of alfalfa can be altered by the strain of rhizobium.” This should enable farmers to obtain the best of both worlds, as it were, by benefiting from the significant growth stimulation produced by the ongoing rise in the air’s CO₂ content while selecting a strain of rhizobium capable of compensating for a possible CO₂-induced reduction in freezing tolerance.

Hanninen *et al.* (2007) note “according to the hypothesis presented by Cannell (1985), climatic warming may paradoxically increase the risk of frost damage in boreal and temperate regions, because the trees will dehardening and even start to grow during intermittent mild periods in winter and get damaged during subsequent periods of frost.” Likewise, they write, “Kellomaki *et al.* (1995) predicted that frost damage caused by a premature dehardening would severely restrict growth of Scots pine under a climatic warming scenario in central Finland.”

Hanninen *et al.* investigated this subject using whole-tree chambers (WTCs) surrounding groups of 40-year-old Norway spruce (*Picea abies* (L.) Karst.) trees growing under natural conditions in northern Sweden, studying the effects of atmospheric CO₂ enrichment (to 700 ppm above the ambient value of 365 ppm) and global warming (ranging from 2.8°C above ambient in summer to 5.6°C above ambient in winter) on the timing of spring bud burst in the trees.

The researchers report the timing of bud burst was unaffected by elevated CO₂, but “the trees growing at an elevated temperature hardened later and dehardened earlier than the control trees.” However, they note, the difference was “much smaller” than that implied by Cannell (1985) and predicted by Kellomaki *et al.* (1995). Hanninen *et al.* conclude, “regardless of the warming taking place during winter, boreal coniferous trees are able to retain their dormancy and frost hardiness until around the spring

equinox,” explaining, “high temperatures during bud dormancy induction increase the chilling requirement of rest completion, or in some other way delay bud burst during spring,” citing Heide (2003) and Junttila *et al.* (2003). These observations thus suggest, they write, “boreal trees may be able to prevent premature dehardening and growth onset under climatic warming,” thereby thwarting scenarios of deleterious frost damage in the face of global warming.

In a study focusing only on temperature, Loik *et al.* (2004) note a warming of the climate may cause plants to come out of winter dormancy earlier in the spring, and “because physiologically active plants are more vulnerable than dormant plants to a transient low-temperature event (Larcher, 1995), earlier acclimation to warmer temperatures and onset of photosynthetic activity ... may make plants more susceptible to damage [caused by temporary but extreme cold weather] that reduces overall functional leaf surface area and productivity.” They tested this hypothesis for specimens of the evergreen shrub *Artemisia tridentata* and the sub-alpine herbaceous *Erythronium grandiflorum* that had been growing at 3,050 meters in the Rocky Mountains of Colorado (USA), “where overhead infrared heaters have continually simulated atmospheric forcing of the future (Harte *et al.*, 1995),” enhancing the downward infrared radiation flux by 22 Wm⁻².

Specifically, they compared the photosynthetic responses of the plants before, during, and after an imposed *in situ* freezing event, where air and leaf temperatures of selected plants were “continually decreased, as would occur during a natural episodic freezing event.” This environmental manipulation started at an ambient temperature of about 10°C and adjusted to -30°C over a period of 10 hours, mimicking what occurs naturally at this site about once every 10 years.

The authors report “the infrared warming treatment did not reduce the ability of the subalpine herbaceous geophyte *Erythronium grandiflorum* to tolerate *in situ* freezing, in contrast to our hypothesis.” The warming treatment in fact “led to a significant increase in photosynthetic tolerance of an experimentally imposed *in situ* freezing event for the Great Basin Desert evergreen shrub *Artemisia tridentata* ... in contrast to our hypothesis.” Loik *et al.* suggest “enhanced tolerance of episodic freezing is a result of enhanced physiological activity, in particular, higher plant water potentials and photosynthetic gas exchange caused by the infrared treatment effects on soil water content and soil temperature,” leading to “an increased level of

photosynthates available for allocation to cryo-protection or other acclimation mechanisms (Iba, 2002).” Loik *et al.* thus conclude that, contrary to prior expectations, some species of plants will not be negatively affected by episodic freezing events in a warmer world, and others “may exhibit enhanced tolerance of subzero air temperatures under a future warmer climate.”

References

- Alam, B., Nair, D.B., and Jacob, J. 2005. Low temperature stress modifies the photochemical efficiency of a tropical tree species *Hevea brasiliensis*: effects of varying concentration of CO₂ and photon flux density. *Photosynthetica* **43**: 247–252.
- Baczek-Kwinta, R. and Koscielniak, J. 2003. Anti-oxidative effect of elevated CO₂ concentration in the air on maize hybrids subjected to severe chill. *Photosynthetica* **41**: 161–165.
- Barker, D.H., Loveys, B.R., Egerton, J.J.G., Gorton, H., Williams, W.E., and Ball, M.C. 2005. CO₂ enrichment predisposes foliage of a eucalypt to freezing injury and reduces spring growth. *Plant, Cell and Environment* **28**: 1506–1515.
- Bertrand, A., Prevost, D., Bigras, F.J., and Castonguay, Y. 2007. Elevated atmospheric CO₂ and strain of rhizobium alter freezing tolerance and cold-induced molecular changes in alfalfa (*Medicago sativa*). *Annals of Botany* **99**: 275–284.
- Bertrand, A., Robitaille, G., Nadeau, P., and Castonguay, Y. 1999. Influence of ozone on cold acclimation in sugar maple seedlings. *Tree Physiology* **19**: 527–534.
- Bigras, F.J. and Bertrand, A. 2006. Responses of *Picea mariana* to elevated CO₂ concentration during growth, cold hardening and dehardening: phenology, cold tolerance, photosynthesis and growth. *Tree Physiology* **26**: 875–888.
- Boese, S.R., Wolfe, D.W., and Melkonian, J. 1997. Elevated CO₂ mitigates chilling-induced water stress and photosynthetic reduction during chilling. *Plant, Cell and Environment* **20**: 624–632.
- Cannell, M.G.R. 1985. Analysis of risks of frost damage to forest trees in Britain. In: Tigerstedt, P.M.A., Puttonen, P., and Koski, V. (Eds.) *Crop Physiology of Forest Trees*, Helsinki University Press, Helsinki, Finland, pp. 153–165.
- Dalen, L.S., Johnsen, O., and Ogner, G. 2001. CO₂ enrichment and development of freezing tolerance in Norway spruce. *Physiologia Plantarum* **113**: 533–540.
- Dole, K.P., Loik, M.E., and Sloan, L.C. 2003. The relative importance of climate change and the physiological effects

Plant Characteristics

- of CO₂ on freezing tolerance for the future distribution of *Yucca brevifolia*. *Global and Planetary Change* **36**: 137–146.
- Graham, D. and Patterson, B.D. 1982. Responses of plants to low, non-freezing temperatures: proteins, metabolism, and acclimation. *Annual Review of Plant Physiology* **33**: 347–372.
- Hanninen, H., Slaney, M., and Linder, S. 2007. Dormancy release of Norway spruce under climatic warming: testing ecophysiological models of bud burst with a whole-tree chamber experiment. *Tree Physiology* **27**: 291–300.
- Harte, J., Torn, M.S., Chang, F., Feifarek, B., Kinzig, A.P., Shaw, R., and Shen, K. 1995. Global warming and soil microclimate: results from a meadow-warming experiment. *Ecological Applications* **5**: 132–150.
- Heide, O.M. 2003. High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. *Tree Physiology* **23**: 931–936.
- Hugly, S. and Somerville, C. 1992. A role for membrane lipid polyunsaturation in chloroplast biogenesis at low temperature. *Plant Physiology* **99**: 197–202.
- Iba, K. 2002. Acclimative response to temperature stress in higher plants: Approaches of gene engineering for temperature tolerance. *Annual Review of Plant Biology* **53**: 225–245.
- Ishizaki-Nishizawa, O., Fujii, T., Azuma, M., Sekiguchi, K., Murata, N., Ohtani, T., and Toguri T. 1996. Low-temperature resistance of higher plants is significantly enhanced by a nonspecific cyanobacterial desaturase. *Nature Biotechnology* **14**: 1003–1006.
- Junttila, O., Nilsen, J., and Igeland, B. 2003. Effect of temperature on the induction of bud dormancy in ecotypes of *Betula pubescens* and *Betula pendula*. *Scandinavian Journal of Forest Research* **18**: 208–217.
- Kellomaki, S., Hanninen, H., and Kolstrom, M. 1995. Computations on frost damage to Scots pine under climatic warming in boreal conditions. *Ecological Applications* **5**: 42–52.
- Kodama, H., Hamada, T., Horiguchi, G., Nishimura, M., and Iba, K. 1994. Genetic enhancement of cold tolerance by expression of a gene for chloroplast w-3 fatty acid desaturase in transgenic tobacco. *Plant Physiology* **105**: 601–605.
- Kodama, H., Horiguchi, G., Nishiuchi, T., Nishimura, M., and Iba, K. 1995. Fatty acid desaturation during chilling acclimation is one of the factors involved in conferring low-temperature tolerance to young tobacco leaves. *Plant Physiology* **107**: 1177–1185.
- Korner, C. 2003. Carbon limitation in trees. *Journal of Ecology* **91**: 4–17.
- Kostiainen, K., Jalkanen, H., Kaakinen, S., Saranpaa, P., and Vapaavuori, E. 2006. Wood properties of two silver birch clones exposed to elevated CO₂ and O₃. *Global Change Biology* **12**: 1230–1240.
- Larcher, W. 1995. *Physiological Plant Ecology*. Springer-Verlag, New York, New York, USA.
- Loik, M.E., Huxman, T.E., Hamerlynck, E.P., and Smith, S.D. 2000. Low temperature tolerance and cold acclimation for seedlings of three Mojave Desert *Yucca* species exposed to elevated CO₂. *Journal of Arid Environments* **46**: 43–56.
- Loik, M.E., Still, C.J., Huxman, T.E., and Harte, J. 2004. *In situ* photosynthetic freezing tolerance for plants exposed to a global warming manipulation in the Rocky Mountains, Colorado, USA. *New Phytologist* **162**: 331–341.
- Lyons, J.M. 1973. Chilling injury in plants. *Annual Review of Plant Physiology* **24**: 445–466.
- Melkonian, J., Owens, T.G., and Wolfe, D.W. 2004. Gas exchange and co-regulation of photochemical and nonphotochemical quenching in bean during chilling at ambient and elevated carbon dioxide. *Photosynthesis Research* **79**: 71–82.
- Moon, B.Y., Higashi, S.-I., Gombos, Z., and Murata, N. 1995. Unsaturation of the membrane lipids of chloroplasts stabilizes the photosynthetic machinery against low-temperature photoinhibition in transgenic tobacco plants. *Proceedings of the National Academy of Sciences, USA* **92**: 6219–6223.
- Obrist, D., Arnone III, J.A., and Korner, C. 2001. *In situ* effects of elevated atmospheric CO₂ on leaf freezing resistance and carbohydrates in a native temperate grassland. *Annals of Botany* **87**: 839–844.
- Piispanen, R. and Saranpaa, P. 2001. Variation of non-structural carbohydrates in silver birch (*Betula pendula* Roth) wood. *Trees* **15**: 444–451.
- Riikonen, J., Lindsberg, M.-M., Holopainen, T., Oksanen, E., Lappi, J., Peltonen, P., and Vapaavuori, E. 2004. Silver birch and climate change: variable growth and carbon allocation responses to elevated concentrations of carbon dioxide and ozone. *Tree Physiology* **24**: 1227–1237.
- Schwanz, P. and Polle, A. 2001. Growth under elevated CO₂ ameliorates defenses against photo-oxidative stress in poplar (*Populus alba* x *tremula*). *Environmental and Experimental Botany* **45**: 43–53.
- Sgherri, C.L.M., Quartacci, M.F., Menconi, M., Raschi, A., and Navari-Izzo, F. 1998. Interactions between drought and elevated CO₂ on alfalfa plants. *Journal of Plant Physiology* **152**: 118–124.
- Sigurdsson, B.D. 2001. Elevated [CO₂] and nutrient status modified leaf phenology and growth rhythm of young

Populus trichocarpa trees in a 3-year field study. *Trees* **15**: 403–413.

Terry, A.C., Quick, W.P., and Beerling, D.J. 2000. Long-term growth of *Ginkgo* with CO₂ enrichment increases leaf ice nucleation temperatures and limits recovery of the photosynthetic system from freezing. *Plant Physiology* **124**: 183–190.

Wayne, P.M., Reekie, E.G., and Bazzaz, F.A. 1998. Elevated CO₂ ameliorates birch response to high temperature and frost stress: implications for modeling climate-induced geographic range shifts. *Oecologia* **114**: 335–342.

2.14 Monoterpenes

- The diverse results of several experimental studies do not paint a clear picture of what should be expected in the way of plant monoterpene emissions in a CO₂-enriched and possibly warmer world of the future.

Monoterpenes constitute a major fraction of the biogenic volatile organic compounds or BVOCs given off by plants; they help protect Earth's terrestrial vegetation by acting as scavengers of reactive oxygen species produced within plants experiencing significant heat stress (Peñuelas and Llusia, 2003). They also function as deterrents of pathogens and herbivores and are known to aid wound-healing after herbivore damage (Pichersky and Gershenzon, 2002). In addition, monoterpenes may attract pollinators and herbivore predators (Peñuelas *et al.*, 1995; Shulaeva *et al.*, 1997), and they have the ability to generate large quantities of organic aerosols that may alter the planet's climate by producing cloud condensation nuclei that can lead to a cooling of Earth's surface (during the day) via an enhanced reflection of incoming solar radiation.

In light of these observations, it is natural to want to know how plant monoterpene production might be affected by the ongoing rise in the atmosphere's CO₂ concentration, as well as by any warming that might yet occur as Earth continues to recover from the global chill of the Little Ice Age. What follows is a review of the findings of studies that have investigated various aspects of this subject.

Vuorinen *et al.* (2004) grew well-watered and fertilized white cabbage plants from seed for 25 days in growth chambers maintained at atmospheric CO₂ concentrations of either 360 or 720 ppm. One group of plants in each CO₂ treatment experienced no larval insect feeding, another experienced 48 hours of

feeding by larvae of a crucifer specialist (*Plutella xylostella*), and yet another group experienced 48 hours of feeding by larvae of a generalist herbivore (*Spodoptera littoralis*), after which several BVOCs released by each group of plants were collected from the air surrounding them and analyzed. The researchers conclude, "total monoterpene emission per shoot dry weight was approximately 27% reduced from plants grown at elevated CO₂," and they report there was no difference in larval-induced damage to the plants between the ambient-air and CO₂-enriched treatments.

An earlier study of holly oak trees by Loreto *et al.* (2001) also found decreases in monoterpene emissions in response to atmospheric CO₂ enrichment, and Constable *et al.* (1999) found no effect of elevated CO₂ on monoterpene emissions from Ponderosa pine and Douglas fir trees. This may mean the effects of atmospheric CO₂ enrichment on plant monoterpene emissions are nil or even negative.

Baraldi *et al.* (2004) exposed sections of a southern California chaparral ecosystem to atmospheric CO₂ concentrations ranging from 250 to 750 ppm in 100-ppm increments for four years within naturally lit glass chambers, measuring net ecosystem CO₂ exchange (NEE) and emission rates of BVOCs, which were mainly monoterpenes. The seven scientists found NEE exhibited a marked linear increase in response to increasing atmospheric CO₂ concentration, more than tripling its rate in going from 400 to 700 ppm at 0400, 1200, and 1600 hours in June, and rising from moderately negative to weak positive values in December. They found "total trace gas emissions expressed on a ground area basis were low and did not respond to increasing CO₂ concentrations" in the winter; in summer, when "BVOC emissions were of an order of magnitude greater than during winter," they found the different levels of CO₂ still "did not affect the emission rates" of monoterpenes.

Rapparini *et al.* (2004) measured BVOC emissions from mature downy and holly oak trees growing close to a natural CO₂ spring in central Italy, where atmospheric CO₂ concentrations averaged about 1,000 ppm, and at a nearby control site where the air's CO₂ content was unaffected by the spring. They too found long-term exposure to high levels of atmospheric CO₂ did not significantly affect BVOC emissions from the trees. However, when leaves of plants grown in the control site were exposed for a short period to an elevated CO₂ level by rapidly switching the CO₂ concentration in the gas-exchange cuvette, monoterpene basal emissions "were clearly

inhibited,” where basal emissions are those that occur at standard measuring conditions of 30°C air temperature and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ light intensity.

The studies thus appear to suggest atmospheric CO₂ enrichment has little or no effect on plant monoterpene emissions, and that if there is any effect at all, it is negative. But the situation is not nearly that straightforward, as demonstrated by Staudt *et al.* (2001). These four researchers also grew holly oak, albeit holly oak seedlings, within two compartments of a controlled-environment greenhouse—one of which was maintained at an atmospheric CO₂ concentration of 350 ppm and one of which was maintained at 700 ppm—where air temperature and vapor pressure deficit were set to track outside ambient conditions and the plants were exposed to natural sunlight and watered every other week. Various growth parameters and physiological responses of the seedlings were measured over a four-month period that began when the trees had been exposed to the two CO₂ treatments for a total of 10 months. They report the elevated CO₂ treatment increased the leaf area of the young oaks by 40%, their leaf biomass by 50%, and their trunk and branch biomass by 90%. The plants in the elevated CO₂ treatment “released 2.8-fold more monoterpenes per plant than plants grown in ambient CO₂,” on top of which Peñuelas and Llusia (2003) state, warming “increases the emission rates of most BVOCs exponentially.”

Raisanen *et al.* (2008) studied to what extent a doubling of the air’s CO₂ content and 2–6°C increases in air temperature (+2°C in summer, +4°C in spring and autumn, +6°C in winter), applied singly or together, might impact emissions of monoterpenes from 20-year-old Scots pine seedlings. They constructed closed-top chambers over parts of a naturally seeded stand of the trees in eastern Finland, which they exposed to these treatments for five years. Over the five-month growing season of May–September, the three researchers found total monoterpene emissions in the elevated-CO₂-only treatment were 5% greater than those in the ambient-CO₂-ambient-temperature treatment, and emissions in the elevated-temperature-only treatment were 9% less than those in ambient air. In the presence of both elevated CO₂ and elevated temperature, there was an increase of fully 126% in the total amount of monoterpenes emitted over the growing season.

The diverse results of these studies do not paint a clear picture of what should be expected in the way of plant monoterpene emissions in a CO₂-enriched and possibly warmer world of the future.

References

- Baraldi, R., Rapparini, F., Oechel, W.C., Hastings, S.J., Bryant, P., Cheng, Y., and Miglietta, F. 2004. Monoterpene emission responses to elevated CO₂ in a Mediterranean-type ecosystem. *New Phytologist* **161**: 17–21.
- Constable, J.V.H., Litvak, M.E., Greenberg, J.P., and Monson, R.K. 1999. Monoterpene emission from coniferous trees in response to elevated CO₂ concentration and climate warming. *Global Change Biology* **5**: 255–267.
- Loreto, F., Fischbach, R.J., Schnitzler, J.P., Ciccioli, P., Brancaleoni, E., Calfapietra, C., and Seufert, G. 2001. Monoterpene emission and monoterpene synthase activities in the Mediterranean evergreen oak *Quercus ilex* L. grown at elevated CO₂ concentrations. *Global Change Biology* **7**: 709–717.
- Peñuelas, J. and Llusia, J. 2003. BVOCs: plant defense against climate warming? *Trends in Plant Science* **8**: 105–109.
- Peñuelas, J., Llusia, J., and Estiarte, M. 1995. Terpenoids: a plant language. *Trends in Ecology and Evolution* **10**: 289.
- Pichersky, E. and Gershenzon, J. 2002. The formation and function of plant volatiles: perfumes for pollinator attraction and defense. *Current Opinion in Plant Biology* **5**: 237–243.
- Raisanen, T., Ryyppo, A., and Kellomaki, S. 2008. Effects of elevated CO₂ and temperature on monoterpene emission of Scots pine (*Pinus sylvestris* L.). *Atmospheric Environment* **42**: 4160–4171.
- Rapparini, F., Baraldi, R., Miglietta, F., and Loreto, F. 2004. Isoprenoid emission in trees of *Quercus pubescens* and *Quercus ilex* with lifetime exposure to naturally high CO₂ environment. *Plant, Cell and Environment* **27**: 381–391.
- Shulaev, V., Silverman, P., and Raskin, I. 1997. Airborne signaling by methyl salicylate in plant pathogen resistance. *Nature* **385**: 718–721.
- Staudt, M., Joffre, R., Rambal, S., and Kesselmeier, J. 2001. Effect of elevated CO₂ on monoterpene emission of young *Quercus ilex* trees and its relation to structural and ecophysiological parameters. *Tree Physiology* **21**: 437–445.
- Vuorinen, T., Reddy, G.V.P., Nerg, A.-M., and Holopainen, J.K. 2004. Monoterpene and herbivore-induced emissions from cabbage plants grown at elevated atmospheric CO₂ concentration. *Atmospheric Environment* **38**: 675–682.

2.15 Nectar

- As the air’s CO₂ content continues to rise, plant

fitness, flower pollination, and nectar production should be enhanced, leading to increases in fruit, grain, and vegetable yields of agricultural crops, as well as similar increases in the productivity of the world's natural vegetation.

Lake and Hughes (1999) grew nasturtiums (*Tropaeolum majus*) from seed through flowering and senescence (77 days) in growth chambers maintained at atmospheric CO₂ concentrations of either 380 or 760 ppm to determine the effects of elevated CO₂ on the vegetative and reproductive growth of the flowers, as well as several of the flowers' characteristics, including nectar quantity and quality. They found the doubled CO₂ concentration increased total plant biomass by 35% and root biomass by 78%, and it increased nectar volume in the CO₂-enriched flowers by 2.4-fold. It did so without lowering the sugar and amino acid characteristics of the nectar.

Dag and Eisikowitch (2000) divided a 0.5-acre greenhouse located in the center of the Arava Valley in the southern part of Israel into two parts, one of which was exposed to ambient air and one of which was exposed to air that had a CO₂ concentration of 1,000 ppm throughout the morning, 400 ppm between 1300 and 1500 hours, and 600 ppm until the next morning. Under these conditions they grew melons (*Cucumis melo*). In the melons' early flowering stage, the scientists collected and measured the volume of nectar produced per flower between 0900 and 1530 hours along with the sugar concentration of the nectar. They found average nectar volumes per flower were significantly higher in the CO₂-enriched sector of the greenhouse than in the control sector, sometimes by as much as 100%; since the sugar concentration of the nectar was found to be the same in both treatments, sugar production per flower was stimulated by an identical amount (as much as 100%) in the CO₂-enriched air. As a result, and noting the only pollinator used in greenhouse production of melons in Israel is the honey bee, the two researchers conclude, "improvement in nectar reward can increase the attractiveness of the flowers to the bees, increase pollination activity and consequently increase the fruit set and the yield."

Erhardt *et al.* (2005) grew well-watered *Epilobium angustifolium* L. plants (perennial temperate clonal herbs that colonize nutrient-rich open habitats) from the seeds of five genotypes in pots containing 12 liters of loamy soil maintained at high and low levels of nutrients by weekly supplying them with 25 ml of either 1.0 N (high level) or 0.5 N (low level) Hoagland's solution. The experiment

lasted from April 1995 to July 1996 (two full growing seasons) and was conducted in naturally lit controlled environment chambers housed within a greenhouse. Half of the chambers were supplied with ambient air having a CO₂ concentration of about 350 ppm and half were supplied with CO₂-enriched air having a concentration of about 650 ppm. Under these conditions, and in the second year of the study when most of the plants were flowering, nectar was extracted from the flowers, and its volume and sugar concentration were determined, along with its amino acid concentration and the total amino acid content per flower. The researchers found "elevated CO₂ significantly increased nectar production per day (+51%, $p < 0.01$), total sugar per flower (+41%, $p < 0.05$), amino acid concentration (+65%, $p < 0.05$) and total amino acids per flower (+192%, $p < 0.001$)." These responses occurred with all genotypes.

Erhardt *et al.* note Galen and Plowright (1985) found "increased nectar rewards led to longer bumblebee tenure on flowers and greater pollen receipt in *E. angustifolium*, and that bees visited more flowers per plant on plants with more nectar." In addition, they report, "in other plant species higher nectar rewards also usually led to increases in components of plant fitness," citing Thomson (1986), Mitchell and Waser (1992), Mitchell (1993), Hodges (1995), and Irwin and Brody (1999).

References

- Dag, A. and Eisikowitch, D. 2000. The effect of carbon dioxide enrichment on nectar production in melons under greenhouse conditions. *Journal of Apicultural Research* **39**: 88–89.
- Erhardt, A., Rusterholz, H.-P., and Stocklin, J. 2005. Elevated carbon dioxide increases nectar production in *Epilobium angustifolium* L. *Oecologia* **146**: 311–317.
- Galen, C. and Plowright, R.C. 1985. The effects of nectar level and flower development on pollen carry-over in inflorescences of fireweed (*Epilobium angustifolium*) (Onagraceae). *Canadian Journal of Botany* **63**: 488–491.
- Hodges, S.A. 1995. The influence of nectar production on hawkmoth behavior, self pollination, and seed production in *Mirabilis multiflora* (Nyctaginaceae). *American Journal of Botany* **82**: 197–204.
- Irwin, R.E. and Brody, A.K. 1999. Nectar-robbing bumble bees reduce the fitness of *Ipomopsis aggregata* (Polemoniaceae). *Ecology* **80**: 1703–1712.
- Lake, J.C. and Hughes, L. 1999. Nectar production and floral characteristics of *Tropaeolum majus* L. grown in

ambient and elevated carbon dioxide. *Annals of Botany* **84**: 535–541.

Mitchell, R.J. 1993. Adaptive significance of *Ipomopsis aggregata* nectar production: observation and experiment in the field. *Evolution* **47**: 25–35.

Mitchell, R.J. and Waser, N.M. 1992. Adaptive significance of *Ipomopsis aggregata* nectar production: pollination success of single flowers. *Ecology* **73**: 633–638.

Thomson, J.D. 1986. Pollen transport and deposition by bumble bees in *Erythronium*: influences of floral nectar and bee grooming. *Journal of Ecology* **74**: 329–341.

2.16 Nitrogen Fixation

Increases in the air's CO₂ content likely will stimulate nitrogen fixation in most herbaceous species that form symbiotic relationships with nitrogen-fixing soil bacteria. This phenomenon likely will lead to increased nitrogen availability in soils and large increases in both agricultural and natural ecosystem productivity. Increases in the air's CO₂ content also will greatly enhance the growth of Earth's leguminous trees, stimulating their fixation of nitrogen and their exudation of the resultant nitrogenous substances to the soils in which they grow, where they become available to neighboring non-leguminous vegetation.

2.16.1 Herbaceous Plants

- Increases in the air's CO₂ content likely will stimulate nitrogen fixation in most legumes, herbaceous species that form symbiotic relationships with nitrogen-fixing soil bacteria. This phenomenon likely will lead to increased nitrogen availability in soils, ultimately leading to large CO₂-induced increases in agricultural and natural ecosystem productivity.

Nearly all of Earth's plants respond to increases in the air's CO₂ content by exhibiting increased rates of photosynthesis and biomass production. Additionally, most leguminous species—i.e., those that form symbiotic relationships with nitrogen-fixing bacteria—also find their ability to acquire nitrogen to be enhanced when exposed to CO₂-enriched air. This phenomenon could increase their positive growth responses to elevated CO₂ even more and ultimately make more soil nitrogen available to co-occurring species. This section reviews several scientific studies of these phenomena that have been conducted on herbaceous plants.

Luscher *et al.* (1998) exposed several different grassland species to elevated levels of atmospheric CO₂ and observed nitrogen-fixing species tend to produce more biomass than non-nitrogen-fixing species, possibly in response to CO₂-induced increases in the nitrogenase activity of symbiotic nitrogen-fixing bacteria associated with their roots. Dakora and Drake (2000) found a 300-ppm increase in the air's CO₂ concentration increased nitrogenase activity in a C₃ and a C₄ wetland species by 35 and 13%, respectively. Marilley *et al.* (1999) found enriching the air with CO₂ increased the dominance of nitrogen-fixing *Rhizobium* bacterial species associated with the roots of white clover. Arnone (1999), however, reported atmospheric CO₂ enrichment had no effect on symbiotic nitrogen fixation in *Trifolium alpinum*, a grassland species common to the Swiss Alps.

In a FACE study conducted on lucerne, plants fumigated with air containing 600 ppm CO₂ significantly increased their total tissue nitrogen content derived from symbiotic nitrogen-fixation (Luscher *et al.*, 2000). Plants grown on soil containing high nitrogen nearly doubled their symbiotically derived tissue nitrogen content, which rose from 21 to 41%, and plants grown on soils containing low nitrogen increased their symbiotically derived nitrogen content from 82 to 88%. In a related study performed on the same species, a doubling of the air's CO₂ content increased root nodule biomass by 40 and 100% in well-watered and water-stressed plants, respectively, as the CO₂-enriched plants obtained 31 and 97% more total nitrogen than control plants under the same conditions (De Luis *et al.* 1999).

Lee *et al.* (2003b) investigated the effects of atmospheric CO₂ concentration (365 and 700 ppm) and nitrogen fertilization (low-N field soil + 0, 4, 8, 12, 16 and 20 g N m⁻² year⁻¹) on leaf net photosynthesis, whole plant growth, and carbon and nitrogen acquisition in the N₂-fixing wild lupine (*Lupinus perennis*) in controlled-environment chambers, where plants were grown from seed in pots for one full growing season. The mean rate of leaf net photosynthesis in the CO₂-enriched chambers was 39% greater than in the ambient-air chambers, irrespective of N treatment, and total plant biomass at final harvest was 80% greater in the CO₂-enriched chambers, again irrespective of N treatment. Elevated CO₂ increased plant total N by 57%, with the extra N coming from enhanced symbiotic N₂ fixation related to an increased number and overall mass of nodules. Although partial photosynthetic acclimation to CO₂

enrichment occurred, the four researchers report the plants maintained significantly higher rates of photosynthesis and more efficient carbon capture per unit leaf N (average + 60%) in elevated CO₂ compared to ambient CO₂, indicating a substantial CO₂-induced increase in nitrogen use efficiency.

In mixed species experiments, Niklaus *et al.* (1998) found artificially constructed calcareous grassland swards were considerably more responsive to CO₂-enriched air when legumes were present than when they were absent. In addition, they found elevated CO₂ stimulated nitrogen fixation, particularly when soil phosphorus was not limiting to growth. Thus, under conditions of adequate soil phosphorus, symbiotically derived nitrogen likely would become available for the use of non-nitrogen-fixing species.

Lee *et al.* (2003a) grew the N₂-fixing *Lupinus perennis* in monoculture and in nine-species plots exposed to ambient air and air enriched to 560 ppm CO₂. The proportion of *Lupinus* N derived from symbiotic N₂ fixation in monoculture increased from 44% in ambient air to 57% in CO₂-enriched air, and in the nine-species plots it increased from 43% in ambient air to 54% in CO₂-enriched air. Combined with the CO₂-induced increases in plant biomass production, this resulted in a doubling of N fixed per plot under elevated compared to ambient CO₂. Hartwig *et al.* (2002) obtained a similar result, observing a 70% increase in the air's CO₂ concentration to roughly double the amount of nitrogen input through symbiotic N₂-fixation by white clover in a clover-ryegrass mixed ecosystem.

These findings indicate increases in the air's CO₂ content likely will stimulate nitrogen fixation in most legumes, and this phenomenon likely will lead to increased nitrogen availability in soils, ultimately leading to increases in agro- and natural ecosystem productivity.

References

- Arnone, J.A., III. 1999. Symbiotic N₂ fixation in a high Alpine grassland: effects of four growing seasons of elevated CO₂. *Functional Ecology* **13**: 383–387.
- Dakora, F.D. and Drake, B.G. 2000. Elevated CO₂ stimulates associative N₂ fixation in a C₃ plant of the Chesapeake Bay wetland. *Plant, Cell and Environment* **23**: 943–953.
- De Luis, J., Irigoyen, J.J., and Sanchez-Diaz, M. 1999. Elevated CO₂ enhances plant growth in droughted N₂-fixing alfalfa without improving water stress. *Physiologia Plantarum* **107**: 84–89.

Hartwig, U.A., Luscher, A., Nosberger, J., and van Kessel, C. 2002. Nitrogen-15 budget in model ecosystems of white clover and perennial ryegrass exposed for four years at elevated atmospheric pCO₂. *Global Change Biology* **8**: 194–202.

Lee, T.D., Reich, P.B., and Tjoelker, M.G. 2003a. Legume presence increases photosynthesis and N concentrations of co-occurring non-fixers but does not modulate their responsiveness to carbon dioxide enrichment. *Oecologia* **10.1007/s00442-003-1309-1**.

Lee, T.D., Tjoelker, M.G., Reich, P.B., and Russelle, M.P. 2003b. Contrasting growth response of an N₂-fixing and non-fixing forb to elevated CO₂: dependence on soil N supply. *Plant and Soil* **255**: 475–486.

Luscher, A., Hartwig, U.A., Suter, D., and Nosberger, J. 2000. Direct evidence that symbiotic N₂ fixation in fertile grassland is an important trait for a strong response of plants to elevated atmospheric CO₂. *Global Change Biology* **6**: 655–662.

Luscher, A., Hendrey, G.R., and Nosberger, J. 1998. Long-term responsiveness to free air CO₂ enrichment of functional types, species and genotypes of plants from fertile permanent grassland. *Oecologia* **113**: 37–45.

Marilley, L., Hartwig, U.A., and Aragno, M. 1999. Influence of an elevated atmospheric CO₂ content on soil and rhizosphere bacterial communities beneath *Lolium perenne* and *Trifolium repens* under field conditions. *Microbial Ecology* **38**: 39–49.

Niklaus, P.A., Leadley, P.W., Stocklin, J., and Korner, C. 1998. Nutrient relations in calcareous grassland under elevated CO₂. *Oecologia* **116**: 67–75.

2.16.2 Woody Plants

- Continued increases in the air's CO₂ content will greatly enhance the growth of Earth's leguminous trees, stimulate their fixation of nitrogen, and increase their root exudations of nitrogenous substances to the soils in which they grow, where they become available for uptake by neighboring non-leguminous vegetation.

Nearly all of Earth's plants respond to increases in the air's CO₂ content by exhibiting enhanced rates of photosynthesis and biomass production. In addition, leguminous species possess the special ability to form symbiotic relationships with nitrogen-fixing bacteria, which can indirectly increase plant responses to elevated CO₂ by making more nitrogen available for plant uptake and utilization. This review summarizes the results of some of the studies that report the

Plant Characteristics

effects of atmospheric CO₂ enrichment on these phenomena in woody plants.

Olesniewicz and Thomas (1999) grew black locust (*Robinia pseudoacacia*) seedlings for approximately two months in controlled environment chambers maintained at atmospheric CO₂ concentrations of 350 and 710 ppm, determining the elevated CO₂ increased total plant biomass by 180%. In addition, the extra CO₂ increased nitrogen-fixation by 69%, nodule mass by 92%, and the amount of seedling nitrogen derived from nitrogen-fixation by 212%. Working with the same species under much the same conditions, Uselman *et al.* (1999) determined between 1 and 2% of the total symbiotically fixed nitrogen is exuded from the tree's roots to become available for uptake by neighboring vegetation.

Schortemeyer *et al.* (1999) grew seedlings of *Acacia melanoxylon*, a leguminous nitrogen-fixing tree native to south-eastern Australia, for six weeks in growth cabinets maintained at atmospheric CO₂ concentrations of 350 and 700 ppm in hydroponic solutions with nitrogen concentrations ranging from 3 to 6,400 mmol m⁻³. Although atmospheric CO₂ enrichment did not stimulate symbiotic nitrogen fixation, averaged across all nitrogen treatments the seedlings grown in elevated CO₂ displayed net photosynthetic rates 22% higher than those of control seedlings, and they did not exhibit any signs of photosynthetic acclimation. These positive responses likely contributed to the doubled final biomass observed in the CO₂-enriched seedlings in all but the two lowest nitrogen concentrations, where final biomass was unaffected by elevated CO₂.

In a subsequent study of seven *Acacia* species native to Australia, Schortemeyer *et al.* (2002) once again grew seedlings in environmental chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm, but this time for nearly five months. They found the elevated CO₂ enhanced rates of net photosynthesis by 19 to 56% among all species and led to an average total plant dry weight increase of 86%. In addition, the elevated CO₂ increased the total amount of nitrogen fixed per plant by an average of 65%.

Temperton *et al.* (2003) measured total biomass and a number of physiological processes of N₂-fixing *Alnus glutinosa* or common alder trees, which were grown for three years (1994–1996) in open-top chambers maintained at either ambient or elevated (ambient + 350 ppm) concentrations of atmospheric CO₂ and two soil nitrogen regimes (full nutrient solution or no fertilizer). The six scientists measured

nitrogen fixation by *Frankia* spp. in the root nodules of the trees, finding nitrogenase activity was consistently higher in the elevated CO₂ treatment in both 1995 and 1996. In addition, they report, “in October 1996, elevated CO₂ had a significant effect on total nodule dry mass, and there was a trend toward heavier nodules in the elevated CO₂ treatment than in the ambient CO₂ treatment.” They conclude, “most single-species studies on the effect of elevated CO₂ on N₂-fixing species have reported stimulation of growth, nodule mass and nitrogenase activity (Norby, 1987; Arnone and Gordon, 1990; Hibbs *et al.*, 1995; Vogel and Curtis, 1995; Tissue *et al.*, 1997; Vogel *et al.*, 1997; Thomas *et al.*, 2000),” which is similar to what they observed.

These findings indicate continued increases in the air's CO₂ content will enhance the growth of Earth's leguminous trees, stimulate their fixation of nitrogen, and increase their root exudations of nitrogenous substances.

References

- Arnone, J.A. and Gordon, J.C. 1990. Effect of nodulation, nitrogen fixation and CO₂ enrichment on the physiology, growth and dry mass allocation of seedlings of *Alnus rubra* Bong. *New Phytologist* **116**: 55–66.
- Hibbs, D.E., Chan, S.S., Castellano, M., and Niu, C.-H. 1995. Response of red alder seedlings to CO₂ enrichment and water stress. *New Phytologist* **129**: 569–577.
- Norby, R.J. 1987. Nodulation and nitrogenase activity in nitrogen fixing woody plants stimulated by CO₂ enrichment of the atmosphere. *Physiologia Plantarum* **71**: 77–82.
- Olesniewicz, K.S. and Thomas, R.B. 1999. Effects of mycorrhizal colonization on biomass production and nitrogen fixation of black locust (*Robinia pseudoacacia*) seedlings grown under elevated atmospheric carbon dioxide. *New Phytologist* **142**: 133–140.
- Schortemeyer, M., Atkin, O.K., McFarlane, N., and Evans, J.R. 1999. The impact of elevated atmospheric CO₂ and nitrate supply on growth, biomass allocation, nitrogen partitioning and N₂ fixation of *Acacia melanoxylon*. *Australian Journal of Plant Physiology* **26**: 737–774.
- Schortemeyer, M., Atkin, O.K., McFarlane, N., and Evans, J.R. 2002. N₂ fixation by *Acacia* species increases under elevated atmospheric CO₂. *Plant, Cell and Environment* **25**: 567–579.
- Temperton, V.M., Grayston, S.J., Jackson, G., Barton, C.V.M., Millard, P., and Jarvis, P.G. 2003. Effects of elevated carbon dioxide concentration on growth and

nitrogen fixation in *Alnus glutinosa* in a long-term field experiment. *Tree Physiology* **23**: 1051–1059.

Thomas, R.B., Bashkin, M.A., and Richter, D.D. 2000. Nitrogen inhibition of nodulation and N₂ fixation of a tropical N₂-fixing tree (*Gliricida sepium*) grown in elevated atmospheric CO₂. *New Phytologist* **145**: 233–243.

Tissue, D.T., Thomas, R.B., and Strain, B.R. 1997. Atmospheric CO₂ enrichment increases growth and photosynthesis of *Pinus taeda*: a 4-year experiment in the field. *Plant, Cell and Environment* **20**: 1123–1134.

Uselman, S.M., Qualls, R.G., and Thomas, R.B. 1999. A test of a potential short cut in the nitrogen cycle: The role of exudation of symbiotically fixed nitrogen from the roots of a N-fixing tree and the effects of increased atmospheric CO₂ and temperature. *Plant and Soil* **210**: 21–32.

Vogel, C.S. and Curtis, P.S. 1995. Leaf gas exchange and nitrogen dynamics of N₂-fixing field-grown *Alnus glutinosa* under elevated atmospheric CO₂. *Global Change Biology* **1**: 55–61.

Vogel, C.S., Curtis, P.S., and Thomas, R.B. 1997. Growth and nitrogen accretion of dinitrogen-fixing *Alnus glutinosa* (L.) Gaertn. under elevated carbon dioxide. *Plant Ecology* **130**: 63–70.

2.17 Nitrogen Use Efficiency

- As the air's CO₂ content continues to rise, Earth's plants likely will reduce the amount of nitrogen invested in rubisco and other photosynthetic proteins while maintaining enhanced rates of photosynthesis and thereby increasing their photosynthetic nitrogen-use efficiencies.

Long-term exposure to elevated atmospheric CO₂ concentrations often, but not always, elicits photosynthetic acclimation or down-regulation in plants, which is typically accompanied by reduced amounts of rubisco and/or other photosynthetic proteins typically present in excess amounts in plants grown in ambient air. As a consequence, foliar nitrogen concentrations often decrease with atmospheric CO₂ enrichment, as nitrogen is mobilized out of leaves and into other areas of the plant to increase its availability for enhancing sink development or stimulating other nutrient-limited processes.

In reviewing the scientific literature on this subject, one quickly notices that even though photosynthetic acclimation has occurred, CO₂-enriched plants still nearly always display rates of photosynthesis greater than those of control plants exposed to ambient air. Consequently, photosynthetic nitrogen-use efficiency—the amount of carbon

converted into sugars during the photosynthetic process per unit of leaf nitrogen—often increases in CO₂-enriched plants.

Davey *et al.* (1999), for example, found CO₂-induced reductions in foliar nitrogen contents and concomitant increases in photosynthetic rates led to photosynthetic nitrogen-use efficiencies in the CO₂-enriched (to 700 ppm CO₂) grass *Agrostis capillaris* 27 and 62% greater than those observed in control plants grown at 360 ppm CO₂ under moderate and low soil nutrient conditions, respectively. Similarly, they found elevated CO₂ enhanced photosynthetic nitrogen-use efficiencies in *Trifolium repens* by 66 and 190% under moderate and low soil nutrient conditions, respectively, and in *Lolium perenne* by 50%, regardless of soil nutrient status. Other researchers report similar CO₂-induced enhancements of photosynthetic nitrogen-use efficiency in wheat (Osborne *et al.*, 1998) and in *Leucadendron* species (Midgley *et al.*, 1999).

In some cases, researchers report nitrogen-use efficiency in terms of the amount of biomass produced per unit of plant nitrogen. Niklaus *et al.* (1998), for example, report intact swards of CO₂-enriched calcareous grasslands grown at 600 ppm CO₂ attained total biomass values 25% greater than those of control swards exposed to ambient air while extracting the same amount of nitrogen from the soil as ambiently grown swards. Deng and Woodward (1998) reported similar results for strawberry, noting the growth-based nitrogen-use efficiencies of plants grown at 560 ppm CO₂ were 23 and 17% greater than those of ambiently grown plants simultaneously subjected to high and low soil nitrogen availability, respectively.

The scientific literature suggests as the air's CO₂ content continues to rise, Earth's plants likely will respond by reducing the amount of nitrogen invested in rubisco and other photosynthetic proteins while maintaining enhanced rates of photosynthesis, which should increase their photosynthetic nitrogen-use efficiencies. As overall plant nitrogen-use efficiency increases, plants likely will grow ever better on soils containing less-than-optimal levels of nitrogen.

References

Davey, P.A., Parsons, A.J., Atkinson, L., Wadge, K., and Long, S.P. 1999. Does photosynthetic acclimation to elevated CO₂ increase photosynthetic nitrogen-use efficiency? A study of three native UK grassland species in open-top chambers. *Functional Ecology* **13**: 21–28.

Deng, X. and Woodward, F.I. 1998. The growth and yield responses of *Fragaria ananassa* to elevated CO₂ and N supply. *Annals of Botany* **81**: 67–71.

Midgley, G.F., Wand, S.J.E., and Pammenter, N.W. 1999. Nutrient and genotypic effects on CO₂-responsiveness: photosynthetic regulation in *Leucadendron* species of a nutrient-poor environment. *Journal of Experimental Botany* **50**: 533–542.

Niklaus, P.A., Leadley, P.W., Stocklin, J., and Korner, C. 1998. Nutrient relations in calcareous grassland under elevated CO₂. *Oecologia* **116**: 67–75.

Osborne, C.P., LaRoche, J., Garcia, R.L., Kimball, B.A., Wall, G.W., Pinter Jr., P.J., LaMorte, R.L., Hendrey, G.R., and Long, S.P. 1998. Does leaf position within a canopy affect acclimation of photosynthesis to elevated CO₂? *Plant Physiology* **117**: 1037–1045.

2.18 Nutrient Acquisition

- As the CO₂ content of the air increases, much of Earth's vegetation likely will display increases in biomass. The larger plants likely will develop more extensive root systems and extract greater amounts of mineral nutrients from the soils in which they are rooted, enabling them to sustain their enhanced growth.

With respect to acquiring nitrogen, Zak *et al.* (2000) found aspen seedlings grown for 2.5 years at twice-ambient CO₂ concentrations displayed an average total seedling nitrogen content 13% greater than that displayed by control seedlings grown in ambient air, in spite of an average reduction in tissue nitrogen concentration of 18%. Elevated CO₂ enhanced total nitrogen uptake from the soil, even though tissue nitrogen concentrations in the CO₂-enriched plants were diluted by the enhanced biomass of the much larger CO₂-enriched seedlings.

On a per-unit-biomass basis, Smart *et al.* (1998) note there were no differences in the total amounts of nitrogen within CO₂-enriched and ambiently grown wheat seedlings after three weeks of exposure to atmospheric CO₂ concentrations of 360 and 1,000 ppm. Nevertheless, the CO₂-enriched seedlings exhibited greater rates of soil nitrate extraction than the ambient-grown plants did.

Similarly, BassiriRad *et al.* (1998) report a doubling of the atmospheric CO₂ concentration doubled the uptake rate of nitrate in the C₄ grass *Bouteloua eriopoda*. However, they also report elevated CO₂ had no effect on the rate of nitrate uptake in *Prosopis*, and it actually decreased the rate of nitrate uptake by 55% in *Larrea*. Nonetheless,

atmospheric CO₂ enrichment increased total biomass in these two species by 55 and 69%, respectively. Thus, although the uptake rate of this nutrient was depressed under elevated CO₂ conditions in the latter species, the much larger CO₂-enriched plants likely still extracted more total nitrate from the soil than did the ambient-grown plants of the experiment.

Nasholm *et al.* (1998) determined trees, grasses, and shrubs can absorb significant amounts of organic nitrogen from soils. Thus, plants do not have to wait for the mineralization of organic nitrogen before they extract the nitrogen they need from soils to support their growth and development. As a result, the forms of nitrogen removed from soils by plants (nitrate vs. ammonium) and their abilities to remove different forms may not be as important as was once thought.

Finzi *et al.* (2002) found, on average, loblolly pine exposed to an extra 200 ppm of CO₂ maintained rates of net primary productivity 25% greater, and produced 32% more biomass, than trees growing in ambient air. The elevated CO₂ also increased the total amount of nitrogen present in the trees' biomass. The average annual requirement for nitrogen rose by 16% for the trees growing in the air enriched with CO₂. To compensate for this increased nitrogen demand, the average uptake of nitrogen from the soil was enhanced by 28% in the CO₂-enriched plot—which says a lot, considering the soils in the study region are characteristically low in available nitrogen. In addition, average nitrogen-use efficiency rose by approximately 10% with atmospheric CO₂ enrichment.

With respect to the uptake of phosphate, Staddon *et al.* (1999) report *Plantago lanceolata* and *Trifolium repens* plants grown at 650 ppm CO₂ for 2.5 months exhibited total plant phosphorus contents much greater than those displayed by plants grown at 400 ppm CO₂, because atmospheric CO₂ enrichment significantly enhanced plant biomass. Similarly, Rouhier and Read (1998) report enriching the air around *Plantago lanceolata* plants with an extra 190 ppm of CO₂ for three months led to increased uptake of phosphorus and greater tissue phosphorus concentrations than were observed in plants growing in ambient air.

Greater uptake of phosphorus also can occur due to CO₂-induced increases in root absorptive surface area or enhancements in specific enzyme activities. In addressing the first of these phenomena, BassiriRad *et al.* (1998) report a doubling of the air's CO₂ concentration significantly increased the belowground biomass of *Bouteloua eriopoda* and doubled its uptake rate of phosphate. However, elevated CO₂ had

no effect on uptake rates of phosphate in *Larrea* and *Prosopis*. Because the CO₂-enriched plants grew so much bigger, however, they still removed more phosphate from the soil on a per-plant basis. With respect to the second phenomenon, activity of phosphatase—the primary enzyme responsible for the conversion of organic phosphate into usable inorganic forms—increased by 30 to 40% in wheat seedlings growing at twice-ambient CO₂ concentrations (Barrett *et al.*, 1998).

With respect to another nutrient, iron, Jin *et al.* (2009) grew 20-day-old plants for an additional seven days within controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 350 or 800 ppm in an iron (Fe)-sufficient medium with a soluble Fe source or under Fe-limited conditions in a medium containing the sparingly soluble hydrous Fe(III)-oxide. Their results indicate plant growth was increased by the elevated CO₂ in both the Fe-sufficient and Fe-limited media, with shoot fresh weight increasing by 22% and 44%, respectively, and root fresh weight increasing by 43% and 97%, respectively. In addition, Jin *et al.* report, “the elevated CO₂ under Fe-limited conditions enhance[d] root growth, root hair development, proton release, root FCR [ferric chelate reductase] activity, and expressions of *LeFR01* and *LeIRT1* genes [which respectively encode FCR and the Fe(II) transporter in tomato], all of which enable plants to access and accumulate more Fe.” They add, “the associated increase in Fe concentrations in the shoots and roots alleviated Fe-deficiency-induced chlorosis.”

Jin *et al.* note the bioavailability of iron to terrestrial plants “is often limited (Guerinot and Yi, 1994), particularly in calcareous soils, which represent 30% of the Earth’s surface (Imsande, 1998),” and thus conclude, “Fe nutrition in plants is likely to be affected by the continued elevation of atmospheric CO₂, which, in turn, will affect crop production.” As their work strongly suggests, those important effects should be highly beneficial. Even wider biospheric benefits are suggested by the work of Sasaki *et al.* (1998), who demonstrated both the ferric reductase activity and Fe uptake capacity of the marine alga *Chlorococcum littorale* cultured in Fe-limited media have been significantly enhanced by elevated CO₂ concentrations.

Haase *et al.* (2008) grew barley (*Hordeum vulgare* L. cv. Europa) plants from seed for four weeks—both hydroponically in nutrient solution having adequate or less-than-adequate iron (Fe) concentrations (+Fe and -Fe, respectively), as well as in rhizobox microcosms filled with soil under the

same two conditions of iron availability—in controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 400 or 800 ppm. The elevated atmospheric CO₂ treatments stimulated biomass production in both Fe-sufficient and Fe-deficient barley plants, in both hydroponics and soil culture. In addition, they found three CO₂-induced modifications in plant activity: “(i) increased internal Fe use efficiency, (ii) stimulation of root growth, and (iii) increased root exudation of Fe-mobilizing phytosiderophores in the sub-apical root zones.” Since phytosiderophores act as metal chelators that mobilize sparingly soluble inorganic forms of iron and zinc and make them more readily available to plants, the researchers suggest atmospheric CO₂ enrichment increases the competitiveness of plants such as barley with rhizosphere microorganisms in their quest for these often difficult-to-obtain trace elements. This phenomenon helps to explain the strong growth response of barley to atmospheric CO₂ enrichment even when iron availability is low.

In a study dealing with multiple nutrients, Schaffer *et al.* (1997) grew two mango ecotypes, one evolving from a warm, humid tropical climate and the other from a cool, dry subtropical region, for 12 months in glasshouses with atmospheres of either 350 or 700 ppm CO₂ to determine the effects of atmospheric CO₂ enrichment on plant growth and leaf mineral nutrient concentrations. According to the researchers, although atmospheric CO₂ enrichment led to partial photosynthetic acclimation in both ecotypes, greater net carbon gains were achieved with elevated CO₂, as indicated by greater plant dry mass values for trees grown at 700 ppm CO₂. Elevated CO₂ also tended to decrease foliar concentrations of mineral nutrients (N, P, K, Ca, Mg, S, Cl, Fe, Zn, Mn, Cu, and B) in both mango cultivars, most likely due to a dilution effect, since atmospheric CO₂ enrichment increased leaf dry mass. Although the instantaneous doubling of the atmospheric CO₂ concentration in this experiment reduced the concentrations of leaf mineral elements, Schaffer *et al.* state, “given the slow rate at which global atmospheric CO₂ concentration is increasing, it is possible that plants will adapt to elevated ambient CO₂ concentrations over time with respect to mineral nutrition,” as did sour orange trees after 85 months of exposure to elevated CO₂ (Peñuelas *et al.*, 1997).

Lieffering *et al.* (2004) analyzed the elemental concentrations of archived grain samples from temperate rice (*Oryza sativa* L. cv. Akitakomachi) crops grown previously under FACE conditions out-

Plant Characteristics

of-doors in a fertile agricultural field (Okada *et al.*, 2001), where an approximate 200-ppm increase in the air's CO₂ concentration increased rice grain yields by about 14% (Kim *et al.*, 2003a,b).

Of the five macro-nutrients they measured (N, P, K, Mg, S), Lieffering *et al.* found “only N showed a decrease in concentration with elevated CO₂ in both years,” and all six of the micro-nutrients studied (Zn, Mn, Fe, Cu, B, Mo) exhibited concentration increases. For Zn and Mn, in particular, they state, “there was a strong tendency [for concentrations] to increase,” and the same could have been said of Fe, which in the second year of the study exhibited a CO₂-induced concentration increase on the order of 68%, as best as can be determined from Lieffering *et al.*'s bar graphs.

Lieffering *et al.* note their study of the effects of elevated CO₂ on grain elemental concentrations under real-world field conditions is “the first such report for a staple food crop: all other previously reported data were obtained from plants growing in pots and in some kind of enclosure.” In contrast to the results obtained in most of these latter root-confining experiments, they note that, other than for N, “no dilution of [the] elements in the grain was observed, contrary to the general conclusions of Loladze (2002).” Therefore, they conclude, “as long as there is a readily available supply of nutrients and the nutrient uptake capacity response to elevated CO₂ is equal [to] or greater than the whole plant biomass response [which was the case in their experiment, except for N], then no dilution should be observed.”

Natali *et al.* (2009) noted “increased production of fine roots with CO₂ enrichment (Norby *et al.*, 2004; Pritchard *et al.*, 2008) may allow plants to match increased carbon assimilation with increased uptake of soil-derived elements.” They “examined CO₂ effects of a suite of metal micronutrients and contaminants in forest trees and soils at two free-air CO₂ enrichment sites—a loblolly pine forest in North Carolina (Duke) and a sweetgum plantation in Tennessee [Oak Ridge National Laboratory (ORNL)]—as well as at an open-top chamber experiment in a scrub-oak community in Florida [Smithsonian Environmental Research Center (SERC)].” They “did not find an overall decline in foliar metal concentrations with CO₂ enrichment,” but they *did* find dilution effects for metal micronutrients were generally “less than for non-essential trace metals,” and “some essential plant metals were greater under elevated CO₂ (for example, a 28% increase in Mn across species and sites).” Natali *et al.* conclude their results “should alleviate some concerns

that rising CO₂ concentrations will result in broad-scale decreases in the concentrations of all elements essential for plant function and animal nutrition,” as proposed by Loladze (2002). They also state their generally opposite results for nonessential trace elements (some of which can be toxic) “may be applicable to contaminated systems,” stating, “elevated CO₂ may, through dilution effects, alleviate aluminum toxicity.”

In a somewhat different type of study, Urabe and Waki (2009) grew three algal species—*Scenedesmus obliquus* (green algae), *Cyclotella* sp. (diatoms), and *Synechococcus* sp. (cyanobacteria)—in mono- and mixed-cultures at ambient (360 ppm) and high (2,000 ppm) CO₂ levels and allowed a planktonic herbivore (*Daphnia*) to feed on the different algal populations thereby produced either individually or in various mixtures, to see if there was any CO₂-induced effect on herbivore growth. The two researchers found “both in the mono- and mixed cultures, algal steady state abundance increased but algal P:C and N:C ratios decreased when they were grown at high CO₂.” They also found “*Daphnia* fed monospecific algae cultured at high CO₂ had decreased growth rates despite increased algal abundance.” But “when fed mixed algae cultured at high CO₂, especially consisting of diatoms and cyanobacteria or the three algal species,” they found “*Daphnia* maintained high growth rates despite lowered P and N contents relative to C in the algal diets.” The findings indicate, they write, “algal diets composed of multiple species can mitigate the adverse effects of elevated CO₂ on herbivore performance,” and “in environments with high CO₂, herbivores may find a new diet producer or a combination of producer species to best meet their nutritional demands.”

The experimental data accumulated to date suggest much of Earth's vegetation likely will display increases in biomass as the air's CO₂ content rises, and considerable evidence suggests the larger plants thereby produced will develop more extensive root systems and extract greater amounts of mineral nutrients from the soils in which they are rooted, enabling them to sustain their enhanced growth.

References

- Barrett, D.J., Richardson, A.E., and Gifford, R.M. 1998. Elevated atmospheric CO₂ concentrations increase wheat root phosphatase activity when growth is limited by phosphorus. *Australian Journal of Plant Physiology* 25: 87–93.

Climate Change Reconsidered II: Biological Impacts

- BassiriRad, H., Reynolds, J.F., Virginia, R.A., and Brunelle, M.H. 1998. Growth and root NO₃⁻ and PO₄³⁻ uptake capacity of three desert species in response to atmospheric CO₂ enrichment. *Australian Journal of Plant Physiology* **24**: 353–358.
- Finzi, A.C., DeLucia, E.H., Hamilton, J.G., Richter, D.D., and Schlesinger, W.H. 2002. The nitrogen budget of a pine forest under free air CO₂ enrichment. *Oecologia* **132**: 567–578.
- Guerinot, M.L. and Yi, Y. 1994. Iron: nutritious, noxious, and not readily available. *Plant Physiology* **104**: 815–820.
- Haase, S., Rothe, A., Kania, A., Wasaki, J., Romheld, V., Engels, C., Kandeler, E., and Neumann, G. 2008. Responses to iron limitation in *Hordeum vulgare* L. as affected by the atmospheric CO₂ concentration. *Journal of Environmental Quality* **37**: 1254–1262.
- Imsande, J. 1998. Iron, sulfur, and chlorophyll deficiencies: a need for an integrative approach in plant physiology. *Physiologia Plantarum* **103**: 139–144.
- Jin, C.W., Du, S.T., Chen, W.W., Li, G.X., Zhang, Y.S., and Zheng, S.J. 2009. Elevated carbon dioxide improves plant iron nutrition through enhancing the iron-deficiency-induced responses under iron-limited conditions in tomato. *Plant Physiology* **150**: 272–280.
- Kim, H.-Y., Lieffering, M., Kobayashi, K., Okada, M., Mitchell, M.W., and Gumpertz, M. 2003b. Effects of free-air CO₂ enrichment and nitrogen supply on the yield of temperate paddy rice crops. *Field Crops Research* **83**: 261–270.
- Kim, H.-Y., Lieffering, M., Kobayashi, K., Okada, M., and Miura, S. 2003a. Seasonal changes in the effects of elevated CO₂ on rice at three levels of nitrogen supply: a free-air CO₂ enrichment (FACE) experiment. *Global Change Biology* **9**: 826–837.
- Lieffering, M., Kim, H.-Y., Kobayashi, K., and Okada, M. 2004. The impact of elevated CO₂ on the elemental concentrations of field-grown rice grains. *Field Crops Research* **88**: 279–286.
- Loladze, I. 2002. Rising atmospheric CO₂ and human nutrition: towards globally imbalanced plant stoichiometry. *Trends in Ecology and Evolution* **17**: 457–461.
- Nasholm, T., Ekblad, A., Nordin, A., Giesler, R., Hogberg, M., and Hogberg, P. 1998. Boreal forest plants take up organic nitrogen. *Nature* **392**: 914–916.
- Natali, S.M., Sañudo-Wilhelmy, S.A., and Lerdau, M.T. 2009. Plant and soil mediation of elevated CO₂ impacts on trace metals. *Ecosystems* **12**: 715–727.
- Norby, R.J., Ledford, J., Reilly, C.D., Miller, N.E., and O'Neill, E.G. 2004. Fine-root production dominates response of a deciduous forest to atmospheric CO₂ enrichment. *Proceedings of the National Academy of Sciences, USA* **101**: 9689–9693.
- Okada, M., Lieffering, M., Nakamura, H., Yoshimoto, M., Kim, H.-Y., and Kobayashi, K. 2001. Free-air CO₂ enrichment (FACE) using pure CO₂ injection: system description. *New Phytologist* **150**: 251–260.
- Peñuelas, J., Idso, S.B., Ribas, A., and Kimball, B.A. 1997. Effects of long-term atmospheric CO₂ enrichment on the mineral concentration of *Citrus aurantium* leaves. *New Phytologist* **135**: 439–444.
- Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., Finzi, A., Jackson, R.B., Matamala, R., Rogers, H.H., and Oren, R. 2008. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO₂-enrichment: a six-year-minirhizotron study. *Global Change Biology* **14**: 588–602.
- Rouhier, H. and Read, D.J. 1998. The role of mycorrhiza in determining the response of *Plantago lanceolata* to CO₂ enrichment. *New Phytologist* **139**: 367–373.
- Sasaki, T., Kurano, N., and Miyachi, S. 1998. Induction of ferric reductase activity and of iron uptake capacity in *Chlorococcum littorale* cells under extremely high-CO₂ and iron-deficient conditions. *Plant & Cell Physiology* **39**: 405–410.
- Schaffer, B., Whiley, A.W., Searle, C., and Nissen, R.J. 1997. Leaf gas exchange, dry matter partitioning, and mineral element concentrations in mango as influenced by elevated atmospheric carbon dioxide and root restriction. *Journal of the American Society of Horticultural Science* **122**: 849–855.
- Smart, D.R., Ritchie, K., Bloom, A.J., and Bugbee, B.B. 1998. Nitrogen balance for wheat canopies (*Triticum aestivum* cv. Veery 10) grown under elevated and ambient CO₂ concentrations. *Plant, Cell and Environment* **21**: 753–763.
- Staddon, P.L., Fitter, A.H., and Graves, J.D. 1999. Effect of elevated atmospheric CO₂ on mycorrhizal colonization, external mycorrhizal hyphal production and phosphorus inflow in *Plantago lanceolata* and *Trifolium repens* in association with the arbuscular mycorrhizal fungus *Glomus mosseae*. *Global Change Biology* **5**: 347–358.
- Urabe, J. and Waki, N. 2009. Mitigation of adverse effects of rising CO₂ on a planktonic herbivore by mixed algal diets. *Global Change Biology* **15**: 523–531.
- Zak, D.R., Pregitzer, K.S., Curtis, P.S., Vogel, C.S., Holmes, W.E., and Lussenhop, J. 2000. Atmospheric CO₂, soil-N availability, and allocation of biomass and nitrogen by *Populus tremuloides*. *Ecological Applications* **10**: 34–46.

2.19 Phenolics

Herbaceous plants often experience increases in foliar and fruit phenolic concentrations in response to atmospheric CO₂ enrichment, and these responses appear to have a number of positive implications for both man and the biosphere. Future increases in the air's CO₂ concentration likely will enhance foliar phenolic concentrations in many trees and shrubs, and this should enhance woody-plant defense mechanisms that help deter herbivory, thereby improving forest health, robustness, and longevity.

2.19.1 Herbaceous Species

- Many, but not all, herbaceous plants experience increases in foliar and fruit phenolic concentrations in response to atmospheric CO₂ enrichment. These responses appear to have a number of positive implications for both man and the biosphere.

In the presence of elevated concentrations of atmospheric CO₂, many of Earth's plants display an enhanced rate of photosynthetic carbon uptake, which leads to an increased production of plant secondary carbon compounds, including phenolics. Since the resulting increases in plant foliar phenolic concentrations often enhance plant resistance to herbivore and pathogen attack, this section reviews the results of some studies that have dealt with this important subject in herbaceous plants.

Hoorens *et al.* (2002) grew two plants common to dune grasslands of the Netherlands (*Calamagrostis epigejos* and *Vicia lathyroides*), along with two species common to Dutch peatlands (*Carex rostrata* and *Sphagnum recurvum*), in greenhouses fumigated with air containing either 390 or 700 ppm CO₂ for five months. Then, after senescence had occurred, they collected the resulting leaf litter and analyzed it for the presence of various substances. Among other things, they found elevated CO₂ had little impact on the presence of phenolics in *Calamagrostis* and *Sphagnum* litter, but it increased phenolic concentrations in *Vicia* and *Carex* litter by 20 and 32%, respectively.

Castells *et al.* (2002) grew 14 genotypes of two perennial grasses common to the Mediterranean area (*Dactylis glomerata* and *Bromus erectus*) in glasshouses maintained at atmospheric CO₂ concentrations of 350 and 700 ppm in order to determine whether elevated CO₂ impacts phenolic

production in a genotypic-dependent manner. Their research indicates doubling the air's CO₂ concentration increased total phenolic concentrations in *Dactylis* and *Bromus* by 15 and 87%, respectively, and there were no significant CO₂ x genotype interactions in either species. As the atmosphere's CO₂ concentration continues to rise, therefore, these two perennial grasses likely will exhibit greater resistance to herbivory without having to sacrifice their genotypic diversity.

Wetzel and Tuchman (2005) grew cattails for three years in open-bottom root boxes out-of-doors within clear-plastic-wall open-top chambers maintained at either ambient (360 ppm) or elevated (720 ppm) atmospheric CO₂ concentrations from early spring through leaf senescence. During this period, green and naturally senesced leaves were collected and analyzed for the fraction of leaf mass composed of total phenolics. The researchers found green leaf material contained 27.6% more total phenolics when the plants were grown in CO₂-enriched as opposed to ambient air, and senesced leaf material grown in CO₂-enriched air contained 40.6% more total phenolics than similar leaves produced in ambient air.

In a study with human health implications, Wang *et al.* (2003) grew strawberry plants in six clear-acrylic open-top chambers, two of which were maintained at the ambient atmospheric CO₂ concentration, two of which were maintained at ambient + 300 ppm CO₂, and two of which were maintained at ambient + 600 ppm CO₂ from early spring 1998 through June 2000. During this time, the researchers harvested the strawberry fruit, they write, "at the commercially ripe stage" in both 1999 and 2000. They analyzed the fruit for the presence of a number of different health-promoting substances with "potent antioxidant properties." They found CO₂ enrichment increased fruit ascorbic acid, glutathione, phenolic acid, flavonol, and anthocyanin concentrations, and plants grown under the CO₂ enriched conditions also had higher oxygen radical absorbance activity against many types of harmful oxygen radicals in the fruit.

References

- Castells, E., Roumet, C., Peñuelas, J., and Roy, J. 2002. Intraspecific variability of phenolic concentrations and their responses to elevated CO₂ in two mediterranean perennial grasses. *Environmental and Experimental Botany* 47: 205–216.

Hoorens, B., Aerts, R., and Stroetenga, M. 2002. Litter quality and interactive effects in litter mixtures: more negative interactions under elevated CO₂? *Journal of Ecology* **90**: 1009–1016.

Wang, S.Y., Bunce, J.A., and Maas, J.L. 2003. Elevated carbon dioxide increases contents of antioxidant compounds in field-grown strawberries. *Journal of Agricultural and Food Chemistry* **51**: 4315–4320.

Wetzel, R.G. and Tuchman, N.C. 2005. Effects of atmospheric CO₂ enrichment and sunlight on degradation of plant particulate and dissolved organic matter and microbial utilization. *Archiv fur Hydrobiologie* **162**: 287–308.

2.19.2 Woody Species

- Future increases in the air's CO₂ concentration likely will enhance foliar phenolic concentrations in many shrubs and trees. This, in turn, should enhance woody-plant defense mechanisms that help deter herbivory and thus improve forest health, robustness, and longevity.

As the air's CO₂ content continues to rise, many of Earth's plants are experiencing enhanced rates of photosynthetic carbon uptake, which commonly leads to increased production of plant secondary carbon compounds, including phenolics that often enhance plant resistance to herbivore and pathogen attack. This section examines the results of several studies dealing with this important subject.

Peñuelas *et al.* (2002) sampled leaves of three species of shrubs growing close to, and further away from, CO₂-emitting springs in Pisa, Italy, to determine the long-term effects of elevated atmospheric CO₂ on foliar concentrations of carbon-based secondary compounds. The researchers found the extra 340 ppm of CO₂ near the springs had very few long-term significant effects on foliar concentrations of most such substances, including phenolics, and those effects that were observed varied according to specific compound and plant species. Their findings are somewhat atypical of what is often observed, as several studies of temperate-region trees have shown leaf phenolic concentrations to rise by 20 to 60% in response to a doubling of the air's CO₂ content (Koricheva *et al.*, 1998; Peñuelas and Estiarte, 1998; McDonald *et al.*, 1999; Agrell *et al.*, 2000; Hartley *et al.*, 2000), as also was reported by Parsons *et al.* (2003) with respect to the total fine-root phenolic concentrations of warm-temperate conifers studied by King *et al.* (1997), Entry *et al.* (1998), and Runion *et*

al. (1999).

Gebauer *et al.* (1998) grew loblolly pine seedlings in glasshouses maintained at atmospheric CO₂ concentrations of 350 and 700 ppm for five months while subjecting them to four levels of soil nitrogen fertilization. Across all of these nitrogen regimes, the extra CO₂ increased the above- and below-ground concentrations of seedling total phenolics by 21 and 35%, respectively.

Booker and Maier (2001) also worked with loblolly pines, measuring concentrations of total soluble phenolics in needles exposed for two years in branch chambers to ambient air and air enriched to as much as 350 ppm CO₂ above ambient. They found needle concentrations of total soluble phenolics increased about 11% in response to the elevated CO₂, noting this response was related to “the balance between carbohydrate sources and sinks,” so “the greater the source:sink ratio, the greater the concentration of phenolic compounds (Herms and Mattson, 1992; Peñuelas and Estiarte, 1998).”

In contrast, Hamilton *et al.* (2004) studied the understory of the loblolly pine plantation in the Duke Forest FACE study, finding no evidence of significant changes in total leaf phenolics in either of two years, in agreement with the results of “another study performed at the Duke Forest FACE site that also found no effect of elevated CO₂ on the chemical composition of leaves of understory trees (Finzi and Schlesinger, 2002).” Nevertheless, they state, “elevated CO₂ led to a trend toward reduced herbivory in [the] deciduous understory in a situation that included the full complement of naturally occurring plant and insect species.” In 1999, for example, they found “elevated CO₂ reduced overall herbivory by more than 40% with elm showing greater reduction than either red maple or sweetgum,” and in 2000 they observed “the same pattern and magnitude of reduction.”

In a similar FACE study of an ecosystem dominated by three species of oak tree (*Quercus myrtifolia*, *Q. chapmanii*, and *Q. geminata*) plus the nitrogen-fixing legume *Galactia elliotii* at the Kennedy Space Center in Florida (USA), Hall *et al.* (2005) detected no significant differences between the CO₂-enriched and ambient-treatment leaves of any single species in terms of condensed tannins, hydrolyzable tannins, total phenolics, or lignin. When all four species were considered together, however, there were always greater concentrations of all four leaf constituents in the CO₂-enriched leaves, with across-species mean increases of 6.8% for condensed tannins, 6.1% for hydrolyzable tannins, 5.1% for total

Plant Characteristics

phenolics, and 4.3% for lignin. In addition, there were large CO₂-induced decreases in all leaf damage categories associated with herbivory: chewing (-48%, $P < 0.001$), mines (-37%, $P = 0.001$), eye spot gall (-45%, $P < 0.001$), leaf tier (-52%, $P = 0.012$), leaf mite (-23%, $P = 0.477$), and leaf gall (-16%, $P = 0.480$). The five researchers conclude the changes in leaf chemical constituents and herbivore damage “suggest that damage to plants may decline as atmospheric CO₂ levels continue to rise.”

Wetzel and Tuchman (2005) grew trembling aspen seedlings for three years in open-bottom root boxes out-of-doors within clear-plastic-wall open-top chambers maintained at either ambient (360 ppm) or elevated (720 ppm) atmospheric CO₂ concentrations from early spring through leaf senescence. Green and naturally senesced leaves were collected and analyzed for the fraction of leaf mass composed of total phenolics. Green leaf material contained 19.1% more total phenolics when the experimental seedlings were grown in CO₂-enriched as opposed to ambient air, and senesced leaf material grown in CO₂-enriched air contained 63.2% more total phenolics than similar leaf material grown in ambient air.

In Finland, Kuokkanen *et al.* (2003) grew two-year-old birch trees in the field in closed-top chambers exposed to either ambient air of 350 ppm CO₂ or air enriched to a CO₂ concentration of 700 ppm at either ambient temperatures or ambient temperatures plus 3°C for one full growing season. During the middle of summer, when carbon-based secondary compounds of birch leaves are usually fairly stable, they picked several leaves from each tree and measured the concentrations of a number of physiologically important substances. The concentration of total phenolics significantly increased in the birch leaves produced in the CO₂-enriched air, as also has been observed in the experiments of Lavola and Julkunen-Titto (1994), Williams *et al.* (1994), Kinney *et al.* (1997), Bezemer and Jones (1998), and Kuokkanen *et al.* (2001).

Coley *et al.* (2002) studied nine species of tropical trees rooted in the ground and grown in their natural environment near the Smithsonian Tropical Research Institute's experiment site in central Panama. Their six-month open-top chamber study produced impressive results, with eight of the nine species exhibiting positive leaf phenolic/tannin responses to a doubling of the air's CO₂ content, the largest of which was a concentration increase of 119%. The single negative response was a 27% decline, and the mean response of all nine species was an increase of 48%. These results are comparable to

those obtained for temperate-region trees, and they provide the basis for Coley *et al.*'s primary conclusion: Although “both temperate and tropical trees show large interspecific variation in the extent of their response to CO₂ ... the overwhelming pattern is for an increase in phenolics by approximately 50%.”

The results of these several studies suggest future increases in the air's CO₂ concentration likely will enhance foliar phenolic concentrations in many shrubs and trees. This phenomenon, in turn, should enhance woody-plant defense mechanisms that help deter herbivory, which should improve forest health, robustness, and longevity.

References

- Agrell, J., McDonald, E.P., and Lindroth, R.L. 2000. Effects of CO₂ and light on tree phytochemistry and insect performance. *Oikos* **88**: 259–272.
- Bezemer, T.M. and Jones, T.H. 1998. Plant-insect herbivore interactions in elevated atmospheric CO₂, quantitative analyses and guild effects. *Oikos* **82**: 212–222.
- Booker, F.L. and Maier, C.A. 2001. Atmospheric carbon dioxide, irrigation, and fertilization effects on phenolic and nitrogen concentrations in loblolly pine (*Pinus taeda*) needles. *Tree Physiology* **21**: 609–616.
- Coley, P.D., Massa, M., Lovelock, C.E., and Winter, K. 2002. Effect of elevated CO₂ on foliar chemistry of saplings of nine species of tropical tree. *Oecologia* **133**: 62–69.
- Entry, J.A., Runion, G.B., Prior, S.A., Mitchell, R.J., and Rogers, H.H. 1998. Influence of CO₂ enrichment and nitrogen fertilization on tissue chemistry and carbon allocation in longleaf pine seedlings. *Plant and Soil* **200**: 3–11.
- Finzi, A.C. and Schlesinger, W.H. 2002. Species control variation in litter decomposition in a pine forest exposed to elevated CO₂. *Global Change Biology* **8**: 1217–1229.
- Gebauer, R.L.E., Strain, B.R., and Reynolds, J.F. 1998. The effect of elevated CO₂ and N availability on tissue concentrations and whole plant pools of carbon-based secondary compounds in loblolly pine (*Pinus taeda*). *Oecologia* **113**: 29–36.
- Hall, M.C., Stiling, P., Moon, D.C., Drake, B.G., and Hunter, M.D. 2005. Effects of elevated CO₂ on foliar quality and herbivore damage in a scrub oak ecosystem. *Journal of Chemical Ecology* **31**: 267–285.
- Hamilton, J.G., Zangerl, A.R., Berenbaum, M.R., Pippen, J., Aldea, M., and DeLucia, E.H. 2004. Insect herbivory in

an intact forest understory under experimental CO₂ enrichment. *Oecologia* **138**: 10.1007/s00442-003-1463-5.

Hartley, S.E., Jones, C.G., Couper, G.C., and Jones, T.H. 2000. Biosynthesis of plant phenolic compounds in elevated atmospheric CO₂. *Global Change Biology* **6**: 497–506.

Herns, D.A. and Mattson, W.J. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology* **67**: 283–335.

King, J.S., Thomas, R.B., and Strain, B.R. 1997. Morphology and tissue quality of seedling root systems of *Pinus taeda* and *Pinus ponderosa* as affected by varying CO₂, temperature, and nitrogen. *Plant and Soil* **195**: 107–119.

Kinney, K.K., Lindroth, R.L., Jung, S.M., and Nordheim, E.V. 1997. Effects of CO₂ and NO₃ availability on deciduous trees, phytochemistry and insect performance. *Ecology* **78**: 215–230.

Koricheva, J., Larsson, S., Haukioja, E., and Keinanen, M. 1998. Regulation of woody plant metabolism by resource availability: hypothesis testing by means of a meta-analysis. *Oikos* **83**: 212–226.

Kuokkanen, K., Julkunen-Titto, R., Keinanen, M., Niemela, P., and Tahvanainen, J. 2001. The effect of elevated CO₂ and temperature on the secondary chemistry of *Betula pendula* seedlings. *Trees* **15**: 378–384.

Kuokkanen, K., Yan, S., and Niemela, P. 2003. Effects of elevated CO₂ and temperature on the leaf chemistry of birch *Betula pendula* (Roth) and the feeding behavior of the weevil *Phyllobius maculicornis*. *Agricultural and Forest Entomology* **5**: 209–217.

Lavola, A. and Julkunen-Titto, R. 1994. The effect of elevated carbon dioxide and fertilization on primary and secondary metabolites in birch, *Betula pendula* (Roth). *Oecologia* **99**: 315–321.

McDonald, E.P., Agrell, J., and Lindroth, R.L. 1999. CO₂ and light effects on deciduous trees: growth, foliar chemistry and insect performance. *Oecologia* **119**: 389–399.

Parsons, W.F.J., Kopper, B.J., and Lindroth, R.L. 2003. Altered growth and fine root chemistry of *Betula papyrifera* and *Acer saccharum* under elevated CO₂. *Canadian Journal of Forest Research* **33**: 842–846.

Peñuelas, J., Castells, E., Joffre, R., and Tognetti, R. 2002. Carbon-based secondary and structural compounds in Mediterranean shrubs growing near a natural CO₂ spring. *Global Change Biology* **8**: 281–288.

Peñuelas, J. and Estiarte, M. 1998. Can elevated CO₂ affect secondary metabolism and ecosystem function? *Trees* **13**: 20–24.

Runion, G.B., Entry, J.A., Prior, S.A., Mitchell, R.J., and Rogers, H.H. 1999. Tissue chemistry and carbon allocation in seedlings of *Pinus palustris* subjected to elevated atmospheric CO₂ and water stress. *Tree Physiology* **19**: 329–335.

Wetzel, R.G. and Tuchman, N.C. 2005. Effects of atmospheric CO₂ enrichment and sunlight on degradation of plant particulate and dissolved organic matter and microbial utilization. *Archiv fur Hydrobiologie* **162**: 287–308.

Williams, R.S., Lincoln, D.E., and Thomas, R.B. 1994. Loblolly pine grown under elevated CO₂ affects early instar pine sawfly performance. *Oecologia* **98**: 64–71.

2.20 Phenology

- The wide range of results obtained by many past and current methods of detecting each year's start-of-spring has led some researchers to claim spring has been arriving earlier over the course of the twentieth century. These observations are used to support the associated claim of twentieth-century CO₂-induced global warming, often said to result in the mistiming of the yearly start-up of the component links of various ecosystems' food chains. Real-world data, however, do not support the bulk of these contentions.

The progressively earlier arrival of spring with each succeeding year is widely viewed as an indicator of global warming. Scheifinger *et al.* (2002) and Schaber and Badeck (2005) claim to have detected earlier spring arrival in Europe over the course of the twentieth century. One difficulty with such studies, however, is the lack of a commonly agreed-upon metric for the arrival of spring.

White *et al.* (2009) compared 10 algorithms for processing satellite Normalized Difference Vegetation Index (NDVI) data for this purpose, based on the expectation that satellite data, with their continental coverage, should allow such trends to be more easily detected. A question that remains, however, is whether the various methods employed measure the same things or correspond to on-the-ground measurements.

White *et al.*'s study covered the period 1982–2006, using 16,000 ground-based phenological measurements from across North America as well as data on snow melt and hydrology. Using the 10 methods of extracting a start-of-spring (SOS) signal from the satellite data, they ended up with a range of fully 60 days around the 10-model mean estimate.

Plant Characteristics

The 10 methods also tended to be biased toward detecting SOS earlier than ground-based phenology data indicated, and to have weak correlations with the ground data, perhaps because there were difficulties classifying pixels in some cases, particularly for desert, semi-tropical, and Mediterranean (California) zones in which the arrival of “spring” is not a well-defined phenomenon.

In the end, the 21 researchers state they “found no evidence for time trends in spring arrival from ground- or model-based data,” and “using an ensemble estimate from two methods that were more closely related to ground observations than other methods, SOS trends could be detected for only 12% of North America,” with 7% showing a trend to earlier spring and 5% exhibiting a trend toward later spring. That suggests the wide range of results obtained by most past and current methods of detecting the start of spring may have led to premature claims of spring’s increasingly earlier annual occurrence over the latter part of the twentieth century. And that finding, in turn, raises significant concerns about the validity of near-surface air temperature measurements that suggest North America has warmed significantly over the past several decades.

In the introduction to another study of the subject, however, Johnston and Reekie (2008) state there have “been marked changes in plant phenology over the past century,” and these changes “have been interpreted as a consequence of the increase in temperature that has been observed over this time.” In an added twist to the subject, they speculate, “the concentration of atmospheric CO₂ may also directly affect time of flowering, even in the absence of temperature change.”

The two researchers examined the effect of elevated atmospheric CO₂ concentration by itself (ambient and ambient + 330 ppm), as well as the combined effect of elevated CO₂ and elevated air temperature (ambient + 1.5°C), on the flowering phenology of 22 species of plants in the Asteraceae family, which were grown under natural, seasonally varying temperature and daylength in separate compartments of a glasshouse in Wolfville, Nova Scotia, Canada. The researchers found, “on average, elevated CO₂ by itself advanced flowering by four days” and “increasing temperature as well as CO₂ advanced flowering by an additional three days.” They also found, “CO₂ was more likely to hasten phenology in long- than in short-day species,” and “early- and late-flowering species did not differ in response to elevated CO₂,” but “the combined effect

of elevated CO₂ and temperature hastened flowering more in early- than late-flowering species.” They conclude, with respect to time of flowering in Asteraceae species, “the direct effect of CO₂ on phenology may be as important as its indirect effect through climate change,” further complicating the interpretation of a progressively earlier start of spring as an indication of regional or global warming.

Some scientists express concern that global warming may “throw off” the timing of lifecycle stages of certain food chain components, leading to a mismatch among the unique needs of different ecosystem trophic levels that could spell disaster for some species. Visser and Both (2005) warn of such an “insufficient adjustment” to climate change.

Bauer *et al.* (2010) studied the effect of 47 years of warming (1961–2007) on the time of leafing-out of dominant English Oak (*Quercus robur*) trees at four research sites in the Czech Republic located in full-grown, multiaged floodplain forests that had been under no forestry management. They also studied the time of appearance of the two most abundant species of caterpillars in the floodplain forests, the Winter Moth (*Operophtera brumata*) and the Tortrix Moth (*Tortrix viridana*), and the first and mean laying dates of two of the ecosystem’s most common birds: Great Tits (*Parus major*) and Collared Flycatchers (*Ficedula albicollis*).

The seven scientists found “mean annual temperature showed a significant increase of 0.27–0.33°C per decade, with approximately the same magnitude of change during spring at all sites.” They also found, “on average (all four sites), the bud burst date for English Oak has advanced by 7.9 days and full foliage by 8.9 days, with approximately the same shifts being recorded for the peak of the beginning and end of frass for herbivorous caterpillars,” which was the observational variable they used to characterize the caterpillars’ presence. Finally, they write, “the first laying date of Great Tits has advanced by between 6.2 to 8.0 days,” and “the mean laying date has advanced by 6.4 to 8.0 days.” They found the “Collared Flycatcher first laying date has advanced by 8.5 to 9.2 days over the past 47 years, and the mean laying date by 7.7 to 9.6 days.”

Bauer *et al.* state, because “trends in the timing of reproduction processes of both bird species are coherent with the trends in development of English Oak and with peak herbivorous caterpillar activity,” it is apparent in this specific food chain the common temporal shifting of the different organisms’ phenological stages toward the beginning of the year “does not appear to have led to mistiming in the

trophic food chain.” Hence, other food chains also may not be as seriously disrupted by global warming as many have postulated they could be. More work of this nature, however, is clearly needed before any generalizations are warranted.

References

Bauer, Z., Trnka, M., Bauerova, J., Mozny, M., Stepanek, P., Bartosova, L., and Zalud, Z. 2010. Changing climate and the phenological response of great tit and collared flycatcher populations in floodplain forest ecosystems in Central Europe. *International Journal of Biometeorology* **54**: 99–111.

Johnston, A. and Reekie, E. 2008. Regardless of whether rising atmospheric carbon dioxide levels increase air temperature, flowering phenology will be affected. *International Journal of Plant Science* **169**: 1210–1218.

Schaber, J. and Badeck, F. 2005. Plant phenology in Germany over the 20th Century. *Regional Environmental Change* **5**: 37–46.

Scheifinger, H., Menzel, A., Koch, E., Peter, C., and Ahas, R. 2002. Atmospheric mechanisms governing the spatial and temporal variability of phenological phases in central Europe. *International Journal of Climatology* **22**: 1739–1755.

Visser, M.E. and Both, C. 2005. Shifts in phenology due to global climate change: the need for yardstick. *Proceedings of the Royal Society B* **272**: 2561–2569.

White, Michael A., de Beurs, K.M., Kidan, K., Inouye, D.W., Richardson, A.D., Jensen, O.P., O’Keefe, J., Zhang, G., Nemani, R.R., van Leeuwen, W.J.D., Brown, J.F., de Wit, A., Schaepman, M., Lin, X., Dettinger, M., Bailey, A.S., Kimball, J., Schwartz, M.D., Baldocchi, D.D., Lee, J.T., and Lauenroth, W.K. 2009. Intercomparison, interpretation, and assessment of spring phenology in North America estimated from remote sensing for 1982–2006. *Global Change Biology* **15**: 2335–2359.

2.21 Protein

- In both managed agricultural crops and the wild plants of Earth’s natural ecosystems, the ongoing rise of the air’s CO₂ concentration likely will have few negative impacts of any consequence on the nutritive value of their grains and foliage in terms of protein concentration. In tree crops such as citrus, CO₂-induced changes in the activities of certain foliar proteins could lead to vast increases in yield potential.

In a review of the scientific literature on the effects of atmospheric CO₂ enrichment on plant constituents of significance to human health, Idso and Idso (2001) cite a number of studies where elevated levels of atmospheric CO₂ either increased, decreased, or had no effect on the protein concentrations of various agricultural crops. The first two of these consequences also were observed by Kaddour and Fuller (2004) and Veisz *et al.* (2005) in wheat.

In the case of this particular crop—which according to Wittwer (1995) was “the most widely grown plant in the world” at that time, contributing “more calories and protein to the human diet than any other food”—Pleijel *et al.* (1999) analyzed the results of 16 open-top chamber experiments that had been conducted on spring wheat in Denmark, Finland, Sweden, and Switzerland between 1986 and 1996. In addition to CO₂ enrichment of the air, these experiments included increases and decreases in atmospheric ozone (O₃). Pleijel *et al.* found when increasing O₃ pollution reduced wheat grain yield, it simultaneously increased the protein concentration of the grain. They also found when O₃ was scrubbed from the air and grain yield was thereby increased, the protein concentration of the grain was decreased. This same relationship described the degree to which grain protein concentration dropped when atmospheric CO₂ enrichment increased grain yield. Hence, whenever the grain yield of the wheat was changed—by CO₂, O₃, or even water stress, which was also a variable in one of the experiments—grain protein concentrations moved up or down along a common linear relationship in the opposite direction to the change in grain yield.

In an earlier study of CO₂ and O₃ effects on wheat grain yield and quality, Rudorff *et al.* (1996) obtained essentially the same result. They observed, for example, “flour protein contents were increased by enhanced O₃ exposure and reduced by elevated CO₂,” but “the combined effect of these gases was minor.” Hence, they conclude, “the concomitant increase of CO₂ and O₃ in the troposphere will have no significant impact on wheat grain quality.”

Evans (1993) found similar relationships for several other crops, further observing them to be greatly affected by soil nitrogen availability. It is highly likely, therefore, that the differing availability of soil nitrogen could have been responsible for some of the results observed in the many other studies reviewed by Idso and Idso (2001). That is precisely what the study of Rogers *et al.* (1996) suggests. Although they observed CO₂-induced reductions in the protein concentration of flour derived from wheat

Plant Characteristics

plants growing at low soil nitrogen concentrations, no such reductions were evident when the soil nitrogen supply was increased. Hence, Pleijel *et al.* conclude, the oft-observed negative impact of atmospheric CO₂ enrichment on grain protein concentration probably would be alleviated by higher applications of nitrogen fertilizers.

Kimball *et al.* (2001) confirmed that hypothesis. They studied the effects of a 50% increase in atmospheric CO₂ concentration on wheat grain nitrogen concentration and the baking properties of the flour derived from that grain throughout four years of free-air CO₂ enrichment experiments. In the first two years of their study, soil water content was an additional variable, and in the last two years, soil nitrogen content was a variable. The most influential factor in reducing grain nitrogen concentration was determined to be low soil nitrogen. Under this condition, atmospheric CO₂ enrichment further reduced grain nitrogen and protein concentrations, although the change was much less than that caused by low soil nitrogen. When soil nitrogen was not limiting, however, increases in the air's CO₂ concentration did not affect grain nitrogen and protein concentrations, nor did they reduce the baking properties of the flour derived from the grain. Hence, it would appear that given sufficient water and nitrogen, atmospheric CO₂ enrichment can increase wheat grain yield without sacrificing grain protein concentration in the process.

Atmospheric CO₂ enrichment has been found in some studies to increase the protein concentration of wheat. Agrawal and Deepak (2003), for example, grew two cultivars of wheat (*Triticum aestivum* L. cv. Malviya 234 and HP1209) in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 600 ppm alone and in combination with 60 ppb SO₂ to study the interactive effects of elevated CO₂ and this major air pollutant on crop growth. They found exposure to the elevated SO₂ caused a 13% decrease in foliar protein concentrations in both cultivars, but when the plants were concomitantly exposed to an atmospheric CO₂ concentration of 600 ppm, leaf protein levels decreased by only 3% in HP1209 and increased by 4% in Malviya 234.

In the case of rice—which according to Wittwer (1995) was “the basic food for more than half the world's population,” supplying “more dietary energy than any other single food”—Jablonski *et al.* (2002) conducted a wide-ranging review of the scientific literature, finding rice, too, appeared to suffer no reduction in grain nitrogen (protein) concentration in response to atmospheric CO₂ enrichment. They also

found no CO₂-induced decrease in seed nitrogen concentration in the studies of legumes they reviewed. This finding is significant because, as Wittwer (1995) notes, legumes “are a direct food resource providing 20% of the world's protein for human consumption” and “about two thirds of the world's protein concentrate for livestock feeding.” In addition, Jablonski *et al.* found the biomass of the CO₂-enriched wheat, rice, and legumes was increased significantly above that of the same crops grown in normal air. Hence, there likely will be a vast increase in the total amount of protein that can be made available to humanity in a future CO₂-enriched world, both directly via food crops and indirectly via livestock.

Thomas *et al.* (2003) noted “oil and protein comprise ~20 and 40%, respectively, of the dry weight of soybean seed.” This “unique chemical composition,” they write, “has made it one of the most valuable agronomic crops worldwide.” In addition, “the intrinsic value of soybean seed is in its supply of essential fatty acids and amino acids in the oil and protein, respectively.” They report Heagle *et al.* (1998) “observed a positive significant effect of CO₂ enrichment on soybean seed oil and oleic acid concentration.”

Legumes and their responses to atmospheric CO₂ enrichment also figure prominently in studies of mixed forage crops. In a study of nitrogen cycling in grazed pastures on the North Island of New Zealand, for example, Allard *et al.* (2003) found under elevated CO₂, leaves of the individual species exhibited lower nitrogen concentrations but higher water-soluble carbohydrate (WSC) concentrations. They also note “there was a significantly greater proportion of legume in the diet at elevated CO₂,” and this “shift in the botanical composition towards a higher proportion of legumes counter-balanced the nitrogen decrease observed at the single species scale, resulting in a nitrogen concentration of the overall diet that was unaffected by elevated CO₂.” They further report, “changes at the species level and at the sward level appeared to combine additively in relation to WSC.” Hence, they note, “as there was a significant correlation between WSC and digestibility (as previously observed by Dent and Aldrich, 1963 and Humphreys, 1989), there was also an increase in digestibility of the high CO₂ forage.” This result, they write, “matches that found in a Mini-FACE experiment under cutting (Teyssonneyre, 2002; Picon-Cochard *et al.*, 2004),” where “digestibility also increased in response to CO₂ despite reduced crude protein concentration.” These data, plus the strong relation-

ship between soluble sugars (rather than nitrogen) and digestibility, led them to suggest “the widespread response to CO₂ of increased soluble sugars might lead to an increase in forage digestibility.”

Luscher *et al.* (2004) found much the same in their review of the subject, which was based primarily on studies conducted at the Swiss FACE facility that hosted what had by then become the world’s longest continuous atmospheric CO₂ enrichment study of a naturally occurring grassland. There, in response to an approximate two-thirds increase in the atmosphere’s CO₂ concentration, leaf nitrogen (N) concentrations of white clover (*Trifolium repens* L.) and perennial ryegrass (*Lolium perenne* L.) were reduced by 7% and 18%, respectively, when they were grown separately in pure stands. As Luscher *et al.* report, “the considerably lower concentration of N under elevated CO₂, observed for *L. perenne* leaves in pure stands, was found to a much lesser extent for *L. perenne* leaves in the bi-species mixture with *T. repens* (Zanetti *et al.*, 1997; Hartwig *et al.*, 2000).” Furthermore, “under elevated CO₂ the proportion of N-rich *T. repens* (40 mg N g⁻¹ dry matter) increased in the mixture at the expense of the N-poor *L. perenne* (24 mg N g⁻¹ dry matter when grown in monoculture),” the end result being “the concentration of N in the harvested biomass of the mixture showed no significant reduction.”

That this phenomenon is likely ubiquitous is suggested by the still more comprehensive review by Campbell *et al.* (2000), who analyzed research conducted between 1994 and 1999 by a worldwide network of 83 scientists associated with the Global Change and Terrestrial Ecosystems (GCTE) Pastures and Rangelands Core Research Project 1 (CRP1). This program had resulted in the publication of more than 165 peer-reviewed scientific journal articles. Campbell *et al.* determined from this massive collection of data the legume content of grass-legume swards typically was increased by approximately 10% in response to a doubling of the air’s CO₂ content.

Luscher *et al.* (2004) state, “the nutritive value of herbage from intensively managed grassland dominated by *L. perenne* and *T. repens* ... is well above the minimum range of the concentration of crude protein necessary for efficient digestion by ruminants (Barney *et al.* 1981).” Hence, they conclude, “a small decrease in the concentration of crude protein in intensively managed forage production systems [which may never occur, as noted above] is not likely to have a negative effect on the nutritive value or on the intake of forage.” In addition, in a CO₂-enriched world of the future there would be

much more such forage produced per unit of land and water devoted to the enterprise, clearly making the ongoing rise in the air’s CO₂ content a big plus for animal husbandry.

Newman *et al.* (2003) investigated the effects of two levels of nitrogen fertilization and an approximate doubling of the air’s CO₂ content on the growth and chemical composition of tall fescue (*Festuca arundinacea* Schreber cv. KY-31), both when infected and uninfected with a mutualistic fungal endophyte (*Neotyphodium coenophialum* Morgan-Jones and Gams). They found the elevated CO₂ reduced the crude protein content of the forage by an average of 21% in three of the four situations studied: non-endophyte-infected plants in both the low and high nitrogen treatments, and endophyte-infected plants in the high nitrogen treatment. There was no protein reduction for endophyte-infected plants in the low nitrogen treatment.

Newman *et al.* note, “the endophyte is present in many native and naturalized populations and the most widely sown cultivars of *F. arundinacea*,” so the first two situations in which the CO₂-induced protein reduction occurred (those involving non-endophyte-infected plants) are not typical of the real world. In addition, since the dry-weight biomass yield of the forage was increased by fully 53% under the low nitrogen regime, and since the 10-times-greater high nitrogen regime boosted yields only by an additional 8%, there would appear to be no need to apply extra nitrogen to *F. arundinacea* in a CO₂-enriched environment.

Consequently, under best management practices in a doubled-CO₂ world of the future, little or no nitrogen would be added to the soil, and there would be little or no reduction in the crude protein content of *F. arundinacea*. But there would be more than 50% more of it produced on the same amount of land.

With respect to the final plant quality (forage digestibility) studied by Newman *et al.*, increasing soil nitrogen lowered *in vitro* neutral detergent fiber digestibility in both ambient and CO₂-enriched air, and this phenomenon was most pronounced in the elevated CO₂ treatment. Under low nitrogen conditions there again was no decline in plant digestibility. Hence, there is a second good reason not to apply extra nitrogen to *F. arundinacea* in a high CO₂ world of the future, and little need to do so.

With respect to the unmanaged world of nature, increases in the air’s CO₂ content often, but not always (Goverde *et al.*, 1999), lead to greater decreases in the concentrations of nitrogen and protein in the foliage of C₃ as compared to C₄ grasses

(Wand *et al.*, 1999). As a result, in the words of Barbehenn *et al.* (2004a), “it has been predicted that insect herbivores will increase their feeding damage on C₃ plants to a greater extent than on C₄ plants (Lincoln *et al.*, 1984, 1986; Lambers, 1993).”

To test this hypothesis, Barbehenn *et al.* (2004a) grew *Lolium multiflorum* Lam. (Italian ryegrass, a common C₃ pasture grass) and *Bouteloua curtipendula* (Michx.) Torr. (sideoats gramma, a native C₄ rangeland grass) in chambers maintained at either the ambient atmospheric CO₂ concentration of 370 ppm or the doubled CO₂ concentration of 740 ppm for two months, after which newly molted sixth-instar larvae of *Pseudaletia unipuncta* (a grass-specialist noctuid) and *Spodoptera frugiperda* (a generalist noctuid) were allowed to feed on the grasses. As expected, foliage protein concentration decreased by 20% in the C₃ grass, but by only 1% in the C₄ grass, when grown in the CO₂-enriched air. However, and “contrary to our expectations,” Barbehenn *et al.* write, “neither caterpillar species significantly increased its consumption rate to compensate for the lower concentration of protein in [the] C₃ grass,” and “this result does not support the hypothesis that C₃ plants will be subject to greater rates of herbivory relative to C₄ plants in future [high-CO₂] atmospheric conditions (Lincoln *et al.*, 1984).” In addition, “despite significant changes in the nutritional quality of *L. multiflorum* under elevated CO₂,” they report “no effect on the relative growth rate of either caterpillar species on either grass species resulted,” and there were “no significant differences in insect performance between CO₂ levels.”

In a similar study, Barbehenn *et al.* (2004b) allowed grasshopper (*Melanoplus sanguinipes*) nymphs reared to the fourth-instar stage to feed on the grasses. Once again, “contrary to the hypothesis that insect herbivores will increase their feeding rates disproportionately in C₃ plants under elevated atmospheric CO₂,” they found “*M. sanguinipes* did not significantly increase its consumption rate when feeding on the C₃ grass grown under elevated CO₂.” They suggest this observation implies “post-ingestive mechanisms enable these grasshoppers to compensate for variable nutritional quality in their host plants,” and some of these post-ingestive responses may include “changes in gut size, food residence time, digestive enzyme levels, and nutrient metabolism (Simpson and Simpson, 1990; Bernays and Simpson, 1990; Hinks *et al.*, 1991; Zanotto *et al.*, 1993; Yang and Joern, 1994a,b).” Their data indicate *M. sanguinipes* growth rates may have increased, perhaps

by as much as 12%, when feeding upon the C₃ foliage that had been produced in the CO₂-enriched air.

With respect to both managed agricultural crops and the wild plants of Earth’s natural ecosystems, it appears the ongoing rise of the air’s CO₂ concentration will have few negative impacts of any consequence on the nutritive value of their grains and foliage in terms of protein concentration. In tree crops such as citrus, CO₂-induced changes in the activities of certain foliar proteins could lead to vast increases in their yield potential, as elucidated by the work of Idso *et al.* (2001).

References

- Agrawal, M. and Deepak, S.S. 2003. Physiological and biochemical responses of two cultivars of wheat to elevated levels of CO₂ and SO₂, singly and in combination. *Environmental Pollution* **121**: 189–197.
- Allard, V., Newton, P.C.D., Lieffering, M., Clark, H., Matthew, C., Soussana, J.-F., and Gray, Y.S. 2003. Nitrogen cycling in grazed pastures at elevated CO₂: N returns by ruminants. *Global Change Biology* **9**: 1731–1742.
- Barbehenn, R.V., Karowe, D.N., and Chen, Z. 2004b. Performance of a generalist grasshopper on a C₃ and a C₄ grass: compensation for the effects of elevated CO₂ on plant nutritional quality. *Oecologia* **140**: 96–103.
- Barbehenn, R.V., Karowe, D.N., and Spickard, A. 2004a. Effects of elevated atmospheric CO₂ on the nutritional ecology of C₃ and C₄ grass-feeding caterpillars. *Oecologia* **140**: 86–95.
- Barney, D.J., Grieve, D.G., Macleod, G.K., and Young, L.G. 1981. Response of cows to a reduction in dietary crude protein from 17 to 13% during early lactation. *Journal of Dairy Science* **64**: 25–33.
- Bernays, E.A. and Simpson, S.J. 1990. Nutrition. In: Chapman, R.F. and Joern, A. (Eds.) *Biology of Grasshoppers*. Wiley, New York, NY, pp. 105–127.
- Campbell, B.D., Stafford Smith, D.M., Ash, A.J., Fuhrer, J., Gifford, R.M., Hiernaux, P., Howden, S.M., Jones, M.B., Ludwig, J.A., Manderscheid, R., Morgan, J.A., Newton, P.C.D., Nosberger, J., Owensby, C.E., Soussana, J.F., Tuba, Z., and ZuoZhong, C. 2000. A synthesis of recent global change research on pasture and rangeland production: reduced uncertainties and their management implications. *Agriculture, Ecosystems and Environment* **82**: 39–55.
- Dent, J.W. and Aldrich, D.T.A. 1963. The inter-relationships between heading date, yield, chemical composition and digestibility in varieties of perennial

Climate Change Reconsidered II: Biological Impacts

- ryegrass, timothy, cooksfoot and meadow fescue. *Journal of the National Institute of Agricultural Botany* **9**: 261–281.
- Evans, L.T. 1993. *Crop Evolution, Adaptation and Yield*. Cambridge University Press, Cambridge, UK.
- Goverde, M., Bazin, A., Shykoff, J.A., and Erhardt, A. 1999. Influence of leaf chemistry of *Lotus corniculatus* (Fabaceae) on larval development of *Polyommatus icarus* (Lepidoptera, Lycaenidae): effects of elevated CO₂ and plant genotype. *Functional Ecology* **13**: 801–810.
- Hartwig, U.A., Luscher, A., Daepf, M., Blum, H., Soussana, J.F., and Nosberger, J. 2000. Due to symbiotic N₂ fixation, five years of elevated atmospheric pCO₂ had no effect on litter N concentration in a fertile grassland ecosystem. *Plant and Soil* **224**: 43–50.
- Heagle, A.S., Miller, J.E., and Pursley, W.A. 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment: III. Yield and seed quality. *Crop Science* **38**: 128–134.
- Hinks, C.R., Cheeseman, M.T., Erlandson, M.A., Olfert, O., and Westcott, N.D. 1991. The effects of kochia, wheat and oats on digestive proteinases and the protein economy of adult grasshoppers, *Malanoplus sanguinipes*. *Journal of Insect Physiology* **37**: 417–430.
- Humphreys, M.O. 1989. Water-soluble carbohydrates in perennial ryegrass breeding. III. Relationships with herbage production, digestibility and crude protein content. *Grass and Forage Science* **44**: 423–430.
- Idso, K.E., Hooper, J.K., Idso, S.B., Wall, G.W., and Kimball, B.A. 2001. Atmospheric CO₂ enrichment influences the synthesis and mobilization of putative vacuolar storage proteins in sour orange tree leaves. *Environmental and Experimental Botany* **48**: 199–211.
- Idso, S.B. and Idso, K.E. 2001. Effects of atmospheric CO₂ enrichment on plant constituents related to animal and human health. *Environmental and Experimental Botany* **45**: 179–199.
- Jablonski, L.M., Wang, X., and Curtis, P.S. 2002. Plant reproduction under elevated CO₂ conditions: a meta-analysis of reports on 79 crop and wild species. *New Phytologist* **156**: 9–26.
- Kaddour, A.A. and Fuller, M.P. 2004. The effect of elevated CO₂ and drought on the vegetative growth and development of durum wheat (*Triticum durum* Desf.) cultivars. *Cereal Research Communications* **32**: 225–232.
- Kimball, B.A., Morris, C.F., Pinter Jr., P.J., Wall, G.W., Hunsaker, D.J., Adamsen, F.J., LaMorte, R.L., Leavitt, S.W., Thompson, T.L., Matthias, A.D., and Brooks, T.J. 2001. Elevated CO₂, drought and soil nitrogen effects on wheat grain quality. *New Phytologist* **150**: 295–303.
- Lambers, H. 1993. Rising CO₂, secondary plant metabolism, plant-herbivore interactions and litter decomposition. Theoretical considerations. *Vegetatio* **104/105**: 263–271.
- Lincoln, D.E., Couvet, D., and Sionit, N. 1986. Responses of an insect herbivore to host plants grown in carbon dioxide enriched atmospheres. *Oecologia* **69**: 556–560.
- Lincoln, D.E., Sionit, N., and Strain, B.R. 1984. Growth and feeding response of *Pseudoplusia includens* (Lepidoptera: Noctuidae) to host plants grown in controlled carbon dioxide atmospheres. *Environmental Entomology* **13**: 1527–1530.
- Luscher, A., Daepf, M., Blum, H., Hartwig, U.A., and Nosberger, J. 2004. Fertile temperate grassland under elevated atmospheric CO₂—role of feed-back mechanisms and availability of growth resources. *European Journal of Agronomy* **21**: 379–398.
- Newman, J.A., Abner, M.L., Dado, R.G., Gibson, D.J., Brookings, A., and Parsons, A.J. 2003. Effects of elevated CO₂, nitrogen and fungal endophyte-infection on tall fescue: growth, photosynthesis, chemical composition and digestibility. *Global Change Biology* **9**: 425–437.
- Picon-Cochard, C., Teyssonneyre, F., and Besle, J.M., et al. 2004. Effects of elevated CO₂ and cutting frequency on the productivity and herbage quality of a semi-natural grassland. *European Journal of Agronomy* **20**: 363–377.
- Pleijel, H., Mortensen, L., Fuhrer, J., Ojanpera, K., and Danielsson, H. 1999. Grain protein accumulation in relation to grain yield of spring wheat (*Triticum aestivum* L.) grown in open-top chambers with different concentrations of ozone, carbon dioxide and water availability. *Agriculture, Ecosystems and Environment* **72**: 265–270.
- Rogers, G.S., Milham, P.J., Gillings, M., and Conroy, J.P. 1996. Sink strength may be the key to growth and nitrogen responses in N-deficient wheat at elevated CO₂. *Australian Journal of Plant Physiology* **23**: 253–264.
- Rudorff, B.F.T., Mulchi, C.L., Fenny, P., Lee, E.H., and Rowland, R. 1996. Wheat grain quality under enhanced tropospheric CO₂ and O₃ concentrations. *Journal of Environmental Quality* **25**: 1384–1388.
- Simpson, S.J. and Simpson, C.L. 1990. The mechanisms of nutritional compensation by phytophagous insects. In: Bernays, E.A. (Ed.) *Insect-Plant Interactions*, Vol. 2. CRC Press, Boca Raton, FL, pp. 111–160.
- Teyssonneyre, F. 2002. Effet d'une augmentation de la concentration atmospherique en CO₂ sur la prairie permanente et sur la competition entre especes prairiales associees. Ph.D. thesis, Orsay, Paris XI, France.
- Thomas, J.M.G., Boote, K.J., Allen Jr., L.H., Gallo-Meagher, M., and Davis, J.M. 2003. Elevated temperature and carbon dioxide effects on soybean seed composition and transcript abundance. *Crop Science* **43**: 1548–1557.

Plant Characteristics

Veisz, O., Bencze, S., and Bedo, Z. 2005. Effect of elevated CO₂ on wheat at various nutrient supply levels. *Cereal Research Communications* **33**: 333–336.

Wand, S.J.E., Midgley, G.F., Jones, M.H., and Curtis, P.S. 1999. Responses of wild C₄ and C₃ grass (Poaceae) species to elevated atmospheric CO₂ concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology* **5**: 723–741.

Wittwer, S.H. 1995. *Food, Climate, and Carbon Dioxide: The Global Environment and World Food Production*. CRC Press, Boca Raton, FL.

Yang, Y. and Joern, A. 1994a. Gut size changes in relation to variable food quality and body size in grasshoppers. *Functional Ecology* **8**: 36–45.

Yang, Y. and Joern, A. 1994b. Influence of diet quality, developmental stage, and temperature on food residence time in the grasshopper *Melanoplus differentialis*. *Physiological Zoology* **67**: 598–616.

Zanetti, S., Hartwig, U.A., Van Kessel, C., Luscher, A., Bebeisen, T., Frehner, M., Fischer, B.U., Hendrey, G.R., Blum, G., and Nosberger, J. 1997. Does nitrogen nutrition restrict the CO₂ response of fertile grassland lacking legumes? *Oecologia* **112**: 17–25.

Zanotto, F.P., Simpson, S.J., and Raubenheimer, D. 1993. The regulation of growth by locusts through post-ingestive compensation for variation in the levels of dietary protein and carbohydrate. *Physiological Entomology* **18**: 425–434.

2.22 Respiration

Nearly all of Earth's plants respond favorably to increases in the air's CO₂ concentration by exhibiting enhanced rates of photosynthesis and biomass production during the light part of each day. However, the observed increases in these parameters (especially biomass production) are also due, in part, to CO₂-induced reductions in carbon losses via respiration during both the day and night (the latter called "dark respiration"). The subsections below examine what has been learned about both of these types of respiration from experiments conducted on various herbaceous and woody plants.

2.22.1 Herbaceous Plants

The growth and biomass production of herbaceous crops generally is enhanced by CO₂-induced decreases in respiration during the dark (nighttime) period. However, fundamental information is still lacking on how respiration and the processes

supported by it are physiologically controlled, thereby preventing sound interpretations of what seem to be species-specific responses of respiration to elevated CO₂. The precise role of plant respiration in augmenting the sink capacity of herbaceous plants remains uncertain.

2.22.1.1 Crops

- The growth and biomass production of herbaceous crops generally is enhanced by CO₂-induced decreases in respiration during the dark (nighttime) period.

Baker *et al.* (2000) grew rice in Soil-Plant-Atmosphere Research (SPAR) units at atmospheric CO₂ concentrations of 350 and 700 ppm during daylight hours. Under these conditions, rates of dark respiration decreased in both CO₂ treatments with short-term increases in the air's CO₂ concentration at night. However, when dark respiration rates were measured at the CO₂ growth concentrations of the plants, they were not significantly different from each other.

Cousins *et al.* (2001) grew sorghum at atmospheric CO₂ concentrations of 370 and 570 ppm in a free-air CO₂ enrichment (FACE) facility near Phoenix, Arizona (USA). Within six days of planting, the photosynthetic rates of the second leaves of the CO₂-enriched plants were 37% greater than those of the second leaves of the ambiently grown plants. This CO₂-induced photosynthetic enhancement slowly declined with time, stabilizing at about 15% between 23 and 60 days after planting. In addition, when measuring photosynthetic rates at a reduced oxygen concentration of 2%, they observed 16 and 9% increases in photosynthesis for the ambient and CO₂-enriched plants, respectively, which suggests the extra 200 ppm of CO₂ was reducing photorespiratory carbon losses, although this phenomenon did not account for all of the CO₂-induced stimulation of photosynthesis.

Das *et al.* (2002) grew tropical nitrogen-fixing mungbean plants in open-top chambers maintained at atmospheric CO₂ concentrations of either 350 or 600 ppm for two growing seasons, with the extra CO₂ being provided between either days 0 and 20 or days 21 and 40 after germination. The elevated CO₂ decreased rates of respiration by 54 to 62%, with the greatest declines occurring during the first 20 days after germination.

Wang *et al.* (2004) grew well-watered and

fertilized South American tobacco plants from seed in 8.4-liter pots (one plant per pot) filled with sand and housed in controlled-environment growth chambers maintained at atmospheric CO₂ concentrations of either 365 or 730 ppm for nine weeks. Over this period they found the ratio of net photosynthesis per unit leaf area (A) to dark respiration per unit leaf area (Rd) “changed dramatically.” Whereas A/Rd was the same in both treatments at the beginning of the measurement period, a month later it had doubled in the CO₂-enriched environment but had risen by only 58% in the ambient CO₂ treatment. Speaking of this finding, the three researchers state, “if the dynamic relationship between A and Rd observed in *N. sylvestris* is applicable to other species, it will have important implications for carbon cycling in terrestrial ecosystems, since plants will assimilate CO₂ more efficiently as they mature.”

Bunce (2005) grew soybeans in the field in open-top chambers maintained at atmospheric CO₂ concentrations of ambient and ambient +350 ppm at the Beltsville Agricultural Research Center in Maryland (USA), where net carbon dioxide exchange rate measurements were performed on a total of 16 days between 18 July and 11 September of 2000 and 2003, during the flowering to early pod-filling stages of the growing season. Averaging his results over the course of the study, Bunce found daytime net photosynthesis per unit leaf area was 48% greater in the plants growing in the CO₂-enriched air, and nighttime respiration per unit leaf area was unaffected by elevated CO₂. However, because the extra 350 ppm of CO₂ increased leaf dry mass per unit area by an average of 23%, respiration per unit of mass was significantly lower for the leaves of the soybeans growing in the CO₂-enriched air.

Wang and Curtis (2002) conducted a meta-analysis of the results of 45 area-based dark respiration (Rda) and 44 mass-based dark respiration (Rdm) assessments of the effects of a doubling of the air’s CO₂ concentration on 33 species of plants derived from 37 scientific studies. The mean leaf Rda of the suite of herbaceous plants studied was significantly higher (+29%, $P < 0.01$) at elevated CO₂ than at ambient CO₂. When the herbaceous plants were separated into groups that had experienced durations of CO₂ enrichment either shorter or longer than 60 days, the short-term studies exhibited a mean Rda increase of 51% ($P < 0.05$), and the long-term studies exhibited no effect. Hence, for conditions of continuous atmospheric CO₂ enrichment, herbaceous plants likely would experience no change in leaf Rda. In addition, the two researchers found plants exposed

to elevated CO₂ for < 100 days “showed significantly less of a reduction in leaf Rdm due to CO₂ enrichment (-12%) than did plants exposed for longer periods (-35%, $P < 0.01$).” Hence, for long-term conditions of continuous atmospheric CO₂ enrichment, herbaceous crops likely would experience an approximate 35% decrease in leaf Rdm.

Bunce (2004) grew six 16-plant batches of soybeans in a single controlled-environment chamber, one to a pot filled with 1.8 liters of vermiculite that was flushed daily with a complete nutrient solution. In three experiments conducted at day/night atmospheric CO₂ concentrations of 370/390 ppm, air temperatures were either 20, 25, or 30°C, and in three other experiments conducted at an air temperature of 25°C, atmospheric CO₂ concentrations were either 40, 370, or 1,400 ppm. At the end of the normal 16 hours of light on the 17th day after planting, half of the plants were harvested and used for the measurement of a number of physical parameters, and measurements of the plant physiological processes of respiration, translocation, and nitrate reduction were made on the other half of the plants over the following eight-hour dark period.

Plotting translocation and nitrate reduction as functions of respiration, Bunce found “a given change in the rate of respiration was accompanied by the same change in the rate of translocation or nitrate reduction, regardless of whether the altered respiration was caused by a change in temperature or by a change in atmospheric CO₂ concentration.” Bunce concludes, “the parallel responses of translocation and nitrate reduction for both the temperature and CO₂ treatments make it unlikely that the response of respiration to one variable [CO₂] was an artifact while the response to the other [temperature] was real.” Hence, there is reason to believe the oft-observed decreases in dark respiration experienced by plants exposed to elevated levels of atmospheric CO₂, as per the review and analysis studies of Drake *et al.* (1999) and Wang and Curtis (2002), are indeed real and not the result of measurement system defects.

References

- Baker, J.T., Allen Jr., L.H., Boote, K.J., and Pickering, N.B. 2000. Direct effects of atmospheric carbon dioxide concentration on whole canopy dark respiration of rice. *Global Change Biology* 6: 275–286.
- Bunce, J.A. 2004. A comparison of the effects of carbon dioxide concentration and temperature on respiration,

translocation and nitrate reduction in darkened soybean leaves. *Annals of Botany* **93**: 665–669.

Bunce, J.A. 2005. Response of respiration of soybean leaves grown at ambient and elevated carbon dioxide concentrations to day-to-day variation in light and temperature under field conditions. *Annals of Botany* **95**: 1059–1066.

Cousins, A.B., Adam, N.R., Wall, G.W., Kimball, B.A., Pinter Jr., P.J., Leavitt, S.W., LaMorte, R.L., Matthias, A.D., Ottman, M.J., Thompson, T.L., and Webber, A.N. 2001. Reduced photorespiration and increased energy-use efficiency in young CO₂-enriched sorghum leaves. *New Phytologist* **150**: 275–284.

Das, M., Zaidi, P.H., Pal, M., and Sengupta, U.K. 2002. Stage sensitivity of mungbean (*Vigna radiata* L. Wilczek) to an elevated level of carbon dioxide. *Journal of Agronomy and Crop Science* **188**: 219–224.

Drake, B.G., Azcon-Bieto, J., Berry, J., Bunce, J., Dijkstra, P., Farrar, J., Gifford, R.M., Gonzalez-Meler, M.A., Koch, G., Lambers, H., Siedow, J., and Wulfschleger, S. 1999. Does elevated atmospheric CO₂ inhibit mitochondrial respiration in green plants? *Plant, Cell and Environment* **22**: 649–657.

Wang, X., Anderson, O.R., and Griffin, K.L. 2004. Chloroplast numbers, mitochondrion numbers and carbon assimilation physiology of *Nicotiana sylvestris* as affected by CO₂ concentration. *Environmental and Experimental Botany* **51**: 21–31.

Wang, X. and Curtis, P. 2002. A meta-analytical test of elevated CO₂ effects on plant respiration. *Plant Ecology* **161**: 251–261.

2.22.1.2 Other Herbaceous Plants

- Fundamental information is still lacking on how respiration and the processes supported by it are physiologically controlled in herbaceous plants, thereby preventing sound interpretations of what seem to be species-specific responses of respiration to elevated CO₂. The role of plant respiration in augmenting the sink capacity of terrestrial ecosystems remains uncertain.

Rabha and Uprety (1998) grew India mustard plants for an entire season in open-top chambers with either ambient or enriched (600 ppm) atmospheric CO₂ concentrations and adequate or inadequate soil moisture levels. The elevated CO₂ concentration reduced leaf dark respiration rates by about 25% in both soil moisture treatments, which suggests a greater proportion of the increased carbohydrate pool

in the CO₂-enriched plants remained within them to facilitate increases in growth and development.

Ziska and Bunce (1999) grew four C₄ plants in controlled environment chambers maintained at either full-day (24-hour) atmospheric CO₂ concentrations of 350 and 700 ppm or a nocturnal-only CO₂ concentration of 700 ppm (with 350 ppm CO₂ during the day) for about three weeks. In this study, 24-hour CO₂ enrichment caused a significant increase in the photosynthesis (+13%) and total dry mass (+21%) of only one of the four C₄ species (*Amaranthus retroflexus*). There was no significant effect of nocturnal-only CO₂ enrichment on this species, indicating the observed increase in biomass, resulting from 24-hour atmospheric CO₂ enrichment, was not facilitated by greater carbon conservation stemming from a CO₂-induced reduction in dark respiration.

Grunzweig and Korner (2001) constructed model grasslands representative of the Negev of Israel and placed them in growth chambers maintained at atmospheric CO₂ concentrations of 280, 440, and 600 ppm for five months. They also found atmospheric CO₂ enrichment had no effect on nighttime respiratory carbon losses.

Van der Heijden *et al.* (2000) grew peat moss hydroponically within controlled environment chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm for up to six months, subjecting the peat moss to three different levels of nitrogen deposition. In all cases, they found the elevated CO₂ reduced rates of dark respiration consistently throughout the study by 40 to 60%.

Gonzalez-Meler *et al.* (2004) reviewed the scientific literature on the effects of atmospheric CO₂ enrichment on plant respiration from the cellular level to the level of entire ecosystems. They report finding, “contrary to what was previously thought, specific respiration rates are generally not reduced when plants are grown at elevated CO₂.” Nevertheless, they note, “whole ecosystem studies show that canopy respiration does not increase proportionally to increases in biomass in response to elevated CO₂.” This suggests respiration per unit biomass likely is reduced somewhat by atmospheric CO₂ enrichment. However, they also found “a larger proportion of respiration takes place in the root system [when plants are grown in CO₂-enriched air],” which once again obfuscates the issue.

The three researchers remark, “fundamental information is still lacking on how respiration and the processes supported by it are physiologically controlled, thereby preventing sound interpretations of what seem to be species-specific responses of

respiration to elevated CO₂,” concluding “the role of plant respiration in augmenting the sink capacity of terrestrial ecosystems is still uncertain.”

References

Gonzalez-Meler, M.A., Taneva, L., and Trueman, R.J. 2004. Plant respiration and elevated atmospheric CO₂ concentration: Cellular responses and global significance. *Annals of Botany* **94**: 647–656.

Grunzweig, J.M. and Korner, C. 2001. Growth, water and nitrogen relations in grassland model ecosystems of the semi-arid Negev of Israel exposed to elevated CO₂. *Oecologia* **128**: 251–262.

Rabha, B.K. and Upreti, D.C. 1998. Effects of elevated CO₂ and moisture stress on *Brassica juncea*. *Photosynthetica* **35**: 597–602.

Van der Heijden, E., Verbeek, S.K., and Kuiper, P.J.C. 2000. Elevated atmospheric CO₂ and increased nitrogen deposition: effects on C and N metabolism and growth of the peat moss *Sphagnum recurvum* P. Beauv. Var. *mucronatum* (Russ.) Warnst. *Global Change Biology* **6**: 201–212.

Ziska, L.H. and Bunce, J.A. 1999. Effect of elevated carbon dioxide concentration at night on the growth and gas exchange of selected C₄ species. *Australian Journal of Plant Physiology* **26**: 71–77.

2.22.2 Woody Plants

- Both above and below the soil surface, coniferous trees appear to exhibit significant reductions in respiration in CO₂-enriched air. However, deciduous trees exhibit both increases and decreases, as well as cases of no change. It again appears atmospheric CO₂ enrichment may either increase or decrease woody-plant respiration, but not to any great degree, so the net result for Earth's trees likely would be of little significance.

Plant growth rates are determined largely by the relative magnitudes of carbon gain via photosynthesis and carbon loss via respiration. Although much is known about the effects of atmospheric CO₂ enrichment on the first of these phenomena, much less is known about its effects on the second. The subsections below examine the various effects of CO₂-enriched air on respiration in various types of woody plants.

2.22.2.1 Coniferous Trees

- Both above and below the soil surface, coniferous trees may exhibit significant reductions in respiration in a high-CO₂ world of the future.

Jach and Ceulemans (2000) grew three-year old Scots pine seedlings out-of-doors and rooted in the ground in open-top chambers maintained at atmospheric CO₂ concentrations of either 350 or 750 ppm for two years. To make the experiment more representative of the natural world, they applied no nutrients or irrigation water to the soils in which the trees grew for the duration of the study. After two years of growth under these conditions, dark respiration on a needle mass basis in the CO₂-enriched seedlings was 27 and 33% lower in current-year and one-year-old needles, respectively. The researchers conclude the greater reduction in the older needles arises from the greater duration of elevated CO₂ exposure experienced by those needles.

Hamilton *et al.* (2001) studied the short- and long-term respiratory responses of loblolly pines in a free-air CO₂-enrichment (FACE) study established in 1996 on 13-year-old trees in a North Carolina (USA) plantation, where the CO₂-enriched trees were exposed to an extra 200 ppm of CO₂. This modest increase in the atmosphere's CO₂ concentration produced no significant short-term suppression of dark respiration rates in the trees' needles. Neither did long-term exposure to elevated CO₂ alter maintenance respiration, the amount of CO₂ that is respired to maintain existing plant tissues. However, growth respiration, the amount of CO₂ respired when constructing new tissues, was reduced by 21%.

McDowell *et al.* (1999) grew five-month-old seedlings of western hemlock in root boxes subjected to various root-space CO₂ concentrations (ranging from 90 to 7,000 ppm) for periods of several hours to determine the effects of soil CO₂ concentration on growth, maintenance, and total root respiration. Although elevated CO₂ had no effect on growth respiration, it significantly affected maintenance and total respiration. At a soil CO₂ concentration of 1585 ppm, for example, total and maintenance respiration rates of roots were 55 and 60% lower, respectively, than at 395 ppm. The impact of elevated CO₂ on maintenance respiration was so strong, in fact, it exhibited an exponential decline of about 37% for every doubling of soil CO₂ concentration. This observation is especially important because maintenance respiration comprised 85% of total root respiration in this study.

George *et al.* (2003) begin their work by noting, “several studies have documented a decrease in the specific rate of fine-root respiration for trees grown in elevated atmospheric CO₂,” citing Callaway *et al.* (1994), BassiriRad *et al.* (1997), and Crookshanks *et al.* (1998). Then, citing Cotrufo *et al.* (1998) as a basis for the idea that “growth under elevated CO₂ causes a decrease in the nitrogen concentration of roots,” which in turn suggests “a reduction in protein concentration,” they hypothesize, “the energy required for protein turnover may decline in elevated CO₂ causing a reduction in maintenance respiration,” and the resultant “decrease in maintenance respiration with elevated CO₂ may contribute to increases in growth respiration.”

To test this hypothesis, George *et al.* measured the maintenance respiration of non-growing fine roots in the absence of nutrients, while quantifying growth respiration from calculated construction costs and the observed production rates of fine roots in two major forest FACE studies: the Duke Forest study of a loblolly pine (*Pinus taeda* L.) plantation and the Oak Ridge National Laboratory (ORNL) Forest study of a sweetgum (*Liquidambar styraciflua* L.) plantation.

Based on unpublished data of R.J. Norby and D.W. Johnson from the ORNL Forest and the data of Finzi *et al.* (2002) from the Duke Forest, George *et al.* report, contrary to their initial assumption, as well as that of Hungate *et al.* (2003), they “were unable to detect an effect of elevated CO₂ on the nitrogen concentration of fine roots for either species.” They found a significant reduction of fine-root maintenance respiration in the loblolly pine plantation, but no significant difference in this parameter between the two sweetgum CO₂ treatments. Assessments of CO₂-induced increases in fine-root production in the study of Matamala and Schlesinger (2000) for the loblolly pines and in the study of Norby *et al.* (2002) for the sweetgum trees revealed fine-root biomass increases of 87% in the first case and 77% in the second case in response to an approximate 200-ppm increase in atmospheric CO₂ concentration.

George *et al.* state, “the C:N ratio of fine roots grown in elevated CO₂ was not altered and consequently did not explain the trend of reduced annual fine-root maintenance respiration and the increase in annual fine-root growth respiration for loblolly pine.” Instead, they conclude, “for these forests it appears that an increase in fine-root production is the primary factor contributing to the increase in annual growth respiration under elevated CO₂.” Hence, they end up rejecting their original hypothesis.

In a non-CO₂-enrichment study, Bronson and Gower (2010) state, “the boreal forest historically has been considered a carbon sink,” but “autotrophic respiration is [supposedly] more sensitive than photosynthesis to increases in temperature (Ryan, 1991; Amthor, 1994).” Therefore, in response to global warming, “most models predict autotrophic respiration will increase at a greater rate than photosynthesis, which infers decreased carbon use efficiency and net primary production (Ryan, 1995; VEMAP Members, 1995; Ryan *et al.*, 1996).” This further implies “a substantial increase in temperature could turn the boreal forest into a carbon source (Goulden *et al.*, 1998),” and this positive feedback could lead to an intensification of global warming.

Bronson and Gower studied black spruce trees (*Picea mariana* (Mill.) B.S.P.) growing in large, enclosed greenhouse chambers about 20 km south of Thompson, Manitoba, Canada (55°53'N, 98°20'W). Soil-heating cables were used to warm air and soil temperatures about 5°C over ambient control temperatures. The researchers measured light-saturated net photosynthesis, foliage respiration, and stem respiration in heated and control forest plots during the 2005, 2006, and 2007 growing seasons. Throughout the study, they found “both the older foliage, which developed before the experiment, and the new foliage, developed during the experiment, had similar rates of light-saturated net photosynthesis, foliage respiration and stem respiration across all treatments,” which, they write, “underscores the ability of black spruce to maintain homeostasis in a 5°C warmer environment.” In addition, while noting many global change models predict a doubling of respiration for every 10°C increase in temperature, Bronson and Gower state in the concluding sentence of their paper, “the results from this and other whole-ecosystem warming experiments do not support this model assumption.”

Lhotakova *et al.* (2012) measured rates of light-saturated net photosynthesis and dark respiration in current-year needles of sun-exposed (3rd whorl) and shaded (6th whorl) parts of the canopies of originally 10-year-old Norway spruce (*Picea abies*) trees that were transplanted into native soil (which was given an initial fertilizer treatment) and grown for an additional eight years in the Beskydy Mountains of the Czech Republic within semi-open glass domes having adjustable windows, where the trees were exposed to either the ambient-air CO₂ concentration (AC, which varied from 365 to 377 ppm over the course of the long-term experiment) or to an enriched-air CO₂ concentration (EC, which was

maintained at a steady value of 700 ppm).

Based on the graphical representations of Lhotakova *et al.*'s findings, it can be calculated that at the end of the eight-year CO₂ enrichment experiment there was a CO₂-induced increase in light-saturated net photosynthesis of approximately 115% in the trees' Sun-exposed needles and about 55% in their shaded needles. It can likewise be calculated there was an approximate 20% decrease in the mean dark respiration rate of the trees' Sun-exposed needles and about 40% in their shaded needles.

The nine Czech scientists conclude, "the positive effect of EC on net CO₂ assimilation rates, as we observed in juvenile Norway spruce trees in the present study, was also shown in other long-term studies on conifers," citing Maier *et al.* (2008), Kosvancova *et al.* (2009), Crous *et al.* (2008), and Logan *et al.* (2009). In addition, "it appears that forest trees, including conifers, suppress respiration rates under long-term CO₂ enrichment," citing Zhou *et al.* (2007) and Gonzalez-Meler *et al.* (2009). Thus they conclude, "the observed stimulation of light-saturated net photosynthesis simultaneously with suppressed dark respiration under EC may lead to higher biomass accumulation," as Runion *et al.* (2006) had observed earlier and reported for longleaf pine trees.

The results of the experiments described in this section suggest coniferous trees may exhibit reductions in respiration both above and below the soil surface in a high-CO₂ world of the future.

References

- Amthor, J.S. 1994. Scaling CO₂ photosynthesis relationships from the leaf to the canopy. *Photosynthesis Research* **39**: 321–350.
- BassiriRad, H., Griffin, K.L., Reynolds, J.F., and Strain, B.R. 1997. Changes in root NH₄⁺ and NO₃⁻ absorption rates of loblolly and ponderosa pine in response to CO₂ enrichment. *Plant and Soil* **190**: 1–9.
- Bronson, D.R. and Gower, S.T. 2010. Ecosystem warming does not affect photosynthesis or aboveground autotrophic respiration for boreal black spruce. *Tree Physiology* **30**: 441–449.
- Callaway, R.M., DeLucia, E.H., Thomas, E.M., and Schlesinger, W.H. 1994. Compensatory responses of CO₂ exchange and biomass allocation and their effects on the relative growth rate of ponderosa pine in different CO₂ and temperature regimes. *Oecologia* **98**: 159–166.
- Cotrufo, M.F., Ineson, P., and Scott, A. 1998. Elevated CO₂ reduces the nitrogen concentration of plant tissues. *Global Change Biology* **4**: 43–54.
- Crookshanks, M., Taylor, G., and Broadmeadow, M. 1998. Elevated CO₂ and tree root growth: contrasting responses in *Fraxinus excelsior*, *Quercus petraea* and *Pinus sylvestris*. *New Phytologist* **138**: 241–250.
- Crous, K.Y., Walters, M.B., and Ellsworth, D.S. 2008. Elevated CO₂ concentration affects leaf photosynthesis-nitrogen relationships in *Pinus taeda* over nine years in FACE. *Tree Physiology* **28**: 607–614.
- Finzi, A.C., DeLucia, E.H., Hamilton, J.G., Richter, D.D., and Schlesinger, W.H. 2002. The nitrogen budget of a pine forest under free air CO₂ enrichment. *Oecologia* **132**: 567–578.
- George, K., Norby, R.J., Hamilton, J.G., and DeLucia, E.H. 2003. Fine-root respiration in a loblolly pine and sweetgum forest growing in elevated CO₂. *New Phytologist* **160**: 511–522.
- Gonzalez-Meler, M.A., Blanc-Betes, E., Flower, C.E., Ward, J.K., and Gomez-Casanovas, N. 2009. Plastic and adaptive responses of plant respiration to changes in atmospheric CO₂ concentration. *Physiologia Plantarum* **137**: 473–484.
- Goulden, M.L., Wofsy, S.C., and Harden, J.W. 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* **279**: 214–217.
- Hamilton, J.G., Thomas, R.B., and DeLucia, E.H. 2001. Direct and indirect effects of elevated CO₂ on leaf respiration in a forest ecosystem. *Plant, Cell and Environment* **24**: 975–982.
- Hungate, B.A., Dukes, J.S., Shaw, M.R., Luo, Y., and Field, C.B. 2003. Nitrogen and climate change. *Science* **302**: 1512–1513.
- Jach, M.E. and Ceulemans, R. 2000. Short- versus long-term effects of elevated CO₂ on night-time respiration of needles of Scots pine (*Pinus sylvestris* L.). *Photosynthetica* **38**: 57–67.
- Kosvancova, M., Urban, O., Sprtova, M., Hrstka, M., Kalina, J., Tomaskova, I., Spunda, V., and Marek, M.V. 2009. Photosynthetic induction in broadleaved *Fagus sylvatica* and coniferous *Picea abies* cultivated under ambient and elevated CO₂ concentrations. *Plant Science* **177**: 123–130.
- Lhotakova, Z., Urban, O., Dubankova, M., Cvikrova, M., Tomaskova, I., Kubinova, L., Zvara, K., Marek, M.W., and Albrechtova, J. 2012. The impact of long-term CO₂ enrichment on Sun and shade needles of Norway spruce (*Picea abies*): Photosynthetic performance, needle anatomy and phenolics accumulation. *Plant Science* **188–189**: 60–70.
- Logan, B.A., Combs, A., Myers, K., Kent, R., Stanley, L., and Tissue, D.T. 2009. Seasonal response of photosynthetic

electron transport and energy dissipation in the eighth year of exposure to elevated atmospheric CO₂ (FACE) in *Pinus taeda* (loblolly pine). *Tree Physiology* **29**: 789–797.

Maier, C.A., Palmroth, S., and Ward, E. 2008. Short-term effects of fertilization on photosynthesis and leaf morphology of field-grown loblolly pine following long-term exposure to elevated CO₂ concentration. *Tree Physiology* **28**: 597–606.

Matamala, R. and Schlesinger, W.H. 2000. Effects of elevated atmospheric CO₂ on fine root production and activity in an intact temperate forest ecosystem. *Global Change Biology* **6**: 967–979.

McDowell, N.G., Marshall, J.D., Qi, J., and Mattson, K. 1999. Direct inhibition of maintenance respiration in western hemlock roots exposed to ambient soil carbon dioxide concentrations. *Tree Physiology* **19**: 599–605.

Norby, R.J., Hanson, P.J., O'Neill, E.G., Tschaplinski, T.J., Weltzin, J.F., Hansen, R.A., Cheng, W., Wullschlegel, S.D., Gunderson, C.A., Edwards, N.T., and Johnson, D.W. 2002. Net primary productivity of a CO₂-enriched deciduous forest and the implications for carbon storage. *Ecological Applications* **12**: 1261–1266.

Runion, G.B., Davis, M.A., Pritchard, S.G., Prior, S.A., Mitchell, R.J., Torbert, H.A., Rogers, H.H., and Dute, R.R. 2006. Effects of elevated atmospheric carbon dioxide on biomass and carbon accumulation in a model regenerating longleaf pine community. *Journal of Environmental Quality* **35**: 1478–1486.

Ryan, M.G. 1991. Effects of climate change on plant respiration. *Ecological Applications* **1**: 157–167.

Ryan, M.G. 1995. Foliar maintenance respiration of sub-alpine and boreal trees and shrubs in relation to nitrogen-content. *Plant, Cell and Environment* **18**: 765–772.

Ryan, M.G., Hunt, E.R., McMurtrie, R.E., Agren, G.I., Aber, J.D., Friend, A.D., Rastetter, E.B., Pulliam, W.M., Raison, R.J., and Linder, S. 1996. Comparing models of ecosystem function for temperate conifer forests. In: Greymeyer, A.I., Hall, D.O., Agren, G.I., and Melillo, J.M. (Eds.) *Global Change: Effects on Coniferous Forests and Grasslands*. John Wiley, New York, New York, USA, pp. 313–361.

VEMAP Members. 1995. Vegetation Ecosystem Modeling and Analysis Project: Comparing biogeography and biogeochemistry models in a continental-scale of terrestrial ecosystem response to climate change and CO₂ doubling. *Global Biogeochemical Cycles* **9**: 407–437.

Zhou, Y.M., Han, S.J., Zhang, H.S., Xin, L.H., and Zheng, J.Q. 2007. Response of needle dark respiration of *Pinus koraiensis* and *Pinus sylvestris* to elevated CO₂ concentrations for four growing seasons' exposure. *Science in China Series D—Earth Sciences* **50**: 613–619.

2.22.2.2 Deciduous Trees

- Several experiments conducted on deciduous trees indicate there are both increases and decreases in respiration rates in response to atmospheric CO₂ enrichment, as well as cases of no change in respiration. More data are needed before any general conclusions may be drawn.

Wang and Curtis (2001) grew cuttings of two male and two female trembling aspen trees for about five months on soils containing low and high nitrogen contents in open-top chambers maintained at atmospheric CO₂ concentrations of 380 and 765 ppm. They found gender had little effect on dark respiration rates, but elevated CO₂ increased them, by 6% and 32% in the low and high soil nitrogen treatments, respectively. On the other hand, Karnosky *et al.* (1999) grew both O₃-sensitive and O₃-tolerant aspen clones for one full year in free-air CO₂-enrichment (FACE) plots maintained at atmospheric CO₂ concentrations of 360 and 560 ppm, finding the extra CO₂ decreased dark respiration rates by 24%.

Gielen *et al.* (2003) measured stem respiration rates of white, black, and robusta poplar trees in a high-density forest plantation in the third year of a FACE experiment in which the CO₂ concentration of the air surrounding the trees was increased to a value of approximately 550 ppm. They write, “stem respiration rates were not affected by the FACE treatment,” and “FACE did not influence the relationships between respiration rate and both stem temperature and relative growth rate.” In addition, they found “no effect of the FACE treatment on R_m [maintenance respiration, which is related to the sustaining of existing cells] and R_g [growth respiration, which is related to the synthesis of new tissues].”

Hamilton *et al.* (2001) studied respiratory responses of sweetgum trees growing in the understory of a loblolly pine plantation (but occasionally reaching the top of the canopy) to an extra 200 ppm of CO₂ in a FACE study conducted in North Carolina (USA). They determined the modest increase in the air's CO₂ concentration did not appear to alter maintenance respiration to any significant degree, but it reduced dark respiration by an average of 10% and growth respiration of leaves at the top of the canopy by nearly 40%.

References

Gielen, B., Scarascia-Mugnozza, G., and Ceulemans, R.

2003. Stem respiration of *Populus* species in the third year of free-air CO₂ enrichment. *Physiologia Plantarum* **117**: 500–507.

Hamilton, J.G., Thomas, R.B., and DeLucia, E.H. 2001. Direct and indirect effects of elevated CO₂ on leaf respiration in a forest ecosystem. *Plant, Cell and Environment* **24**: 975–982.

Karnosky, D.F., Mankovska, B., Percy, K., Dickson, R.E., Podila, G.K., Sober, J., Noormets, A., Hendrey, G., Coleman, M.D., Kubiske, M., Pregitzer, K.S., and Isebrands, J.G. 1999. Effects of tropospheric O₃ on trembling aspen and interaction with CO₂: results from an O₃-gradient and a FACE experiment. *Water, Air, and Soil Pollution* **116**: 311–322.

Wang, X. and Curtis, P.S. 2001. Gender-specific responses of *Populus tremuloides* to atmospheric CO₂ enrichment. *New Phytologist* **150**: 675–684.

2.22.2.3 Multiple Tree Studies

- Experimental results are contradictory, suggesting atmospheric CO₂ enrichment may either increase, decrease, or have little effect on woody-plant respiration.

Amthor (2000) measured dark respiration rates of intact leaves of nine tree species growing naturally in an American deciduous forest. Within a specially designed leaf chamber, the CO₂ concentration surrounding individual leaves was stabilized at 400 ppm for 15 minutes, and their respiration rates were measured for 30 minutes, after which the CO₂ concentration in the leaf chamber was raised to 800 ppm for 15 minutes and respiration data were again recorded for the same leaves. This revealed elevated CO₂ had little effect on leaf dark respiration rates. The extra 400 ppm of CO₂ within the measurement cuvette decreased the median respiration rate by only 1.5% across the nine tree species; this observation led Amthor to state the “rising atmospheric CO₂ concentration has only a small direct effect on tree leaf respiration in deciduous forests.” He calculated that effect could be “more than eliminated by a 0.22°C temperature increase.” He thus concludes, “future direct effects of increasing CO₂ in combination with warming could stimulate tree leaf respiration in their sum,” and this consequence “would translate into only slight, if any, effects on the carbon balance of temperate deciduous forests in a future atmosphere containing as much as [800 ppm] CO₂.”

Amthor’s conclusion is debatable, however, because it is based on extrapolation of the short-term respiratory responses of individual leaves exposed to elevated CO₂ for only an hour or two, to that of entire trees, many of which will experience rising CO₂ levels for a century or more during their lifetimes. Trees are long-lived organisms that should not be expected to reveal the nature of their long-term responses to elevated atmospheric CO₂ concentrations on as short a time scale as 15 minutes. Their respiratory responses may change significantly with the passage of time as they acclimate and optimize their physiology and growth patterns to the gradually rising CO₂ content of Earth’s atmosphere, as evidenced by the findings of two other studies.

In the first study, Wang and Curtis (2002) conducted a meta-analysis of the results of 45 area-based dark respiration (R_{da}) and 44 mass-based dark respiration (R_{dm}) assessments of the effects of an approximate doubling of the air’s CO₂ concentration on 33 species of plants (both herbaceous and woody) derived from 37 scientific publications. The mean leaf R_{da} of the woody plants they analyzed was unaffected by elevated CO₂. There was, however, an effect on mean leaf R_{dm}, and it was determined to be time-dependent. The woody plants exposed to elevated CO₂ for less than 100 days, the reviewing scientists write, “showed significantly less of a reduction in leaf R_{dm} due to CO₂ enrichment (-12%) than did plants exposed for longer periods (-35%, *P* < 0.01).” Hence, for conditions of continuous long-term atmospheric CO₂ enrichment, the results of Wang and Curtis’s analysis suggest woody plants may experience an approximate 35% decrease in leaf R_{dm}.

In the second study, Drake *et al.* (1999) also conducted a comprehensive analysis of the peer-reviewed scientific literature to determine the effects of elevated atmospheric CO₂ concentrations on plant respiration rates. They found atmospheric CO₂ enrichment typically decreased respiration rates in mature foliage, stems, and roots of CO₂-enriched plants relative to rates measured in plants grown in ambient air. When normalized on a biomass basis, they determined a doubling of the atmosphere’s CO₂ concentration likely would reduce plant respiration rates by an average of 18%. To determine the potential effects of this phenomenon on annual global carbon cycling, which the 12 researchers say “will enhance the quantity of carbon stored by forests,” they put a 15% CO₂-induced respiration reduction into a carbon sequestration model, finding an additional 6 to 7 Gt of carbon would remain seques-

Plant Characteristics

tered within the terrestrial biosphere each year, substantially strengthening the terrestrial carbon sink.

Davey *et al.* (2004) reached a different conclusion, noting, “Averaged across many previous investigations, doubling the CO₂ concentration has frequently been reported to cause an instantaneous reduction of leaf dark respiration measured as CO₂ efflux.” But they point out “no known mechanism accounts for this effect, and four recent studies [Amthor (2000); Amthor *et al.* (2001); Jahnke (2001); Jahnke and Krewitt (2002)] have shown that the measurement of respiratory CO₂ efflux is prone to experimental artifacts that could account for the reported response.”

Davey *et al.* employed a high-resolution dual channel oxygen analyzer in an open gas exchange system to measure the respiratory O₂ uptake of nine species of plants in response to a short-term increase in atmospheric CO₂ concentration, as well as the response of seven species to long-term elevation of the air’s CO₂ content in four field experiments. They found “[more than] six hundred separate measurements of respiration failed to reveal any decrease in respiratory O₂ uptake with an instantaneous increase in CO₂.” Nor could they detect any response to a fivefold increase in the air’s CO₂ concentration or the total removal of CO₂ from the air. They also note, “this lack of response of respiration to elevated CO₂ was independent of treatment method, developmental stage, beginning or end of night, and the CO₂ concentration at which the plants had been grown.” In the long-term field studies, there was a respiratory response, but it was small (7% on a leaf mass basis), and it was positive, not negative.

The most reasonable conclusion from these contradictory results is that atmospheric CO₂ enrichment induces both increases and decreases in respiration rates, as well as cases of no change in respiration. More data are needed before any general conclusions may be drawn.

References

Amthor, J.S. 2000. Direct effect of elevated CO₂ on nocturnal in situ leaf respiration in nine temperate deciduous tree species is small. *Tree Physiology* **20**: 139–144.

Amthor, J.S., Koch, G.W., Willms, J.R., and Layzell, D.B. 2001. Leaf O₂ uptake in the dark is independent of coincident CO₂ partial pressure. *Journal of Experimental Botany* **52**: 2235–2238.

Davey, P.A., Hunt, S., Hymus, G.J., DeLucia, E.H., Drake,

B.G., Karnosky, D.F., and Long, S.P. 2004. Respiratory oxygen uptake is not decreased by an instantaneous elevation of [CO₂], but is increased with long-term growth in the field at elevated [CO₂]. *Plant Physiology* **134**: 520–527.

Drake, B.G., Azcon-Bieto, J., Berry, J., Bunce, J., Dijkstra, P., Farrar, J., Gifford, R.M., Gonzalez-Meler, M.A., Koch, G., Lambers, H., Siedow, J., and Wulfschleger, S. 1999. Does elevated atmospheric CO₂ inhibit mitochondrial respiration in green plants? *Plant, Cell and Environment* **22**: 649–657.

Jahnke, S. 2001. Atmospheric CO₂ concentration does not directly affect leaf respiration in bean or poplar. *Plant, Cell and Environment* **24**: 1139–1151.

Jahnke, S. and Krewitt, M. 2002. Atmospheric CO₂ concentration may directly affect leaf respiration measurement in tobacco, but not respiration itself. *Plant, Cell and Environment* **25**: 641–651.

Wang, X. and Curtis, P. 2002. A meta-analytical test of elevated CO₂ effects on plant respiration. *Plant Ecology* **161**: 251–261.

2.23 Roots

As indicated in the subsections below, elevated CO₂ nearly always increases root biomass—often even more than shoot biomass—by increasing the size of taproots and the number and size of lateral roots, along with fine-root biomass and a number of other important root properties.

2.23.1 Crops

- As the air’s CO₂ content continues to rise, most crops will develop larger and more extensive root systems that should help them to better cope with periods of reduced soil moisture. This chain of events should make the soil environment more favorable for plant growth and development in a high-CO₂ world of the future.

Hodge and Millard (1998) grew narrowleaf plantain (*Plantago lanceolata*) seedlings for six weeks in controlled environment growth rooms maintained at atmospheric CO₂ concentrations of either 400 or 800 ppm. By the end of this period, the plants in the 800-ppm air exhibited increases in shoot and root dry matter production 159 and 180% greater, respectively, than the corresponding dry matter increases experienced by the plants growing in 400-ppm air, and the amount of plant carbon recovered from the potting medium (sand) was 3.2 times greater in the

elevated-CO₂ treatment. Thus, the belowground growth stimulation provided by atmospheric CO₂ enrichment was greater than that experienced aboveground.

Wechsung *et al.* (1999) grew spring wheat (*Triticum aestivum*) in rows in a FACE study employing atmospheric CO₂ concentrations of 370 and 550 ppm and irrigation treatments that periodically replaced either 50 or 100% of prior potential evapotranspiration, in an effort to determine the effects of elevated CO₂ and water stress on root growth. They found elevated CO₂ increased in-row root dry weight by an average of 22% during the growing season under both the wet and dry irrigation regimes. In addition, during the vegetative growth phase, atmospheric CO₂ enrichment increased inter-row root dry weight by 70%, indicating plants grown in elevated CO₂ developed greater lateral root systems than plants grown at ambient CO₂. During the reproductive growth phase, elevated CO₂ stimulated the branching of lateral roots into inter-row areas, but only when water was limiting to growth. In addition, the CO₂-enriched plants tended to display greater root dry weights at a given depth than did ambiently grown plants.

In a comprehensive review of all prior FACE experiments conducted on agricultural crops, Kimball *et al.* (2002) determined for a 300-ppm increase in atmospheric CO₂ concentration, the root biomass of wheat, ryegrass, and rice experienced an average increase of 70% at ample water and nitrogen, 58% at low nitrogen, and 34% at low water. Clover experienced a 38% increase at ample water and nitrogen and a 32% increase at low nitrogen. Cotton exhibited a 96% increase in root biomass at ample water and nitrogen.

Zhao *et al.* (2000) germinated pea (*Pisum sativum*) seeds and exposed the young plants to various atmospheric CO₂ concentrations in controlled environment chambers to determine whether elevated CO₂ affects root border cells, which are major contributors of root exudates in this and most other agronomic plants. They found elevated CO₂ increased the production of root border cells in pea seedlings. In going from ambient air to air enriched to 3,000 and 6,000 ppm CO₂, border-cell numbers increased by more than 50 and 100%, respectively. Hence, as the CO₂ content of the air continues to rise, peas (and possibly many other crop plants) likely will produce greater numbers of root border cells, which should increase the amounts of root exudations occurring in their rhizospheres, which further suggests associated soil microbial and fungal activities will be stimulated

as a result of the increases in plant-derived carbon inputs these organisms require to meet their energy needs.

Van Ginkel *et al.* (1996) grew perennial ryegrass (*Lolium perenne*) plants from seed in two growth chambers for 71 days under continuous ¹⁴CO₂-labeling of the atmosphere at CO₂ concentrations of 350 and 700 ppm at two soil nitrogen levels. At the conclusion of this part of the experiment, the plants were harvested and their roots dried, pulverized, and mixed with soil in one-liter pots placed in two wind tunnels in an open field, one of which had ambient air of 361 ppm CO₂ flowing through it, and one of which had air of 706 ppm CO₂ flowing through it. Several of the containers were then seeded with more *Lolium perenne*, others were similarly seeded the following year, and still others were kept bare for two years. At the ends of the first and second years, the different degrees of decomposition of the original plant roots were assessed.

The scientists determined shoot and root growth were enhanced by 13 and 92%, respectively, by the extra CO₂ in the initial 71-day portion of the experiment, again demonstrating the significant benefits often conferred on plant roots by atmospheric CO₂ enrichment. They also found the decomposition of the high-CO₂-grown roots in the high-CO₂ wind tunnel was 19% lower than that of the low-CO₂-grown roots in the low-CO₂ wind tunnel at the end of the first year. Decomposition was 14% lower at the end of the second year in the low-nitrogen-grown plants but equivalent in the high-nitrogen-grown plants. It was also determined the presence of living roots reduced the decomposition rate of dead roots below the dead-root-only decomposition rate observed in the bare soil treatment. Van Ginkel *et al.* conclude, “the combination of higher root yields at elevated CO₂ combined with a decrease in root decomposition will lead to a longer residence time of C in the soil and probably to a higher C storage.”

References

- Hodge, A. and Millard, P. 1998. Effect of elevated CO₂ on carbon partitioning and exudate release from *Plantago lanceolata* seedlings. *Physiologia Plantarum* **103**: 280–286.
- Kimball, B.A., Kobayashi, K., and Bindi, M. 2002. Responses of agricultural crops to free-air CO₂ enrichment. *Advances in Agronomy* **77**: 293–368.
- Van Ginkel, J.H., Gorissen, A., and van Veen, J.A. 1996. Long-term decomposition of grass roots as affected by

elevated atmospheric carbon dioxide. *Journal of Environmental Quality* 25: 1122–1128.

Wechsung, G., Wechsung, F., Wall, G.W., Adamsen, F.J., Kimball, B.A., Pinter Jr., P.J., LaMorte, R.L., Garcia, R.L., and Kartschall, T. 1999. The effects of free-air CO₂ enrichment and soil water availability on spatial and seasonal patterns of wheat root growth. *Global Change Biology* 5: 519–529.

Zhao, X., Misaghi, I.J., and Hawes, M.C. 2000. Stimulation of border cell production in response to increased carbon dioxide levels. *Plant Physiology* 122: 181–188.

2.23.2 Grasses

- Root biomass in grasslands may have increased markedly as the air's CO₂ content rose following the termination of the last glacial period, but even more substantial increases are expected if the air's CO₂ content continues to rise as projected, implying ever-greater grassland root biomass.

Many and varied experiments have addressed how the roots of grasses respond to increases in the air's CO₂ concentration and/or soil temperature. Regarding warming, Fitter *et al.* (1999) studied a site on the Great Dun Fell in the United Kingdom, where they determined root birth and death rates from biweekly minirhizotron video images obtained over one experiment of six months' duration and another of 18 months' duration in an upland grassland, where the soils of half of the treatment replications were artificially maintained 2.8°C above ambient at a depth of 2 cm. This warming increased both root production and root death by approximately equivalent amounts. Therefore, they conclude, "the effect of a warmer climate will be a similar acceleration in both [root] birth and death processes and these will have no direct effect on the soil carbon store."

Regarding atmospheric CO₂ enrichment, Crookshanks *et al.* (1998) sprouted seeds of the small and fast-growing *Arabidopsis thaliana* plant on agar medium in Petri dishes and grew the resulting immature plants in controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 355 or 700 ppm. Visual assessments of root growth were made after emergence of the roots from the seeds, and microscopic investigations of root cell properties were conducted. The scientists found the CO₂-enriched plants directed a greater proportion of their newly produced biomass into root- as opposed to shoot-growth, and the young plants produced longer

primary roots and more and longer lateral roots. These effects were found to be related to the CO₂-induced stimulation of mitotic activity, accelerated cortical cell expansion, and increased cell wall plasticity.

Milchunas *et al.* (2005) conducted a five-year open-top chamber study (ambient CO₂ = 360 ppm, enriched CO₂ = 720 ppm) in semiarid shortgrass steppe grassland at the USDA-ARS Central Plains Experimental Range in north central Colorado (USA), where 88% of the ecosystem's biomass was provided by three codominant species—*Bouteloua gracilis* (H.B.K.) Lag., *Stipa comata* (Trin and Rupr.), and *Pascopyrum smithii* (Rybd.)—and where a subfrutescent shrub (*Artemisia frigida* Willd.) was also abundant. They obtained video-image data on root growth and decay in each treatment-replicate from 18 minirhizotron tubes that acquired video images to a depth of 40 cm four to five times a year. Root biomass data were obtained from two 20-cm-diameter cylinders driven into the ground within each chamber and collected yearly in the autumn.

They found root-length growth was 52% greater in the CO₂-enriched chambers than in the ambient-air chambers, and root-length losses were 37% greater in the elevated-CO₂ air. The difference between the CO₂-induced growth and decay stimulations was largely attributable to the 41% longer lifespan of the CO₂-enriched roots, which resulted in a CO₂-induced root-length pool size increase of 41%. In the upper part of the soil profile, root diameters typically were observed to be larger in the CO₂-enriched chambers, leading to an ultimate CO₂-induced root biomass increase of 59%. The four researchers conclude the "slower turnover of new soil carbon, and increased life span of roots suggest an increased storage of carbon under elevated CO₂."

Ayres *et al.* (2008) report the responses of belowground nematode herbivores to atmospheric CO₂ enrichment to approximately 350 ppm above ambient in experiments conducted on three grassland ecosystems in Colorado and California (USA) and Montpellier, France. They found soil moisture increased in response to elevated CO₂ in all three experiments, citing Hungate *et al.* (1997), Nijs *et al.* (2000), and Morgan *et al.* (2004), and "elevated CO₂ increased root biomass by approximately 3–32% in the first five years of the Coloradoan study (Pendall *et al.*, 2004), by 23% after six years in the Californian study (Rillig *et al.*, 1999), and by 31% after six months in the French study (Dhillon *et al.*, 1996)." With respect to the nematodes, they state, "CO₂ enrichment did not significantly affect the family

richness, diversity, or plant parasitic nematode index of herbivorous nematodes in the Colorado, California, or French study,” noting “in each experiment, neutral effects were the most frequent response to CO₂ enrichment.” The seven researchers conclude, “one consequence of increased root production, without changes in belowground herbivore populations, might be greater plant inputs to soil,” which “may lead to greater soil organic matter pools in grassland ecosystems, potentially enhancing soil carbon sequestration.”

Adair *et al.* (2009) employed mass balance calculations to quantify the effects of biodiversity, atmospheric CO₂ concentration, and soil nitrogen (N) content on the total amount of carbon (C) allocated belowground by plants (total belowground C allocation or TBCA), and ecosystem C storage, in an eight-year experiment that was part of the BioCON study of a periodically burned Minnesota grassland. They found annual TBCA increased in response to all three treatment variables—elevated CO₂, enriched N, and increasing diversity—and it was also “positively related to standing root biomass.” Upon removing the influence of root biomass, however, the effects of N and diversity became neutral or even negative (depending on the year), but “the effect of elevated CO₂ remained positive.” In years with fire, they found “greater litter production in high diversity, elevated CO₂, and enhanced N treatments increased annual ecosystem C loss.” Therefore, under non-fire conditions, elevated CO₂, N, and biodiversity generally would tend to increase ecosystem carbon gain, but if grasslands are frequently burned, they could remain neutral in this regard.

Anderson *et al.* (2010) studied various root responses of a C₃-C₄ grassland community at Temple, Texas (USA) over a CO₂ concentration gradient stretching from 230 to 550 ppm, which they created in two CO₂-gradient above-ground “tunnels” of clear polyethylene film. One of the 60-m-long and 1.5-m-wide chambers had ambient air pumped into one end of it; by the time that air exited the chamber through its other end, its CO₂ concentration was reduced by the photosynthetic activity of the plants within the chamber to a value of approximately 230 ppm. The other chamber had air enriched to a CO₂ concentration of 550 ppm pumped into one end of it; as this air exited out the other end of that chamber, its CO₂ concentration was reduced to a value approximately equivalent to that of the ambient air (~380 ppm). The researchers assessed community ingrowth root biomass along the lengths of the tunnels every two to four months from May 1997 through

November 1999, using two ingrowth cores in each five-meter chamber section, and they calculated root biomass response as the ratio of each measurement date’s result to that prevailing at the start of the experiment in May 1997.

Based on the linear relationship they derived from the 20 ingrowth biomass assessments they conducted, Anderson *et al.* found “a 40% increase in the ingrowth root biomass ratio from 380 to 480 ppm as compared with a 36% increase from 280 to 380 ppm.” When excluding one extremely variable data point and using a power function they fit to the data, “the contrast is even greater: a 50% increase from 380 to 480 ppm vs. a 41% increase from 280 to 380 ppm.” In going from the linear relationship to the power function, the *r*² value of the relationship jumped from 0.10 to 0.50, and *P* dropped from 0.095 to less than 0.001.

The six scientists conclude, “root biomass in grasslands may have changed markedly as atmospheric CO₂ increased since the last glacial period, but ... more substantial changes are ahead if the air’s CO₂ content doubles by the end of this century as predicted.” Those anticipated “changes” should all be positive, implying greater grassland root biomass—and all the good things that phenomenon implies—as the air’s CO₂ content continues to climb.

References

- Adair, E.C., Reich, P.B., Hobbie, S.E., and Knops, J.M.H. 2009. Interactive effects of time, CO₂, N, and diversity on total belowground carbon allocation and ecosystem carbon storage in a grassland community. *Ecosystems* **12**: 1037–1052.
- Anderson, L.J., Derner, J.D., Polley, H.W., Gordon, W.S., Eissenstat, D.M., and Jackson, R.B. 2010. Root responses along a subambient to elevated CO₂ gradient in a C₃-C₄ grassland. *Global Change Biology* **16**: 454–468.
- Ayres, E., Wall, D.H., Simmons, B.L., Field, C.B., Milchunas, D.G., Morgan, J.A., and Roy, J. 2008. Belowground nematode herbivores are resistant to elevated atmospheric CO₂ concentrations in grassland ecosystems. *Soil Biology & Biochemistry* **40**: 978–985.
- Crookshanks, M., Taylor, G., and Dolan, L. 1998. A model system to study the effects of elevated CO₂ on the developmental physiology of roots: the use of *Arabidopsis thaliana*. *Journal of Experimental Botany* **49**: 593–597.
- Dhillion, S.D., Roy, J., and Abrams, M. 1996. Assessing the impact of elevated CO₂ on soil microbial activity in a Mediterranean model ecosystem. *Plant & Soil* **187**: 333–342.

Fitter, A.H., Self, G.K., Brown, T.K., Bogie, D.S., Graves, J.D., Benham, D., and Ineson, P. 1999. Root production and turnover in an upland grassland subjected to artificial soil warming respond to radiation flux and nutrients, not temperature. *Oecologia* **120**: 575–581.

Hungate, B.A., Holland, E.A., Jackson, R.B., Chapin, F.S., Mooney, H.A., and Field, C.B. 1997. The fate of carbon in grasslands under carbon dioxide enrichment. *Nature* **388**: 576–579.

Milchunas, D.G., Morgan, J.A., Mosier, A.R., and LeCain, D.R. 2005. Root dynamics and demography in shortgrass steppe under elevated CO₂, and comments on minirhizotron methodology. *Global Change Biology* **11**: 1837–1855.

Morgan, J.A., Mosier, A.R., Milchunas, D.G., LeCain, D.R., Nelson, J.A., and Parton, W.J. 2004. CO₂ enhances productivity, alters species composition, and reduces digestibility of shortgrass steppe vegetation. *Ecological Applications* **14**: 208–219.

Nijs, I., Roy, J., Salager, J.-L., and Fabreguettes, J. 2000. Elevated CO₂ alters carbon fluxes in early successional Mediterranean ecosystems. *Global Change Biology* **6**: 981–994.

Pendall, E., Mosier, A.R., and Morgan, J.A. 2004. Rhizodeposition stimulated by elevated CO₂ in a semiarid grassland. *New Phytologist* **162**: 447–458.

Rillig, M.C., Field, C.B., and Allen, M.F. 1999. Soil biota responses to long-term atmospheric CO₂ enrichment in two California annual grasslands. *Oecologia* **119**: 572–577.

2.23.3 Trees

The ongoing rise in the air's CO₂ content enables Earth's conifers and deciduous trees to increase the volume of soil from which they access water and nutrients, thus allowing them to more thoroughly explore that enlarged volume of soil and acquire greater amounts of these essential resources needed for growth. Numerous experimental findings indicate possible concurrent increases in air temperature and nitrogen deposition will enable them to become even more robust and productive.

2.23.3.1 Conifers

- The ongoing rise in the air's CO₂ content enables Earth's conifers to increase the volume of soil from which they access water and nutrients, allowing them to more thoroughly explore that enlarged volume of soil and acquire more of these essential resources for growth, the aerial fertilization effect of atmospheric CO₂ enrichment.

Janssens *et al.* (1998) grew three-year-old Scots pine seedlings for six months in open-top chambers maintained at ambient and 700 ppm atmospheric CO₂ concentrations. They found the extra CO₂ increased total root length by 122% and total root dry mass by 135%. In a study that employed close to the same degree of enhancement of the atmosphere's CO₂ content, Pritchard *et al.* (2001a) grew ecosystems representative of regenerating longleaf pine forests of the southeastern USA for 18 months in large soil bins located within open-top chambers. They found the aboveground parts of the seedlings experienced a growth enhancement of only 20%, but the root biomass of the trees was increased by more than three times as much (62%).

Working with FACE technology, Pritchard *et al.* (2001b) studied 14-year-old loblolly pine trees after a year of exposure to an extra 200 ppm of CO₂. They found total root length and root numbers were 16 and 34% greater, respectively, in the CO₂-enriched plots than in the ambient-air plots. In addition, the elevated CO₂ increased the diameter of living and dead roots by 8 and 6%, respectively, and annual root production was 26% greater in the CO₂-enriched plots. For the degree of CO₂ enrichment used in the prior two studies, this latter increase corresponded to a root biomass increase of about 45%.

In an open-top chamber study of a model ecosystem composed of a mixture of spruce and beech seedlings, Wiemken *et al.* (2001) investigated the effects of a 200-ppm increase in the air's CO₂ concentration that prevailed for four years. On nutrient-poor soils, the extra CO₂ led to a 30% increase in fine-root biomass, and on nutrient-rich soils it led to a 75% increase. As before, these numbers corresponded to increases of about 52% and 130%, respectively, for atmospheric CO₂ enhancements on the order of those employed by Janssens *et al.* (1998) and Pritchard *et al.* (2001a).

Wiemken *et al.* also found the extra CO₂ increased the amount of symbiotic fungal biomass associated with the trees' fine roots by 31% on nutrient-poor soils and 100% on nutrient-rich soils, which for the degree of atmospheric CO₂ enrichment used in the studies of Janssens *et al.* (1998) and Pritchard *et al.* (2001a) translate into increases of about 52% and 175%, respectively.

Tingey *et al.* (2005) used minirhizotron tubes to study the effects of atmospheric CO₂ enrichment (to approximately 350 ppm above ambient) on the fine-root architecture of seedlings of Ponderosa pine (*Pinus ponderosa*) growing in open-top chambers at the U.S. Forest Service's Institute of Forest Genetics

near Placerville, California (USA), over a period of four years. They found elevated CO₂ increased both fine root extensity (the degree of soil exploration) and intensity (the extent that roots use explored areas) but had no effect on mycorrhizae. They presume the latter observation to be due to the fact that soil nitrogen was not limiting to growth in their study. More specifically, they report, “extensity increased 1.5- to 2-fold in elevated CO₂ while intensity increased only 20% or less,” noting similar extensity results were obtained over shorter periods of four months to two years by Arnon (1997), Berntson and Bazzaz (1998), DeLucia *et al.* (1997), and Runion *et al.* (1997), and similar intensity results had been obtained by Berntson (1994).

Phillips *et al.* (2006) grew well-watered (via drip irrigation) 1.5-year-old ponderosa pine seedlings for four additional years in open-top chambers maintained at the ambient atmospheric CO₂ concentration and at ambient + 175 ppm and ambient + 300 ppm CO₂, while imposing three levels of soil nitrogen (N) fertilization (0, 10 and 20 g N m⁻² year⁻¹) upon the plants. Every two months throughout this period, they collected video images of the roots that were visible on the surfaces of three minirhizotron tubes installed in each chamber. They learned yearly values of fine-root standing crop, production, and mortality were consistently higher in the elevated CO₂ treatments throughout the study. They also report, “in this same study, Johnson *et al.* (2000) found elevated CO₂ increased fine-root life span,” and because the elevated CO₂ increased fine-root length, the amount of root length that died each year was greater in the CO₂ enriched treatments. Therefore, they write, “the higher rates of mortality in absolute terms for elevated CO₂ are driven by increased standing crop and not reduced life spans.”

The work of Phillips *et al.* came to bear upon the progressive nitrogen limitation (PNL) hypothesis, which posits the benefits of atmospheric CO₂ enrichment must ultimately dwindle away because the productivity of Earth's temperate forests often is limited by insufficient soil nitrogen, as is typically the case in the southeastern United States, where the growth of pine and hardwood forests can remove so much nitrogen from the soils on which the forests grow that it induces what Finzi and Schlesinger (2003) have described as “a state of acute nutrient deficiency that can only be reversed with fertilization.” Phillips *et al.* found, however, the increased fine-root length they observed “explains how additional N was provided to support the increased whole plant growth observed in [their]

elevated CO₂ treatments, and corresponds with the increased extent and intensity of the root system architecture discussed by Tingey *et al.* (2005).” This “mining of soil N,” as they describe it, “can in some cases go on for substantial lengths of time,” and there was “no evidence that PNL occurred during the course of [their] study,” citing Johnson *et al.* (2006).

Pritchard *et al.* (2008) described what they learned from minirhizotrons they employed in work conducted at the Duke Forest FACE facility to characterize the influence of free-air-CO₂-enrichment (ambient + 200 ppm) on fine roots for six years (Autumn 1998 through Autumn 2004) in an 18-year-old loblolly pine (*Pinus taeda*) plantation near Durham, North Carolina (USA). Over six years they observed the extra 200 ppm of CO₂ increased average fine-root standing crop by 23%, in line with the overall stimulation of forest net primary productivity of 18–24% they observed for 1996–2002. They found “the positive effects of CO₂ enrichment on fine root growth persisted six years following minirhizotron tube installation (eight years following initiation of the CO₂ fumigation),” and no hint of any progressive nitrogen limitation of the stimulatory effect of atmospheric CO₂ enrichment in a situation where one might have been expected it. In partial explanation of this important finding, Pritchard *et al.* conclude the distal tips of fine roots are “the primary site for initiation of mycorrhizal partnerships which are critical for resource acquisition and could also influence whether or not forests can sustain higher productivity in a CO₂-enriched world.”

Phillips *et al.* (2009) write, “O₃ stress often decreases carbon allocation to roots, leading to reductions in root biomass and growth,” citing Andersen (2003) and Grantz *et al.* (2006). They add, “reduced carbohydrate stores in roots can lead to increased susceptibility to other stresses even after O₃ exposure ends,” citing Andersen *et al.* (1997), but stating, on the other hand, CO₂ tends to promote just the opposite behavior by promoting fine-root production and the benefits this phenomenon provides, citing Norby *et al.* (2004, 2005). In an experiment designed to determine which of the two trace gases (CO₂ or O₃) has the greater impact on the growth and development of the fine roots of ponderosa pine trees, they grew *Pinus ponderosa* seedlings for three years in one-meter-deep containers filled with reconstructed pine-forest soil within sunlit controlled-environment chambers maintained at mean atmospheric CO₂ concentrations of either 420 or 690 ppm, and at mean O₃ conditions described by daily SUM06 index values of either 0 or 15.7 ppm h

(representing the sum of hourly O₃ concentrations $\geq$ 0.06 ppm). Images of fine roots growing along the upper surfaces of four minirhizotron tubes installed within each soil bin were collected every 28 days by a color video camera.

The researchers found “elevated CO₂ increased both the number of fine roots produced and their life span,” and “increased O₃ did not reduce the effect of elevated CO₂.” Fine root biomass at the end of the study in the CO₂-enriched treatment was consistently higher in each soil horizon and 16% higher in total. In addition, the greater fine-root survivorship in the elevated CO₂ treatment was associated with increasing root depth and increasing fine-root diameter, as also has been observed by Eissenstat *et al.* (2000), Guo *et al.* (2008), and Joslin *et al.* (2006). Averaged over the course of the experiment, they found a slight (3.3%) decrease in soil respiration in the elevated CO₂ treatment, as observed by Tingey *et al.* (2006). Consequently, in the words of the four U.S. Environmental Protection Agency scientists who conducted the work, “elevated O₃ did not result in significant negative impacts on ponderosa pine seedling fine-root survival ... or in countering the increased survivorship caused by elevated CO₂.”

Johansson *et al.* (2009) write, “ectomycorrhizal (ECM) fungi, forming the dominant type of symbiotic association with trees in boreal forests, receive as much as 25% of the total carbon assimilated by plants,” and in return, “the extraradical fungal mycelium is directly involved in mobilization and uptake of nutrients which are, in part, passed on to the host plant.” This important function is performed by the fungal exudation of a variety of low molecular weight organic compounds, polymer degrading enzymes, siderophores, polymeric carbohydrates, and fatty acids, the dominant components of which “play important roles in enhancing mineral weathering, nutrient mobilization and uptake by plants.” They investigated certain aspects of this complex suite of phenomena in seedlings of Scots pine (*Pinus sylvestris*) trees grown in the laboratory in liquid culture for six weeks with either no ECM fungi or one of eight such species associated with their roots, during which period they were exposed to air of either 350 or 700 ppm CO₂, and after which a number of analyses were performed to identify and quantify the variety of exudates produced by the fungi.

Johansson *et al.* observed “a clear impact of elevated CO₂ on exudation of soluble low molecular weight organic compounds,” and these exudates “increased by 120–270%” due to “the increased carbon availability to the plant-fungus system.” This

process was driven by the elevated atmospheric CO₂ concentration that increased net CO₂ assimilation rates by approximately 40% for both ECM and non-mycorrhizal seedlings. It led to a mean increase of 27% in the total biomass production of the seedlings infected with the eight species of ECM fungi, but it led to only a 14% increase in the biomass of the non-infected seedlings. Therefore, the four researchers conclude the phenomena they observed “may contribute to nutritional feedback mechanisms to sustain tree growth when nutrients become limiting,” such as some have hypothesized might occur over time in trees growing on low-fertility soils in CO₂-enriched air. (For much more on this subject, see the Progressive Limitation Hypothesis, Section 3.11, this volume.) The findings of this study, however, as well as those of the study of de Graaff *et al.* (2009)—which was published in the same issue of *Soil Biology & Biochemistry*—clearly indicate Earth’s plants should be well-equipped to deal with this hypothetical and now largely discredited roadblock to higher plant productivity in a CO₂-enriched world of the future.

The results described above add to the growing body of evidence suggesting the ongoing rise in the atmosphere’s CO₂ concentration will enable conifers to continue to increase the volume of soil from which they can access water and nutrients, enabling them to more thoroughly explore that enlarged volume of soil. Both of these responses should allow them to acquire more of these essential resources and thereby realize the enhanced potential for growth that is provided them by the aerial fertilization effect of atmospheric CO₂ enrichment. The ongoing rise in the air’s CO₂ content thus bodes well for the growth of the planet’s coniferous forests and for all the creatures that depend upon them for food and shelter, as well as for the ability of the trees to provide lumber for mankind and to sequester carbon while doing so. These consequences have great virtue in and of themselves, and the latter one provides a powerful negative feedback or brake on CO₂-induced global warming.

References

- Andersen, C.P. 2003. Source-sink balance and carbon allocation below ground in plants exposed to ozone. *New Phytologist* **157**: 213–228.
- Andersen, C.P., Wilson, R., Plocher, M., and Hogsett, W.E. 1997. Carry-over effects of O₃ on root growth and carbohydrate concentration of ponderosa pine seedlings. *Tree Physiology* **17**: 805–811.
- Arnone, J.A. 1997. Temporal responses of community fine

Climate Change Reconsidered II: Biological Impacts

- root populations to long-term elevated atmospheric CO₂ and soil nutrient patches in model tropical ecosystems. *Acta Oecologia* **18**: 367–376.
- Berntson, G.M. 1994. Modeling root architecture: are there tradeoffs between efficiency and potential of resource acquisition? *New Phytologist* **127**: 483–493.
- Berntson, G.M. and Bazzaz, F.A. 1998. Regenerating temperate forest mesocosms in elevated CO₂: belowground growth and nitrogen cycling. *Oecologia* **113**: 115–125.
- De Graaff, M.-A., Van Kessel, C., and Six, J. 2009. Rhizodeposition-induced decomposition increases N availability to wild and cultivated wheat genotypes under elevated CO₂. *Soil Biology & Biochemistry* **41**: 1094–1103.
- DeLucia, E.H., Callaway, R.M., Thomas, E.M., and Schlesinger, W.H. 1997. Mechanisms of phosphorus acquisition for ponderosa pine seedlings under high CO₂ and temperature. *Annals of Botany* **79**: 111–120.
- Eissenstat, D.M., Wells, C.E., Yanai, R.D., and Whitbeck, J.L. 2000. Building roots in a changing environment: Implications for root longevity. *New Phytologist* **147**: 33–42.
- Finzi, A.C. and Schlesinger, W.H. 2003. Soil-nitrogen cycling in a pine forest exposed to 5 years of elevated carbon dioxide. *Ecosystems* **6**: 444–456.
- Grantz, D.A., Gunn, S., and Vu, H.-B. 2006. O₃ impacts on plant development: a meta-analysis of root/shoot allocation and growth. *Plant, Cell and Environment* **29**: 1193–1209.
- Guo, D., Mitchell, R.J., Han, W., Hendricks, J.J., Fahey, T.J., and Hendrick, R.L. 2008. Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. *New Phytologist* **177**: 443–456.
- Janssens, I.A., Crookshanks, M., Taylor, G., and Ceulemans, R. 1998. Elevated atmospheric CO₂ increases fine root production, respiration, rhizosphere respiration and soil CO₂ efflux in Scots pine seedlings. *Global Change Biology* **4**: 871–878.
- Johansson, E.M., Fransson, P.M.A., Finlay, R.D., and van Hees, P.A.W. 2009. Quantitative analysis of soluble exudates produced by ectomycorrhizal roots as a response to ambient and elevated CO₂. *Soil Biology & Biochemistry* **41**: 1111–1116.
- Johnson, D.W., Hoylman, A.M., Ball, J.T., and Walker, R.F. 2006. Ponderosa pine responses to elevated CO₂ and nitrogen fertilization. *Biogeochemistry* **77**: 157–175.
- Johnson, M.G., Phillips, D.L., Tingey, D.T., and Storm, M.J. 2000. Effects of elevated CO₂, N-fertilization, and season on survival of ponderosa pine fine roots. *Canadian Journal of Forest Research* **30**: 220–228.
- Joslin, J.D., Gaudinski, J.B., Torn, M.S., Riley, W.J., and Hanson, P.J. 2006. Fine-root turnover patterns and their relationship to root diameter and soil depth in a ¹⁴C-labeled hardwood forest. *New Phytologist* **172**: 523–535.
- Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, S.J., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., De Angelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarasci-Mugnozza, G.E., Schlesinger, W.H., and Oren, R. 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences USA* **102**: 18,052–18,056.
- Norby, R.J., Ledford, J., Reilly, C.D., Miller, N.E., and O'Neill, E.G. 2004. Fine-root production dominates response of a deciduous forest to atmospheric CO₂ enrichment. *Proceedings of the National Academy of Sciences, USA* **101**: 9689–9693.
- Phillips, D.L., Johnson, M.G., Tingey, D.T., and Storm, M.J. 2009. Elevated CO₂ and O₃ effects on fine-root survivorship in ponderosa pine mesocosms. *Oecologia* **160**: 827–837.
- Phillips, D.L., Johnson, M.G., Tingey, D.T., Storm, M.J., Ball, J.T., and Johnson, D.W. 2006. CO₂ and N-fertilization effects on fine-root length, production, and mortality: a 4-year ponderosa pine study. *Oecologia* **148**: 517–525.
- Pritchard, S.G., Davis, M.A., Mitchell, R.J., Prior, A.S., Boykin, D.L., Rogers, H.H., and Runion, G.B. 2001a. Root dynamics in an artificially constructed regenerating longleaf pine ecosystem are affected by atmospheric CO₂ enrichment. *Environmental and Experimental Botany* **46**: 35–69.
- Pritchard, S.G., Rogers, H.H., Davis, M.A., Van Santen, E., Prior, S.A., and Schlesinger, W.H. 2001b. The influence of elevated atmospheric CO₂ on fine root dynamics in an intact temperate forest. *Global Change Biology* **7**: 829–837.
- Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., Finzi, A.C., Jackson, R.B., Matamala, R., Rogers, H.H., and Oren, R. 2008. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO₂-enrichment: a six-year-minirhizotron study. *Global Change Biology* **14**: 588–602.
- Runion, G.B., Mitchell, R.J., Rogers, H.H., Prior, S.A., and Counts, T.K. 1997. Effects of nitrogen and water limitation and elevated atmospheric CO₂ on ectomycorrhiza of longleaf pine. *New Phytologist* **137**: 681–689.
- Tingey, D.T., Johnson, M.G., Lee, E.H., Wise, C., Waschmann, R., Olszyk, D.M., Watrud, L.S., and Donegan, K.K. 2006. Effects of elevated CO₂ and O₃ on soil respiration under ponderosa pine. *Soil Biology & Biochemistry* **38**: 1764–1778.

Tingey, D.T., Johnson, M.G., and Phillips, D.L. 2005. Independent and contrasting effects of elevated CO₂ and N-fertilization on root architecture in *Pinus ponderosa*. *Trees* **19**: 43–50.

Wiemken, V., Ineichen, K., and Boller, T. 2001. Development of ectomycorrhizas in model beech-spruce ecosystems on siliceous and calcareous soil: a 4-year experiment with atmospheric CO₂ enrichment and nitrogen fertilization. *Plant and Soil* **234**: 99–108.

2.23.3.2 Deciduous

- Experimental findings indicate the ongoing rise in the air's CO₂ content, together with possible concurrent increases in air temperature and nitrogen deposition, will make Earth's deciduous woody plants increasingly robust and productive.

Although life-sustaining photosynthesis occurs aboveground in the presence of light, what happens in the darkness beneath the surface of the soil is equally important to the welfare of Earth's higher plants and the many benefits they provide for the rest of the biosphere. This section highlights the findings of some of the scientific literature germane to this subject, focusing on root responses of deciduous trees to atmospheric CO₂ enrichment.

Berntsen and Bazzaz (1998) removed intact chunks of soil from the Hardwood-White Pine-Hemlock forest region of New England and placed them in plastic containers within controlled environment glasshouses maintained at either 375 or 700 ppm CO₂ for two years to study the effects of elevated CO₂ on the regeneration of plants from seeds and rhizomes in the soil. At the conclusion of the study, total mesocosm plant biomass (more than 95% of which was supplied by yellow and white birch tree seedlings) was 31% higher in the elevated CO₂ treatment than in ambient air, with a mean enhancement of 23% aboveground and 62% belowground. The extra CO₂ also increased the mycorrhizal colonization of root tips by 45% in white birch and 71% in yellow birch, and the CO₂-enriched yellow birch seedlings exhibited 322% greater root length and 305% more root surface area than did the yellow birch seedlings growing in ambient air.

Kubiske *et al.* (1998) grew cuttings of four quaking aspen genotypes in open-top chambers for five months at atmospheric CO₂ concentrations of either 380 or 720 ppm and low or high soil nitrogen concentrations. The cuttings grown in elevated CO₂ displayed no discernible increases in aboveground

growth. However, the extra CO₂ significantly increased fine-root length and root turnover rates at high soil nitrogen by increasing fine-root production, which would be expected to produce benefits, not the least of which would be a larger belowground water- and nutrient-gathering system, that would eventually lead to enhanced aboveground growth as well. The many positive aboveground growth responses of quaking aspen trees to atmospheric CO₂ enrichment are documented in Appendices 2 and 3 of this volume (see *Populus tremuloides* Michx.).

Expanding on this study, Pregitzer *et al.* (2000) grew six quaking aspen genotypes for 2.5 growing seasons in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm with both adequate and inadequate supplies of soil nitrogen. The trees exposed to elevated CO₂ developed thicker and longer roots than the trees growing in ambient air, and the fine-root biomass of the CO₂-enriched trees was enhanced by 17% in the nitrogen-poor soils and by 65% in the nitrogen-rich soils.

Another study of quaking aspen, conducted by King *et al.* (2001), demonstrates trees exposed to an atmospheric CO₂ concentration 560 ppm in a FACE experiment produced 133% more fine-root biomass than trees grown in ambient air of 360 ppm, which roughly equates to 233% more fine-root biomass for the degree of CO₂ enrichment employed in the prior study of Pregitzer *et al.* where the CO₂ concentration was 700 ppm. When simultaneously exposed to air of 1.5 times the normal ozone concentration, the degree of fine-root biomass stimulation produced by the extra CO₂ was still as great as 66%, or roughly 115% when extrapolated to the greater CO₂ enrichment employed by Pregitzer *et al.*

King *et al.* (1999) grew four clones at two temperature regimes (separated by 5°C) and two levels of soil nitrogen (N) availability (high and low) for 98 days, measuring photosynthesis, growth, biomass allocation, and root production and mortality. They found the higher of the two temperature regimes increased rates of photosynthesis by 65% and rates of whole-plant growth by 37%, simultaneously enhancing root production and turnover. They conclude, “trembling aspen has the potential for substantially greater growth and root turnover under conditions of warmer soil at sites of both high and low N-availability” and “an immediate consequence of this will be greater inputs of C and nutrients to forest soils.”

These several findings pertaining to quaking aspen trees indicate increases in atmospheric CO₂ concentration, air temperature, and soil nitrogen

content all enhance the trees' belowground growth, which positively affects their aboveground growth.

Regarding other deciduous trees, Gleadow *et al.* (1998) grew eucalyptus seedlings for six months in glasshouses maintained at atmospheric CO₂ concentrations of either 400 or 800 ppm, fertilizing them twice daily with low or high nitrogen solutions. The elevated CO₂ increased total plant biomass by 98 and 134% relative to plants grown at ambient CO₂ in the high and low nitrogen treatments, respectively. In addition, in the low nitrogen treatment, elevated CO₂ stimulated greater root growth, as indicated by a 33% higher root:shoot ratio.

Day *et al.* (1996) studied the effects of elevated CO₂ on fine-root production in open-top chambers erected over a regenerating oak-palmetto scrub ecosystem in Florida (USA). They found a 350-ppm increase in the atmosphere's CO₂ concentration increased fine-root length densities by 63% while enhancing the distribution of fine roots at the soil surface (0–12 cm) and at a depth of 50–60 cm. These findings suggest the ongoing rise in the atmosphere's CO₂ concentration likely will increase the distribution of fine roots near the soil surface, where the greatest concentrations of nutrients are located, and at a depth that coincides with the upper level of the site's water table, both of which should increase the trees' ability to acquire the nutrients and water they will need to support CO₂-enhanced biomass production in the future.

Uselman *et al.* (2000) grew seedlings of the nitrogen-fixing black locust tree for 100 days in controlled environments maintained at atmospheric CO₂ concentrations of 350 and 700 ppm and air temperatures of 26°C (ambient) and 30°C, with either some or no additional nitrogen fertilization. The extra CO₂ increased total seedling biomass by 14%, the elevated temperature increased it by 55%, and nitrogen fertilization increased it by 157%. Root exudation showed a similar pattern. Plants grown in elevated CO₂ exuded 20% more organic carbon compounds than plants grown in ambient air, and elevated temperature and fertilization increased root exudation by 71 and 55%, respectively. Hence, as the air's CO₂ content continues to rise, black locust trees likely will exhibit enhanced rates of biomass production and exudation of dissolved organic compounds from their roots. Moreover, if air temperature also rises, even by as much as 4°C, its positive effect on biomass production and root exudation likely will be even greater than that resulting from the increasing atmospheric CO₂ concentration. The same would appear to hold true for

anthropogenic nitrogen deposition, reinforcing what was learned about the impacts of these three environmental factors on the growth of quaking aspen trees.

McDowell *et al.* (1999) grew five-month-old seedlings of western hemlock in root boxes, subjecting them for several hours to various root-space CO₂ concentrations, ranging from approximately 90 to 7,000 ppm, to determine the effect of soil CO₂ concentration on growth, maintenance, and total root respiration. Although they could detect no effect of atmospheric CO₂ enrichment on growth respiration, it significantly affected maintenance and total respiration rates. At a soil CO₂ concentration of 1,585 ppm, for example, total and maintenance respiration rates were 55 and 60% lower, respectively, than they were at a soil CO₂ concentration of 395 ppm. The impact of elevated soil CO₂ on maintenance respiration (which comprised 85% of the total respiration in this study) was so strong it exhibited an exponential decline of about 37% for every doubling of the soil CO₂ concentration.

These several experimental findings allow confidence in the conclusion that the ongoing rise in the air's CO₂ content, together with possible concurrent increases in air temperature and nitrogen deposition, likely will make Earth's woody plants increasingly robust and productive.

References

- Berntson, G.M. and Bazzaz, F.A. 1998. Regenerating temperate forest mesocosms in elevated CO₂: belowground growth and nitrogen cycling. *Oecologia* **113**: 115–125.
- Day, F.P., Weber, E.P., Hinkle, C.R., and Drake, B.G. 1996. Effects of elevated atmospheric CO₂ on fine root length and distribution in an oak-palmetto scrub ecosystem in central Florida. *Global Change Biology* **2**: 143–148.
- Gleadow, R.M., Foley, W.J., and Woodrow, I.E. 1998. Enhanced CO₂ alters the relationship between photosynthesis and defense in cyanogenic *Eucalyptus cladocalyx* F. Muell. *Plant, Cell and Environment* **21**: 12–22.
- King, J.S., Pregitzer, K.S., and Zak, D.R. 1999. Clonal variation in above- and below-ground growth responses of *Populus tremuloides* Michaux: Influence of soil warming and nutrient availability. *Plant and Soil* **217**: 119–130.
- King, J.S., Pregitzer, K.S., Zak, D.R., Sober, J., Isebrands, J.G., Dickson, R.E., Hendrey, G.R., and Karnosky, D.F. 2001. Fine-root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO₂ and tropospheric O₃. *Oecologia* **128**: 237–250.

Kubiske, M.E., Pregitzer, K.S., Zak, D.R., and Mikan, C.J. 1998. Growth and C allocation of *Populus tremuloides* genotypes in response to atmospheric CO₂ and soil N availability. *New Phytologist* **140**: 251–260.

McDowell, N.G., Marshall, J.D., Qi, J., and Mattson, K. 1999. Direct inhibition of maintenance respiration in western hemlock roots exposed to ambient soil carbon dioxide concentrations. *Tree Physiology* **19**: 599–605.

Pregitzer, K.S., Zak, D.R., Maziasz, J., DeForest, J., Curtis, P.S., and Lussenhop, J. 2000. Interactive effects of atmospheric CO₂ and soil-N availability on fine roots of *Populus tremuloides*. *Ecological Applications* **10**: 18–33.

Uselman, S.M., Qualls, R.G., and Thomas, R.B. 2000. Effects of increased atmospheric CO₂, temperature, and soil N availability on root exudation of dissolved organic carbon by a N-fixing tree (*Robinia pseudoacacia* L.). *Plant and Soil* **222**: 191–202.

2.23.4 Other

In reviewing the scientific literature pertaining to atmospheric CO₂ enrichment effects on belowground plant growth and development, Weihong *et al.* (2000) briefly summarize what was known about this subject at the turn of the century. They report atmospheric CO₂ enrichment typically enhances the growth rates of roots, especially those of fine roots, and CO₂-induced increases in root production eventually lead to increased carbon inputs to soils, due to enhanced root turnover and exudation of various organic carbon compounds, which can lead to greater soil carbon sequestration. In addition, they note, increased soil carbon inputs stimulate the growth and activities of soil microorganisms that utilize plant-derived carbon as their primary energy source, and they report subsequently enhanced activities of fungal and bacterial plant symbionts often lead to increased plant nutrient acquisition.

In a more narrowly focused study, Gouk *et al.* (1999) grew specimens of an orchid plantlet, Mokara Yellow, in plastic bags flushed with 350 and 10,000 ppm CO₂ for three months, in order to study the effects of elevated CO₂ on this epiphytic CAM species. The super-elevated CO₂ of their experiment enhanced the total dry weight of the orchid plantlets more than twofold, while increasing the growth of existing roots and stimulating the induction of new roots from internodes located on the orchid stems. Total chlorophyll content also was increased in CO₂-enriched air, by 64 percent in young leaves and by 118 percent in young roots. This phenomenon permit-

ted greater light harvesting during photosynthesis and likely led to the tissue starch contents of the CO₂-enriched plantlets rising nearly 20-fold higher than those of the control-plantlets. In spite of this large CO₂-induced accumulation of starch, however, no damage or disruption of chloroplasts was evident in the leaves and roots of the CO₂-enriched plants.

A final question that has periodically intrigued researchers is whether plants take up carbon through their roots in addition to through their leaves. Although a definitive answer remains elusive, Idso (1989) described various aspects of the issue a quarter-century ago:

“Although several investigators have claimed that plants should receive little direct benefit from dissolved CO₂ (Stolwijk *et al.*, 1957; Skok *et al.*, 1962; Splittstoesser, 1966), a number of experiments have produced significant increases in root growth (Erickson, 1946; Leonard and Pinckard, 1946; Geisler, 1963; Yorgalevitch and Janes, 1988), as well as yield itself (Kursanov *et al.*, 1951; Grinfeld, 1954; Nakayama and Bucks, 1980; Baron and Gorski, 1986), with CO₂-enriched irrigation water. Early on, Misra (1951) suggested that this beneficent effect may be related to CO₂-induced changes in soil nutrient availability; and this hypothesis may well be correct. Arteca *et al.* (1979), for example, have observed K, Ca and Mg to be better absorbed by potato roots when the concentration of CO₂ in the soil solution is increased; while Mauney and Hendrix (1988) found Zn and Mn to be better absorbed by cotton under such conditions, and Yurgalevitch and Janes (1988) found an enhancement of the absorption of Rb by tomato roots. In all cases, large increases in either total plant growth or yield accompanied the enhanced uptake of nutrients. Consequently, as it has been suggested that CO₂ concentration plays a major role in determining the porosity, plasticity and charge of cell membranes (Jackson and Coleman, 1959; Mitz, 1979), which could thereby alter ion uptake and organic acid production (Yorgalevitch and Janes, 1988), it is possible that some such suite of mechanisms may well be responsible for the plant productivity increases often observed to result from enhanced concentrations of CO₂ in the soil solution.”

References

Arteca, R.N., Pooviah, B.W., and Smith, O.E. 1979. Changes in carbon fixation, tuberization, and growth induced by CO₂ applications to the root zones of potato plants. *Science* **205**: 1279–1280.

Climate Change Reconsidered II: Biological Impacts

Baron, J.J. and Gorski, S.F. 1986. Response of eggplant to a root environment enriched with CO₂. *HortScience* **21**: 495–498.

Erickson, L.C. 1946. Growth of tomato roots as influenced by oxygen in the nutrient solution. *American Journal of Botany* **33**: 551–556.

Geisler, G. 1963. Morphogenetic influence of (CO₂ + HCO₃⁻) on roots. *Plant Physiology* **38**: 77–80.

Gouk, S.S., He, J., and Hew, C.S. 1999. Changes in photosynthetic capability and carbohydrate production in an epiphytic CAM orchid plantlet exposed to super-elevated CO₂. *Environmental and Experimental Botany* **41**: 219–230.

Grinfeld, E.G. 1954. On the nutrition of plants with carbon dioxide through the roots. *Dokl. Akad. Nauk SSSR* **94**: 919–922.

Idso, S.B. 1989. *Carbon Dioxide and Global Change: Earth in Transition*. IBR Press, Tempe, AZ.

Jackson, W.A. and Coleman, N.T. 1959. Fixation of carbon dioxide by plant roots through phosphoenolpyruvate carboxylase. *Plant and Soil* **11**: 1–16.

Kursanov, A.L., Kuzin, A.M., and Mamul, Y.V. 1951. On the possibility for assimilation by plants of carbonates taken in with the soil solution. *Dokl. Akad. Nauk SSSR* **79**: 685–687.

Leonard, O.A. and Pinckard, J.A. 1946. Effect of various oxygen and carbon dioxide concentrations on cotton root development. *Plant Physiology* **21**: 18–36.

Mauney, J.R. and Hendrix, D.L. 1988. Responses of glasshouse grown cotton to irrigation with carbon dioxide-saturated water. *Crop Science* **28**: 835–838.

Misra, R.K. 1951. Further studies on the carbon dioxide factor in the air and soil layers near the ground. *Indian Journal of Meteorology and Geophysics* **2**: 284–292.

Mitz, M.A. 1979. CO₂ biodynamics: A new concept of cellular control. *Journal of Theoretical Biology* **80**: 537–551.

Nakayama, F.S. and Bucks, D.A. 1980. Using subsurface trickle system for carbon dioxide enrichment. In Jensen, M.H. and Oebker, N.F. (Eds.) *Proceedings of the 15th Agricultural Plastics Congress*, National Agricultural Plastics Association, Manchester, MO, pp. 13–18.

Skok, J., Chorney, W., and Broecker, W.S. 1962. Uptake of CO₂ by roots of Xanthium plants. *Botanical Gazette* **124**: 118–120.

Splittstoesser, W.E. 1966. Dark CO₂ fixation and its role in the growth of plant tissue. *Plant Physiology* **41**: 755–759.

Stolwijk, J.A.J. and Thimann, K.V. 1957. On the uptake of

carbon dioxide and bicarbonate by roots and its influence on growth. *Plant Physiology* **32**: 513–520.

Weihong, L., Fusuo, Z., and Kezhi, B. 2000. Responses of plant rhizosphere to atmospheric CO₂ enrichment. *Chinese Science Bulletin* **45**: 97–101.

Yorgalevitch, C.M. and Janes, W.H. 1988. Carbon dioxide enrichment of the root zone of tomato seedlings. *Journal of Horticultural Science* **63**: 265–270.

2.24 Rubisco

Rubisco is the primary carboxylating enzyme used by C₃ plants during photosynthesis to incorporate CO₂ into sugars needed for growth and development. Even C₄ and CAM plants, which use PEP-carboxylase as their primary carboxylating enzyme, utilize rubisco during subsequent secondary CO₂ assimilation events. Thus rubisco is universally present in all the planet's vegetation and is, in fact, the most abundant plant enzyme on the face of the Earth, comprising 40 to 50% of total foliage protein and representing an enormous sink for nitrogen and other valuable resources within plants.

However, rubisco is a bifunctional enzyme that also possesses oxygenation activity, and when oxygenation reactions occur, photorespiration is enhanced, resulting in an increased loss of carbon from plant tissues. Thus, CO₂ and O₂ compete for active sites on rubisco in order to drive photosynthesis and photorespiration, respectively. The following subsections explore how these biochemical processes are affected by the rising CO₂ content of the atmosphere, as well as the implications of these changes for the content and/or activity of rubisco.

2.24.1 Agricultural Species

- There is a reduced need for nitrogen investment in leaf rubisco in agricultural crops growing in CO₂-enriched air because under such conditions plants typically reallocate some of their “surplus” nitrogen to other processes essential for optimal growth and development, without compromising enhanced carbon gains via photosynthesis.

Voluminous experimental data demonstrate atmospheric CO₂ enrichment favors the process of carboxylation over that of oxygenation, which thereby increases photosynthetic rates while decreasing photorespiratory rates. Thus the rising CO₂ content of the air invariably leads to greater rates of net

photosynthesis and a more efficient process of carbon fixation, requiring less rubisco to obtain the carbon needed for plant growth and development under CO₂-enriched conditions.

As a consequence, plants grown in elevated CO₂ environments often, but not always (Farage *et al.*, 1998), exhibit a certain degree of photosynthetic acclimation or down-regulation, which is typically characterized by reduced amounts of rubisco (Sims *et al.*, 1998; Theobald *et al.*, 1998) and/or decreases in its activation state (Pritchard *et al.*, 2000; Reid *et al.*, 1998). However, in nearly every reported case of CO₂-induced photosynthetic acclimation, net photosynthetic rates displayed by CO₂-enriched plants have been significantly greater than those exhibited by plants growing at ambient CO₂ concentrations. This section briefly reviews the photosynthetic acclimation of rubisco within agricultural species subjected to elevated CO₂ concentrations.

Sicher and Bunce (1999) grew potato plants at atmospheric CO₂ concentrations of 350, 530, and 700 ppm over a three-year period, documenting 13 and 21% CO₂-induced reductions in rubisco concentrations at 530 and 700 ppm CO₂, respectively. Nevertheless, the rates of photosynthesis in the CO₂-enriched plants were still 28 and 49% greater than those observed in control plants grown in ambient air. Similarly, Maroco *et al.* (1999) report a tripling of the ambient air's CO₂ concentration increased photosynthetic rates in maize (a C₄ plant) by about 15%, in spite of foliar reductions in both rubisco and PEP-carboxylase concentrations. And Theobald *et al.* (1998) grew spring wheat at twice-ambient CO₂ concentrations, discovering the elevated CO₂ reduced the amount of rubisco required to sustain enhanced rates of photosynthesis, which consequently led to a significant increase in plant nitrogen-use efficiency.

Interestingly, when elevated CO₂ induces photosynthetic acclimation, the phenomenon generally does not occur in every leaf of the plant. Osborne *et al.* (1998), for example, grew wheat plants with an additional 200 ppm of CO₂ and reported CO₂-induced reductions in foliar rubisco concentrations occurred in a depth-dependent manner, with the reductions increasing with depth in the canopy. Sims *et al.* (1999) observed similar canopy-depth-dependent reductions in the rubisco content of sunflowers. Thus, because CO₂-induced reductions in rubisco typically occur within only a portion of a plant's total leaf area, most plants still exhibit biomass increases in response to elevated CO₂ exposure in spite of acclimation.

CO₂-induced photosynthetic acclimation also often results from insufficient plant sink strength,

which can lead to carbohydrate accumulation in source leaves and the subsequent triggering of photosynthetic end-product feedback inhibition that reduces foliar rubisco concentrations. Gesch *et al.* (1998), for example, report rice plants—which have a relatively limited potential for developing additional carbon sinks—grown at an atmospheric CO₂ concentration of 700 ppm exhibited increased leaf carbohydrate contents, which likely reduced *rbcS* mRNA levels and ultimately leaf rubisco protein contents.

In another experiment, Gesch *et al.* (2000) took rice plants growing in ambient air and placed them in an atmospheric CO₂ concentration of 175 ppm, which reduced their photosynthesis rates by 45%. After five days of exposure to this sub-ambient CO₂ concentration, however, the plants manifested an up-regulation of rubisco, which stimulated photosynthetic rates by 35%. Thus, plant acclimation responses can involve both increases and decreases in specific enzymes, depending on the nature of the change in atmospheric CO₂ concentration.

These observations demonstrate the reduced need for nitrogen investment in leaf rubisco in plants growing in CO₂-enriched environments. Under such conditions, plants are able to reallocate some of their “surplus” nitrogen to other processes essential to optimal growth and development without compromising enhanced carbon gains via photosynthesis. The end result, as almost always observed in well-run experiments, is increased biomass production in CO₂-enriched air (see Section 1.1.1, this volume).

References

- Farage, P.K., McKee, I.F., and Long, S.P. 1998. Does a low nitrogen supply necessarily lead to acclimation of photosynthesis to elevated CO₂? *Plant Physiology* **118**: 573–580.
- Gesch, R.W., Boote, K.J., Vu, J.C.V., Allen Jr., L.H., and Bowes, G. 1998. Changes in growth CO₂ result in rapid adjustments of ribulose-1,5-bisphosphate carboxylase/oxygenase small subunit gene expression in expanding and mature leaves of rice. *Plant Physiology* **118**: 521–529.
- Gesch, R.W., Vu, J.C.V., Boote, K.J., Allen Jr., L.H., and Bowes, G. 2000. Subambient growth CO₂ leads to increased Rubisco small subunit gene expression in developing rice leaves. *Journal of Plant Physiology* **157**: 235–238.
- Maroco, J.P., Edwards, G.E., and Ku, M.S.B. 1999. Photosynthetic acclimation of maize to growth under elevated levels of carbon dioxide. *Planta* **210**: 115–125.

Osborne, C.P., LaRoche, J., Garcia, R.L., Kimball, B.A., Wall, G.W., Pinter Jr., P.J., LaMorte, R.L., Hendrey, G.R., and Long, S.P. 1998. Does leaf position within a canopy affect acclimation of photosynthesis to elevated CO₂? *Plant Physiology* **117**: 1037–1045.

Pritchard, S.G., Ju, Z., van Santen, E., Qiu, J., Weaver, D.B., Prior, S.A., and Rogers, H.H. 2000. The influence of elevated CO₂ on the activities of antioxidative enzymes in two soybean genotypes. *Australian Journal of Plant Physiology* **27**: 1061–1068.

Reid, C.D., Fiscus, E.L., and Burkey, K.O. 1998. Combined effects of chronic ozone and elevated CO₂ on rubisco activity and leaf components in soybean (*Glycine max*). *Journal of Experimental Botany* **49**: 1999–2011.

Sicher, R.C. and Bunce, J.A. 1999. Photosynthetic enhancement and conductance to water vapor of field-grown *Solanum tuberosum* (L.) in response to CO₂ enrichment. *Photosynthesis Research* **62**: 155–163.

Sims, D.A., Cheng, W., Luo, Y., and Seeman, J.R. 1999. Photosynthetic acclimation to elevated CO₂ in a sunflower canopy. *Journal of Experimental Botany* **50**: 645–653.

Sims, D.A., Luo, Y., and Seeman, J.R. 1998. Comparison of photosynthetic acclimation to elevated CO₂ and limited nitrogen supply in soybean. *Plant, Cell and Environment* **21**: 945–952.

Theobald, J.C., Mitchell, R.A.C., Parry, M.A.J., and Lawlor, D.W. 1998. Estimating the excess investment in ribulose-1,5-bisphosphate carboxylase/oxygenase in leaves of spring wheat grown under elevated CO₂. *Plant Physiology* **118**: 945–955.

2.24.2 Grassland Species

- The reduced need for nitrogen investment in leaf rubisco in grassland plants growing in CO₂-enriched environments enables them to reallocate some of this “surplus” nitrogen to other limiting processes required for optimal growth and development without compromising enhanced carbon gains via photosynthesis.

As is the case with agricultural plants, voluminous experimental data demonstrate atmospheric CO₂ enrichment also favors carboxylation over oxygenation in grassland species, which in turn increases their photosynthetic rates and decreases their photorespiratory rates. That means the rising CO₂ content of the air invariably leads to greater rates of net photosynthesis and a more efficient process of carbon fixation, where once again less rubisco is needed to obtain the carbon required for maximum

plant growth and development under CO₂-enriched conditions.

Thus, plants grown in elevated atmospheric CO₂ environments often, but not always (Ziska *et al.*, 1999), exhibit some degree of photosynthetic acclimation or down-regulation, typically characterized by reduced amounts of rubisco and/or decreases in its activation state. However, in nearly every reported case of CO₂-induced photosynthetic acclimation, net photosynthetic rates displayed by CO₂-enriched plants were still significantly greater than those exhibited by plants growing in ambient air.

Cheng *et al.* (1998), for example, grew the herbaceous plant *Arabidopsis thaliana* at an atmospheric CO₂ concentration of 1,000 ppm for 40 days; they found the elevated CO₂ reduced foliar rubisco contents by 34%. However, the elevated CO₂ enhanced foliar contents of glucose and fructose more than twofold, and starch concentrations were increased more than 3.5-fold. Thus, although elevated CO₂ reduced the amount of rubisco in leaves, photosynthetically derived sugars and starch still accumulated.

Midgley *et al.* (1999) grew four *Leucadendron* species from South Africa in air of twice-ambient CO₂ concentrations, observing a 30% reduction in the activity of rubisco. However, rates of net photosynthesis in the CO₂-enriched plants were still about 40% greater than rates measured in ambiently grown plants. Bryant *et al.* (1998) reported similar results for chalk grassland species exposed to an atmospheric CO₂ concentration of 600 ppm for 14 months. They note elevated CO₂ caused an average reduction of 32% in the rubisco activity of two forbs and one C₃ grass, while still maintaining photosynthetic rates about 28% greater than those observed in ambiently growing plants. Likewise, after growing three grasslands species from the United Kingdom for two full years at 700 ppm CO₂, Davey *et al.* (1999) reported elevated CO₂ reduced rubisco activity by an average of 27% and increased photosynthetic rates from 12 to 74% in a nutrient-dependent manner.

In the illuminating study of Rogers *et al.* (1998), swards of perennial ryegrass grown in air containing an extra 240 ppm of CO₂ did not exhibit any reductions in rubisco content as long as they were supplied with high levels of soil nitrogen. In contrast, at low soil nitrogen contents the CO₂-enriched plants displayed a 25% reduction in rubisco levels prior to mechanical cutting. After cutting, however, which removed a large portion of the plants' leaf area, the CO₂-enriched plants in low nitrogen completely reversed their acclimation response and increased

their levels of rubisco to facilitate greater carbon uptake to repair the damage.

The bottom-line message of these observations is that the reduced need for nitrogen investment in leaf rubisco in plants growing in CO₂-enriched environments enables them to reallocate some of this “surplus” nitrogen to other limiting processes required for optimal growth and development—without compromising enhanced carbon gains via photosynthesis.

References

Bryant, J., Taylor, G., and Frehner, M. 1998. Photosynthetic acclimation to elevated CO₂ is modified by source:sink balance in three component species of chalk grassland swards grown in a free air carbon dioxide enrichment (FACE) experiment. *Plant, Cell and Environment* **21**: 159–168.

Cheng, S.-H., Moore, B.D., and Seemann, J.R. 1998. Effects of short- and long-term elevated CO₂ on the expression of ribulose-1,5-bisphosphate carboxylase/oxygenase genes and carbohydrate accumulation in leaves of *Arabidopsis thaliana* (L.) Heynh. *Plant Physiology* **116**: 715–723.

Davey, P.A., Parsons, A.J., Atkinson, L., Wadge, K., and Long, S.P. 1999. Does photosynthetic acclimation to elevated CO₂ increase photosynthetic nitrogen-use efficiency? A study of three native UK grassland species in open-top chambers. *Functional Ecology* **13**: 21–28.

Midgley, G.F., Wand, S.J.E., and Pammenter, N.W. 1999. Nutrient and genotypic effects on CO₂-responsiveness: photosynthetic regulation in *Leucadendron* species of a nutrient-poor environment. *Journal of Experimental Botany* **50**: 533–542.

Rogers, A., Fischer, B.U., Bryant, J., Frehner, M., Blum, H., Raines, C.A., and Long, S.P. 1998. Acclimation of photosynthesis to elevated CO₂ under low-nitrogen nutrition is affected by the capacity for assimilate utilization. Perennial ryegrass under free-air CO₂ enrichment. *Plant Physiology* **118**: 683–689.

Ziska, L.H., Sicher, R.C. and Bunce, J.A. 1999. The impact of elevated carbon dioxide on the growth and gas exchange of three C₄ species differing in CO₂ leak rates. *Physiologia Plantarum* **105**: 74–80.

2.24.3 Tree Species

- Woody species growing in CO₂-enriched environments have a reduced need for nitrogen investment in rubisco, which enables them to

reallocate some of the “surplus” nitrogen they might possess to other processes required for optimal growth and development without compromising enhanced carbon gains via photosynthesis.

Experimental data typically demonstrate atmospheric CO₂ enrichment favors carboxylation over oxygenation in rubisco, which increases photosynthetic rates while reducing photorespiratory rates. Thus the rising CO₂ content of the air usually leads to greater rates of net photosynthesis and more efficient carbon fixation, such that less rubisco is needed to obtain the carbon required for plant growth and development under CO₂-enriched conditions.

As a consequence, trees grown in elevated CO₂ environments often, but not always (Stylinski *et al.*, 2000; Beerling *et al.*, 1998), exhibit some degree of photosynthetic acclimation or down-regulation, which typically is characterized by reduced amounts of rubisco (Gleadow *et al.*, 1998) and/or decreases in its activation state (Hamerlynck *et al.*, 2002; Kubiske *et al.*, 2002). In nearly every reported case of CO₂-induced photosynthetic acclimation, however, the net photosynthetic rates displayed by CO₂-enriched plants have been significantly greater than those exhibited by plants growing in ambient-air CO₂ concentrations (Murray *et al.*, 2000).

Tjoelker *et al.* (1998), for example, found a 210-ppm increase in the air’s CO₂ content increased the average rate of net photosynthesis in aspen and birch seedlings by 57% even while inducing a 24% reduction in foliar rubisco content. Similarly, Takeuchi *et al.* (2001) report aspen seedlings grown at an atmospheric CO₂ concentration of 560 ppm exhibited photosynthetic rates in upper-canopy leaves 26% greater than those displayed by upper-canopy leaves of control plants grown in ambient air, in spite of a 28% decrease in foliar rubisco concentrations. CO₂-induced reductions in foliar rubisco contents that did not offset CO₂-induced photosynthetic enhancements also have been reported in oak (Blaschke *et al.*, 2001) and pine (Turnbull *et al.*, 1998) trees.

In another manifestation of photosynthetic acclimation, Centritto *et al.* (1999) observe elevated CO₂ reduced the activity of rubisco without negating CO₂-induced increases in photosynthesis, and Centritto and Jarvis (1999) report twice-ambient atmospheric CO₂ concentrations reduced rubisco activity in Sitka spruce needles by 36% while enhancing photosynthetic rates by 62%. Similarly, Turnbull *et al.*, (1998) report pine seedlings grown at 650 ppm CO₂ displayed 40% reductions in rubisco

activity while exhibiting photosynthetic rates 31% greater than those observed in ambiently grown control seedlings. Rey and Jarvis (1998) also documented this phenomenon in young silver birch trees.

These observations demonstrate the reduced need for nitrogen investment in rubisco in woody species growing in CO₂-enriched environments, which enables them to reallocate some of the resultant “surplus” nitrogen they might possess to other processes required for optimal growth and development without compromising enhanced carbon gains via photosynthesis.

References

- Beerling, D.J., McElwain, J.C., and Osborne, C.P. 1998. Stomatal responses of the ‘living fossil’ *Ginkgo biloba* L. to changes in atmospheric CO₂ concentrations. *Journal of Experimental Botany* **49**: 1603–1607.
- Blaschke, L., Schulte, M., Raschi, A., Slee, N., Rennenberg, H., and Polle, A. 2001. Photosynthesis, soluble and structural carbon compounds in two Mediterranean oak species (*Quercus pubescens* and *Q. ilex*) after lifetime growth at naturally elevated CO₂ concentrations. *Plant Biology* **3**: 288–297.
- Centritto, M. and Jarvis, P.G. 1999. Long-term effects of elevated carbon dioxide concentration and provenance on four clones of Sitka spruce (*Picea sitchensis*). II. Photosynthetic capacity and nitrogen use efficiency. *Tree Physiology* **19**: 807–814.
- Centritto, M., Magnani, F., Lee, H.S.J., and Jarvis, P.G. 1999. Interactive effects of elevated [CO₂] and drought on cherry (*Prunus avium*) seedlings. II. Photosynthetic capacity and water relations. *New Phytologist* **141**: 141–153.
- Gleadow, R.M., Foley, W.J., and Woodrow, I.E. 1998. Enhanced CO₂ alters the relationship between photosynthesis and defense in cyanogenic *Eucalyptus cladocalyx* F. Muell. *Plant, Cell and Environment* **21**: 12–22.
- Hamerlynck, E.P., Huxman, T.E., Charlet, T.N., and Smith, S.D. 2002. Effects of elevated CO₂ (FACE) on the functional ecology of the drought-deciduous Mojave Desert shrub, *Lycium andersonii*. *Environmental and Experimental Botany* **48**: 93–106.
- Kubiske, M.E., Zak, D.R., Pregitzer, K.S., and Takeuchi, Y. 2002. Photosynthetic acclimation of overstory *Populus tremuloides* and understory *Acer saccharum* to elevated atmospheric CO₂ concentration: interactions with shade and soil nitrogen. *Tree Physiology* **22**: 321–329.
- Murray, M.B., Smith, R.I., Friend, A., and Jarvis, P.G. 2000. Effect of elevated [CO₂] and varying nutrient application rates on physiology and biomass accumulation of Sitka spruce (*Picea sitchensis*). *Tree Physiology* **20**: 421–434.
- Rey, A. and Jarvis, P.G. 1998. Long-term photosynthetic acclimation to increased atmospheric CO₂ concentration in young birch (*Betula pendula*) trees. *Tree Physiology* **18**: 441–450.
- Stylinski, C.D., Oechel, W.C., Gamon, J.A., Tissue, D.T., Miglietta, F., and Raschi, A. 2000. Effects of lifelong [CO₂] enrichment on carboxylation and light utilization of *Quercus pubescens* Willd. examined with gas exchange, biochemistry and optical techniques. *Plant, Cell and Environment* **23**: 1353–1362.
- Takeuchi, Y., Kubiske, M.E., Isebrands, J.G., Pregitzer, K.S., Hendrey, G., and Karnosky, D.F. 2001. Photosynthesis, light and nitrogen relationships in a young deciduous forest canopy under open-air CO₂ enrichment. *Plant, Cell and Environment* **24**: 1257–1268.
- Tjoelker, M.G., Oleksyn, J., and Reich, P.B. 1998. Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO₂ and temperature. *Tree Physiology* **18**: 715–726.
- Turnbull, M.H., Tissue, D.T., Griffin, K.L., Rogers, G.N.D., and Whitehead, D. 1998. Photosynthetic acclimation to long-term exposure to elevated CO₂ concentration in *Pinus radiata* D. Don. is related to age of needles. *Plant, Cell and Environment* **21**: 1019–1028.

2.25 Seeds

Atmospheric CO₂ enrichment has been shown to increase amount, size, weight, carbohydrate content, lipid content, protein content, earlier production, earlier germination, and greater percent germination of various plant seeds, all of which bode well for the future of Earth’s biosphere.

2.25.1 Crops

- Rising atmospheric CO₂ concentrations will confer several benefits on the seeds of crop plants, including an increase in seed quantity and improvements in seed quality.

When dealing with agricultural commodities such as grain crops, seeds comprise the yield, and in such cases the biomass of one (seeds) is the biomass of the other (yield). Therefore, when looking for effects of elevated CO₂ on the seeds of such crops, there is a natural interest in something more than just their final

biomass. A number of pertinent papers are explored in this section that consider the sources of biomass production as well as seed properties that go beyond biomass.

In a greenhouse study of the various components of seed biomass production, Palta and Ludwig (2000) grew narrow-leaved lupine in pots filled with soil within Mylar-film tunnels maintained at either 355 or 700 ppm CO₂. They found the extra CO₂ increased the final number of pods and the number of pods that filled large seeds, while it reduced to zero the number of pods that had small seeds, reduced the number of pods with unfilled seeds from 16 to 1 pod per plant, and increased pod set and dry matter accumulation on the developing branches. These CO₂-induced improvements in key physiological processes resulted in 47 to 56% increases in dry matter per plant, which led to increases of 44 to 66% in seed yield per plant.

Sanhewe *et al.* (1996) grew winter wheat in polyethylene tunnels maintained at atmospheric CO₂ concentrations of 380 and 680 ppm from the time of seed germination to the time of plant maturity, maintaining a temperature gradient of approximately 4°C in each tunnel. In addition to the elevated CO₂ increasing seed yield per unit area, they found it also increased seed weight, but not seed survival or germination. Increasing air temperature, on the other hand, increased seed longevity across the entire range of temperatures investigated (14 to 19°C).

Thomas *et al.* (2003) grew soybean plants to maturity in sunlit controlled-environment chambers under sinusoidally varying day/night-max/min temperatures of 28/18, 32/22, 36/26, 40/30, and 44/34°C and two levels of atmospheric CO₂ concentration (350 and 700 ppm). The effect of temperature on seed composition and gene expression was “pronounced,” but “there was no effect of CO₂.” However, they note, “Heagle *et al.* (1998) observed a positive significant effect of CO₂ enrichment on soybean seed oil and oleic acid concentration,” and Thomas *et al.* did find the latter parameters increased with rising temperature, from 28/18 to 44/34°C. In addition, they found, “32/22°C is optimum for producing the highest oil concentration in soybean seed,” “the degree of fatty acid saturation in soybean oil was significantly increased by increasing temperature,” and crude protein concentration increased with temperature to 40/30°C.

Thomas *et al.* note “the intrinsic value of soybean seed is in its supply of essential fatty acids and amino acids in the oil and protein, respectively.” Thus the temperature-driven changes they identified in these parameters, as well as the CO₂ effect observed by

Heagle *et al.*, bode well for the future production of this important crop and its value to society in a CO₂-enriched and warming world. They do note, however, “temperatures during the soybean-growing season in the southern USA are at, or slightly higher than, 32/22°C,” and warming could negatively impact the soybean oil industry in this region. For the world as a whole, however, warming would be a positive development for soybean production, and in the southern United States, shifts in planting zones could accommodate changing weather patterns associated with this phenomenon.

Ziska *et al.* (2001) grew one modern and eight ancestral soybean genotypes in glasshouses maintained at atmospheric CO₂ concentrations of 400 and 710 ppm, finding the extra CO₂ increased photosynthetic rates by an average of 75%. This enhancement in photosynthetic sugar production led to increases in seed yield that averaged 40% for all cultivars, except for one ancestral variety that exhibited an 80% increase in seed yield. Hence, if plant breeders utilize the highly CO₂-responsive ancestral cultivar identified in this study in their breeding programs, soybean seed yields could rise even faster and higher in the future.

Fiscus *et al.* (2007) grew well-watered and well-fertilized soybean (*Glycine max* (L.) Merr. cv. Essex) plants from seed to maturity for one full growing season out-of-doors near Raleigh, North Carolina (USA) within open-top chambers, either rooted in the ground or in 21-liter pots (one plant per pot) at equal plant densities per unit ground area, while exposing the plants to charcoal-filtered air maintained at CO₂ concentrations of either 370 or 700 ppm.

Although seed yields in the container-grown plants were about 17% less than those of the plants rooted directly in the ground, the CO₂-induced enhancement ratios of both sets of plants were not significantly different from each other, averaging approximately 20%. In addition, the six researchers state, “there was a small (3–4%) but highly significant increase in the seed oil concentration due to elevated CO₂,” and this increase was experienced in both rooting environments. Fiscus *et al.* note, “the 3 to 4% increase in oil per seed would amount to a very substantial increase in oil production on a regional, national, or international scale.” For the year 2005, for example, they calculated “an increase of 3.5% of seed oil concentration could result in an additional 2.9 Tg of seed oil in a future climate with CO₂ concentrations well above current ambient levels.”

Derner *et al.* (2004) determined above- and below-ground responses of three generations of two

genotypes of spring wheat to atmospheric CO₂ enrichment to 336 ppm above ambient. This experiment was conducted in glasshouse bays, where the second- and third-generation plants were progeny of seeds produced by plants grown at either ambient or enriched atmospheric CO₂ concentrations under well-watered and high soil-nutrient conditions.

Neither genotype in the first generation exhibited enhanced growth in response to the increased concentration of atmospheric CO₂. However, Derner *et al.* report, “relative enhancement occurred in both the second and third generations for both above- and below-ground variables,” and the “relative enhancement of measured variables was generally greater in the third than second generation when plants were in the seedling or vegetative stage.” They also determined “intergenerational above- and below-ground responses of this C₃ annual plant to CO₂ enrichment are not driven by genetic change (selection) that occurred between generations, but rather CO₂-induced changes in seeds that affected seedling responses to CO₂ enrichment.”

References

Derner, J.D., Tischler, C.R., Polley, H.W., and Johnson, H.B. 2004. Intergenerational above- and belowground responses of spring wheat (*Triticum aestivum* L.) to elevated CO₂. *Basic and Applied Ecology* 5: 145–152.

Fiscus, E.L., Booker, F.L., Dubois, J.-J. B., Rufty, T.W., Burton, J.W., and Pursley, W.A. 2007. Carbon dioxide enhancement effects in container- versus ground-grown soybean at equal planting densities. *Crop Science* 47: 2486–2494.

Heagle, A.S., Miller, J.E., and Pursley, W.A. 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment: III. Yield and seed quality. *Crop Science* 38: 128–134.

Palta, J.A. and Ludwig, C. 2000. Elevated CO₂ during pod filling increased seed yield but not harvest index in indeterminate narrow-leaved lupine. *Australian Journal of Agricultural Research* 51: 279–286.

Sanhewe, A.J., Ellis, R.H., Hong, T.D., Wheeler, T.R., Batts, G.R., Hadley, P., and Morison, J.I.L. 1996. The effect of temperature and CO₂ on seed quality development in wheat (*Triticum aestivum* L.). *Journal of Experimental Botany* 47: 631–637.

Thomas, J.M.G., Boote, K.J., Allen Jr., L.H., Gallo-Meagher, M., and Davis, J.M. 2003. Elevated temperature and carbon dioxide effects on soybean seed composition and transcript abundance. *Crop Science* 43: 1548–1557.

Ziska, L.H., Bunce, J.A., and Caulfield, F.A. 2001. Rising atmospheric carbon dioxide and seed yields of soybean genotypes. *Crop Science* 41: 385–391.

2.25.2 Grasslands

- Atmospheric CO₂ enrichment typically increases the amount, size, and weight of seeds produced and dispersed each year by various grassland species, as well as their carbon/nitrogen ratios and germination percentage. Concomitant increases in air temperature may result in advancements of flowering and fruiting phenology, which can increase spread rates of plant populations because wind conditions in spring tend to produce higher spread rates than wind conditions later in the year.

Steinger *et al.* (2000) collected seeds from *Bromus erectus* plants grown at atmospheric CO₂ concentrations of 360 and 650 ppm, and then germinated some of both groups of seeds under those same two sets of conditions. In the first part of their study, they found the elevated CO₂ treatment increased individual seed mass by about 9% and increased the seed carbon-to-nitrogen ratio by almost 10%. These changes in seed properties had little impact on subsequent seedling growth; when the seeds produced by ambient or CO₂-enriched plants were germinated and grown in ambient air, there was no significant size difference between the two groups of resultant seedlings after a period of 19 days. Likewise, when the seeds produced from the ambient and CO₂-enriched plants were germinated and grown in the high CO₂ treatment, there was no significant difference between the sizes of the seedlings derived from the two groups of seeds. However, the CO₂-enriched seedlings produced from both groups of seeds were almost 20% larger than the seedlings produced from both groups of seeds grown in ambient air, demonstrating the direct effects of atmospheric CO₂ enrichment on seedling growth and development were more important than the differences in seed characteristics produced by the elevated atmospheric CO₂ concentration in which their parent plants grew.

Edwards *et al.* (2001) employed a FACE experiment where daytime atmospheric CO₂ concentrations above a sheep-grazed pasture in New Zealand were increased by 115 ppm, in order to study the effects of elevated CO₂ on seed production, seedling recruitment, and species compositional changes. In the two years of their study, the extra

daytime CO₂ increased seed production and dispersal in seven of the eight most abundant species, including the grasses *Anthoxanthum odoratum*, *Lolium perenne*, and *Poa pratensis*, the legumes *Trifolium repens* and *T. subterranean*, and the herbs *Hypochaeris radicata* and *Leontodon saxatilis*. In some of these plants, elevated CO₂ also increased the number of seeds per reproductive structure, and all exhibited CO₂-induced increases in the number of reproductive structures per unit of ground area. In addition, the CO₂-induced increases in seed production contributed to the increase in the numbers of species found within the CO₂-enriched plots.

In a five-year study of a nutrient-poor calcareous grassland in Switzerland, Thurig *et al.* (2003) used screen-aided CO₂ control (SACC) technology (Leadley *et al.*, 1997) to enrich the air over half of their experimental plots with an extra 300 ppm of CO₂. They found “the effect of elevated CO₂ on the number of flowering shoots (+24%) and seeds (+29%) at the community level was similar to above ground biomass response.” In terms of species functional groups, there was a 42% increase in the mean seed number of graminoids and a 33% increase in the mean seed number of forbs, but no change in legume seed numbers. In most species, mean seed weight also tended to be greater in plants grown in CO₂-enriched air (+12%), and Thurig *et al.* note many studies have shown heavier seeds result in seedlings “more robust than seedlings from lighter seeds (Baskin and Baskin, 1998).”

Wang and Griffin (2003) grew dioecious white campion plants from seed to maturity in sand-filled pots maintained at optimum moisture and fertility conditions in environmentally controlled growth chambers in which the air was continuously maintained at CO₂ concentrations of either 365 or 730 ppm. In response to this doubling of the air’s CO₂ content, the vegetative mass of both male and female plants rose by approximately 39%. Reproductive mass rose by 82% in male plants and by 97% in females. In the female plants, this was accomplished, in part, by increases of 36% and 44% in the number and mass of seeds per plant, and by a 15% increase in the mass of individual seeds, in harmony with the findings of Jablonski *et al.* (2002), which they derived from a meta-analysis of the results of 159 CO₂ enrichment experiments conducted on 79 species of agricultural and wild plants. Dioecious plants comprise nearly half of all angiosperm families, so their allocation of a greater proportion of plant biomass to reproduction in a high-CO₂ world of the future bodes well for the biodiversity of Earth’s ecosystems.

Wang (2005) grew well-watered and -fertilized specimens of *Silene latifolia* from seed to maturity in pots within controlled environment chambers maintained at mean CO₂ concentrations of 386 and 696 ppm, documenting reproductive responses during growth and at final harvest. Then, the seeds produced by the plants in this experiment were used to grow a second generation of plants under the same environmental conditions in which the parent plants had been grown.

In the first experiment, the total reproductive biomass of the plants grown in CO₂-enriched air was 32% greater than that of the plants grown in ambient air, as was the total number of fruit produced. In the second experiment, for seeds from female plants grown in ambient air, 55% of all emergence occurred within six days of sowing, and for seeds from plants grown in CO₂-enriched air, 67% of total emergence occurred during the same period. In addition, 87% of the seeds from the elevated-CO₂-grown plants ultimately germinated, whereas only 67% of the seeds from the ambient-CO₂-grown plants did so. Finally, the plants produced a greater percentage of female progeny in the CO₂-enriched air than in ambient-air (56.3% vs. 52.7%).

The combined effect of a greater number of seeds being produced per female plant, a higher percentage of seed germination, and more female-biased seed production in CO₂-enriched air suggest white campion plants will fare well in a high-CO₂ world of the future, which might cause some to worry, as it is a rather cosmopolitan and somewhat weedy species. However, any plants of agricultural value with which it might compete also will be doing better in such conditions. Hence, the greater importance of this study is what it may imply about other dioecious species, especially in light of the fact that *Silene latifolia*, in the words of Wang, “has become a model system for studying sexual dimorphism and sex-determination mechanisms and is likely the most extensively studied dioecious species.”

Kuparinen *et al.* (2009) investigated the effects of a warming-induced increase in local convective turbulence (caused by a postulated 3°C increase in local temperature) on the long-distance dispersal (LDD) of seeds and pollen based on mechanistic models of wind dispersal (Kuparinen *et al.*, 2007) and population spread (Clark *et al.*, 2001) in a boreal forest of southern Finland. For light-seeded herbs, the group of researchers report spread rates increased by 35–42 m/yr (6.3–9.2%), and for heavy-seeded herbs the increase was 0.01–0.06 m/yr (1.9–6.7%). In addition, they note, “climate change driven advance-

ments of flowering and fruiting phenology can increase spread rates of plant populations because wind conditions in spring tend to produce higher spread rates than wind conditions later in the year.”

The four researchers from France, Germany, Israel, and the United States conclude—in addition to the obvious benefits of greater LDD (being better able to move toward more hospitable locations)—the increased wind dispersal of seeds and pollen may “promote gene flow between populations, thus increasing their genetic diversity and decreasing the risk of inbreeding depression,” citing Ellstrand (1992) and Aguilar *et al.* (2008). They further note, “increased gene flow between neighboring populations can accelerate adaptation to environmental change,” citing Davis and Shaw (2001) and Savolainen *et al.* (2007). The scientists report the “dispersal and spread of populations are widely viewed as a means by which species can buffer negative effects of climate change.”

References

Aguilar, R., Quesada, M., Ashworth, L., Herrerias-Diego, Y., and Lobo, J. 2008. Genetic consequences of habitat fragmentation in plant populations: susceptible signals in plant traits and methodological approaches. *Molecular Ecology* **17**: 5177–5188.

Baskin, C.C. and Baskin, J.M. 1998. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, CA.

Clark, J.S., Lewis, M., and Hovarth, L. 2001. Invasion by extremes; population spread with variation in dispersal and reproduction. *American Naturalist* **157**: 537–544.

Davis, M.B. and Shaw, R.G. 2001. Range shifts and adaptive responses to quaternary climate change. *Science* **292**: 673–679.

Edwards, G.R., Clark, H., and Newton, P.C.D. 2001. The effects of elevated CO₂ on seed production and seedling recruitment in a sheep-grazed pasture. *Oecologia* **127**: 383–394.

Ellstrand, N.C. 1992. Gene flow by pollen: Implications for plant conservation genetics. *Oikos* **63**: 77–86.

Jablonski, L.M., Wang, X., and Curtis, P.S. 2002. Plant reproduction under elevated CO₂ conditions: a meta-analysis of reports on 79 crop and wild species. *New Phytologist* **156**: 9–26.

Kuparinen, A., Katul, G., Nathan, R., and Schurr, F.M. 2009. Increases in air temperature can promote wind-driven dispersal and spread of plants. *Proceedings of the Royal Society B* **276**: 3081–3087.

Leadley, P.W., Niklaus, P.A., and Stocker, R., *et al.* 1997. Screen-aided CO₂ control (SACC): a middle ground between FACE and open-top chambers. *Acta Oecologica* **18**: 39–49.

Savolainen, O., Pyhajarvi, T., and Knurr, T. 2007. Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution and Systematics* **38**: 595–619.

Steinger, T., Gall, R., and Schmid, B. 2000. Maternal and direct effects of elevated CO₂ on seed provisioning, germination and seedling growth in *Bromus erectus*. *Oecologia* **123**: 475–480.

Thurig, B., Korner, C., and Stocklin, J. 2003. Seed production and seed quality in a calcareous grassland in elevated CO₂. *Global Change Biology* **9**: 873–884.

Wang, X. 2005. Reproduction and progeny of *Silene latifolia* (Caryophyllaceae) as affected by atmospheric CO₂ concentration. *American Journal of Botany* **92**: 826–832.

Wang, X. and Griffin, K.L. 2003. Sex-specific physiological and growth responses to elevated atmospheric CO₂ in *Silene latifolia* Poir. *Global Change Biology* **9**: 612–618.

2.25.3 Trees

- Atmospheric CO₂ enrichment typically increases seed amount, size, weight, carbohydrate content, lipid content, and protein content, and also causes earlier production, earlier germination, and greater percent of germination.

LaDeau and Clark (2001) investigated how enriching the air with CO₂ impacts the reproductive capacity of trees by determining various responses of loblolly pines to atmospheric CO₂ enrichment at the Duke Forest in the Piedmont region of North Carolina (USA). In August 1996 three 30-m-diameter FACE rings had been set up around three groups of the 13-year-old trees to enrich the air about them to 200 ppm above the atmosphere’s normal background concentration; three identical FACE rings served as control plots. The trees were not mature at the start of the experiment, so they did not produce any cones until a few rare ones appeared in 1998. By the fall of 1999, however, the scientists found the CO₂-enriched trees were twice as likely as trees growing in ambient air to be reproductively mature, and they produced three times more cones per tree. Similarly, the trees growing in the CO₂-enriched air produced 2.4 times more cones in the fall of 2000, and from August 1999 through July 2000, the scientists collected three times

Plant Characteristics

as many seeds in the CO₂-fertilized FACE rings as in the control rings.

Hussain *et al.* (2001) also worked on this aspect of the Duke Forest FACE study. They report seeds collected from the CO₂-enriched trees were 91% heavier than those collected from the trees growing in ambient air, and the CO₂-enriched seeds had a lipid content 265% greater than that of the seeds produced on the ambient-treatment trees. They also noted the germination success for seeds developed under atmospheric CO₂ enrichment was more than three times greater than for control seeds developed at ambient CO₂, regardless of germination CO₂ concentration. Seeds from the CO₂-enriched trees germinated approximately five days earlier than their ambiently produced counterparts, again regardless of germination CO₂ concentration, and seedlings developing from seeds collected from CO₂-enriched trees displayed significantly greater root lengths and needle numbers than seedlings developing from trees exposed to ambient air, also regardless of growth CO₂ concentration.

The propensity for elevated levels of atmospheric CO₂ to hasten the production of more plentiful seeds on the trees of this valuable timber species bodes well for naturally regenerating loblolly pine stands of the southeastern United States, where LaDeau and Clark report the trees “are profoundly seed-limited for at least 25 years.” Hence, as the air’s CO₂ content continues to climb, they conclude, “this period of seed limitation may be reduced.” In addition, the observations of Hussain *et al.* suggest loblolly pine trees in a CO₂-enriched world of the future likely will display significant increases in their photosynthetic rates. Enhanced carbohydrate supplies resulting from this phenomenon likely will increase seed weight and lipid content. Such seeds consequently should exhibit significant increases in germination success, and their enhanced lipid supplies likely will lead to greater root lengths and needle numbers in developing seedlings. Consequently, when CO₂-enriched loblolly pine seedlings become photosynthetically active, they likely will produce biomass at greater rates than those exhibited by seedlings growing under current CO₂ concentrations.

Five years later, LaDeau and Clark (2006a) conducted a follow-up study extending this work. They found “carbon dioxide enrichment affected mean cone production both through early maturation and increased fecundity,” so “trees in the elevated CO₂ plots produced twice as many cones between 1998 and 2004 as trees in the ambient plots.” In addition, the trees grown in elevated CO₂ “made the

transition to reproductive maturation at smaller [trunk] diameters,” and they “not only reached reproductive maturation at smaller diameters, but also at younger ages.” By 2004, for example, “roughly 50% of ambient trees and 75% of fumigated trees [had] produced cones.” In addition, “22% of the trees in high CO₂ produced between 40 and 100 cones during the study, compared with only 9% of ambient trees.”

“In this 8-year study,” the two researchers write, they found “previous short-term responses indeed persist,” in contradiction of those who downplay the immense biological benefits of atmospheric CO₂ enrichment. In addition, they note, “*P. taeda* trees that produce large seed crops early in their life span tend to continue to be prolific producers (Schultz, 1997),” and they conclude this fact, together with their findings, suggests “individual responses seen in this young forest may be sustained over their life span.”

LaDeau and Clark (2006b) additionally analyzed the seed and pollen responses of the loblolly pines to atmospheric CO₂ enrichment, finding the “trees grown in high-CO₂ plots first began producing pollen while younger and at smaller sizes relative to ambient-grown trees.” Cone pollen and airborne pollen grain abundances were significantly greater in the CO₂-enriched stands. They write, “by spring 2005, 63% of all trees growing in high CO₂ had produced both pollen and seeds vs. only 36% of trees in the ambient plots.”

This propensity for elevated concentrations of atmospheric CO₂ to hasten and increase the production of pollen by this valuable timber species bodes well for naturally regenerated loblolly pine stands, which have a continuous range from Maryland south to Florida and west to Texas, where they currently are profoundly seed-limited for at least 25 years. In addition, the two researchers indicate precocious pollen production “could enhance the production of viable seeds by increasing the percentage of fertilized ovules,” and “more pollen disseminated from multiple-source trees may also increase rates of gene flow among stands, and could further reduce rates of self-pollination, indirectly enhancing the production of viable seeds.” Also of importance, in view of the negative twists some attempt to put on even overwhelmingly positive research findings, they state, “pine pollen is not a dangerous allergen for the public at large.”

Another major study of the reproductive responses of trees to elevated levels of atmospheric CO₂ was conducted at the Kennedy Space Center, Florida (USA), where in 1996 researchers enclosed

three species of scrub-oak (*Quercus myrtifolia*, *Q. chapmanii*, and *Q. geminata*) within 16 open-top chambers, half of which were maintained at 379 ppm CO₂ and half at 704 ppm. Five years later—in August, September, and October 2001—Stiling *et al.* (2004) counted the acorns on randomly selected twigs of each species, and in November they counted fallen acorns of each species within equal-size quadrates of ground area, additionally evaluating mean acorn weight, acorn germination rate, and degree of acorn infestation by weevils.

Acorn germination rate and degree of predation by weevils were unaffected by elevated CO₂, and acorn size was enhanced by a small amount: 3.6% for *Q. myrtifolia*, 7.0% for *Q. chapmanii*, and 7.7% for *Q. geminata*. Acorn number responses, on the other hand, were enormous, but for only two of the three species, as *Q. geminata* did not register any CO₂-induced increase in reproductive output, in harmony with its unresponsive overall growth rate. For *Q. myrtifolia*, however, Stiling *et al.* report, “there were four times as many acorns per 100 twigs in elevated CO₂ as in ambient CO₂ and for *Q. chapmanii* the increase was over threefold.” On the ground, the enhancement was greater still, with the researchers reporting “the number of *Q. myrtifolia* acorns per meter squared in elevated CO₂ was over seven times greater than in ambient CO₂ and for *Q. chapmanii*, the increase was nearly sixfold.”

Stiling *et al.* thus conclude “there will be large increases in seedling production in scrub-oak forests in an atmosphere of elevated CO₂,” noting “this is important because many forest systems are ‘recruitment-limited’ (Ribbens *et al.*, 1994; Hubbell *et al.*, 1999).” This conclusion echoes that of LaDeau and Clark with respect to loblolly pines. Therefore, and if other trees behave similarly, the rising CO₂ content of Earth’s atmosphere likely will be a great boon to the regenerative prowess of the planet’s forests.

A third major study of CO₂ effects on seed production in trees was conducted at the FACE facility near Rhinelander, Wisconsin (USA), where young paper birch (*Betula papyrifera* Marsh.) seedlings were planted in 1997 and had been growing since 1998 in open-top chambers maintained at atmospheric CO₂ concentrations of either 360 or 560 ppm, as well as at atmospheric ozone (O₃) concentrations of either ambient or 1.5 times ambient. Darbah *et al.* (2007) collected many types of data pertaining to flowering, seed production, seed germination, and new seedling growth and development over the 2004–2006 growing seasons.

They found “elevated CO₂ had significant positive effect[s] on birch catkin size, weight, and germination success rate.” Specifically, “elevated CO₂ increased germination rate of birch by 110%, compared to ambient CO₂ concentrations, decreased seedling mortality by 73%, increased seed weight by 17% [and] increased [new seedling] root length by 59%.”

The six researchers found “the opposite was true of elevated O₃”; it “decreased the germination rate of birch by 62%, decreased seed weight by 25%, and increased [new seedling] root length by [only] 15%.” In addition, they note, “the seeds produced under elevated O₃ had much less stored carbohydrate, lipids, and proteins for the newly developing seedling to depend on and, hence, the slow growth rate.” They also report “the total number of trees that flowered increased by 139% under elevated CO₂ [but only] 40% under elevated O₃.” Likewise, they state, “with respect to the quantity of flowers produced, elevated CO₂ had [a] 262% increase, while that of elevated O₃ had [only a] 75% increase compared to the control treatment.”

Darbah *et al.* state their findings imply seedling recruitment in paper birch “will be enhanced under elevated CO₂ but reduced under elevated O₃.”

References

- Darbah, J.N.T., Kubiske, M.E., Nelson, N., Oksanen, E., Vaapavuori, E., and Karnosky, D.F. 2007. Impacts of elevated atmospheric CO₂ and O₃ on paper Birch (*Betula papyrifera*): Reproductive fitness. *The Scientific World Journal* 7(S1): 240–246.
- Hubbell, S.P., Foster, R.B., O’Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J., and Loo de Lao, S. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283: 554–557.
- Hussain, M., Kubiske, M.E., and Connor, K.F. 2001. Germination of CO₂-enriched *Pinus taeda* L. seeds and subsequent seedling growth responses to CO₂ enrichment. *Functional Ecology* 15: 344–350.
- LaDeau, S.L. and Clark, J.S. 2001. Rising CO₂ levels and the fecundity of forest trees. *Science* 292: 95–98.
- LaDeau, S.L. and Clark, J.S. 2006a. Elevated CO₂ and tree fecundity: the role of tree size, interannual variability, and population heterogeneity. *Global Change Biology* 12: 822–833.
- LaDeau, S.L. and Clark, J.S. 2006b. Pollen production by *Pinus taeda* growing in elevated atmospheric CO₂. *Functional Ecology* 20: 541–547.
- Ribbens, E., Silander, J.A., and Pacala, S.W. 1994.

Plant Characteristics

Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology* **75**: 1794–1806.

Schultz, R.P. 1997. *Loblolly Pine—The Ecology and Culture of Loblolly Pine (Pinus taeda L.)*. USDA Forest Service Agricultural Handbook 713. USDA Forest Service, Washington, DC, USA.

Stiling, P., Moon, D., Hymus, G., and Drake, B. 2004. Differential effects of elevated CO₂ on acorn density, weight, germination, and predation among three oak species in a scrub-oak forest. *Global Change Biology* **10**: 228–232.

2.26 Starch

- As the air's CO₂ content rises, most of Earth's vegetation responds with enhanced rates of photosynthesis and greater production of carbohydrates. Many of these carbohydrates are exported from leaves and needles to provide energy or carbon skeletons to facilitate increased biomass production, after which remaining carbohydrates are generally converted into starch and stored within leaves or roots for future use.

CO₂-induced starch accumulation is occurring in a variety of plants. Janssens *et al.* (1998) found a six-month period of atmospheric CO₂ exposure of 700 ppm caused a 90% increase in root starch accumulation in Scots pine seedlings relative to control seedlings exposed to ambient CO₂ of 350 ppm. Studying the same species, Kainulainen *et al.* (1998) report a significant enhancement in needle starch concentrations after three years of atmospheric CO₂ enrichment to 300 ppm above ambient. Similar results have been reported in tropical trees, where 10 (Lovelock *et al.*, 1998) and four (Wurth *et al.*, 1998) species exhibited approximate doublings of their leaf starch contents in response to a doubling of the atmospheric CO₂ content. In other tree studies, Rey and Jarvis (1998) noted a 100% CO₂-induced increase in leaf starch contents of birch seedlings exposed to an atmospheric CO₂ concentration of 700 ppm, and Pan *et al.* (1998) report a 17-fold increase in this parameter for apple seedlings grown at an atmospheric CO₂ concentration of 1600 ppm.

Liu *et al.* (2005) found the combined effects of elevated CO₂ and ozone (O₃) produced a significant increase in leaf nonstructural carbohydrates of three- and four-year-old European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst) seedlings under both mixed and monoculture conditions, which was similar to what was observed

under CO₂ enrichment alone. Hence, they conclude, “since the responses to the combined exposure were more similar to elevated pCO₂ than to elevated pO₃, apparently elevated pCO₂ overruled the effects of elevated pO₃ on nonstructural carbohydrates.”

Kostiainen *et al.* (2006) also studied the combined effects of elevated carbon dioxide and ozone, examining fast-growing silver birch (*Betula pendula* Roth) clones grown out-of-doors at Suonenjoki, Finland, in open-top chambers maintained at ambient and 1.9x ambient CO₂ concentrations in combination with ambient and 1.5x ambient O₃ concentrations.

Among other findings, the five researchers report the elevated CO₂ treatment increased trunk starch concentration by 7%. Recognizing “the concentration of nonstructural carbohydrates (starch and soluble sugars) in tree tissues is considered a measure of carbon shortage or surplus for growth (Korner, 2003),” the Finnish researchers state the “starch accumulation observed under elevated CO₂ in this study indicates a surplus of carbohydrates produced by enhanced photosynthesis of the same trees (Riikonen *et al.*, 2004).” In addition, they report, “during winter, starch reserves in the stem are gradually transformed to soluble carbohydrates involved in freezing tolerance (Bertrand *et al.*, 1999; Piispanen and Saranpää, 2001), so the increase in starch concentration may improve acclimation in winter.” The ongoing rise in the air's CO₂ content should be a boon to silver birch (and likely many other trees) in both summer and winter in both pristine and ozone-polluted air.

It should also be noted elevated CO₂ concentrations increase starch concentrations within non-woody herbaceous plants. Reid *et al.* (1998), for example, documented a doubling of the atmospheric CO₂ concentration led to a 148% increase in soybean leaf starch contents at both normal and elevated concentrations of ozone. Exposure to 1,000 ppm CO₂ caused a 10-fold increase in leaf starch concentrations of potato (Ludewig *et al.*, 1998).

It is therefore highly likely that rising atmospheric CO₂ concentrations will significantly boost starch production in plants, increasing the availability of an important raw material that can be metabolized to help sustain enhanced growth under a variety of stressful conditions.

References

Bertrand, A., Robitaille, G., Nadeau, P., and Castonguay,

Y. 1999. Influence of ozone on cold acclimation in sugar maple seedlings. *Tree Physiology* **19**: 527–534.

Janssens, I.A., Crookshanks, M., Taylor, G., and Ceulemans, R. 1998. Elevated atmospheric CO₂ increases fine root production, respiration, rhizosphere respiration and soil CO₂ efflux in Scots pine seedlings. *Global Change Biology* **4**: 871–878.

Kainulainen, P., Holopainen, J.K., and Holopainen, T. 1998. The influence of elevated CO₂ and O₃ concentrations on Scots pine needles: Changes in starch and secondary metabolites over three exposure years. *Oecologia* **114**: 455–460.

Korner, C. 2003. Carbon limitation in trees. *Journal of Ecology* **91**: 4–17.

Kostiainen, K., Jalkanen, H., Kaakinen, S., Saranpää, P., and Vapaavuori, E. 2006. Wood properties of two silver birch clones exposed to elevated CO₂ and O₃. *Global Change Biology* **12**: 1230–1240.

Liu, X.-P., Grams, T.E.E., Matyssek, R., and Rennenberg, H. 2005. Effects of elevated pCO₂ and/or pO₃ on C-, N-, and S-metabolites in the leaves of juvenile beech and spruce differ between trees grown in monoculture and mixed culture. *Plant Physiology and Biochemistry* **43**: 147–154.

Lovelock, C.E., Winter, K., Mersits, R., and Popp, M. 1998. Responses of communities of tropical tree species to elevated CO₂ in a forest clearing. *Oecologia* **116**: 207–218.

Ludewig, F., Sonnewald, U., Kauder, F., Heineke, D., Geiger, M., Stitt, M., Müller-Rober, B.T., Gillissen, B., Kuhn, C., and Frommer, W.B. 1998. The role of transient starch in acclimation to elevated atmospheric CO₂. *FEBS Letters* **429**: 147–151.

Pan, Q., Wang, Z., and Quebedeaux, B. 1998. Responses of the apple plant to CO₂ enrichment: changes in photosynthesis, sorbitol, other soluble sugars, and starch. *Australian Journal of Plant Physiology* **25**: 293–297.

Piispanen, R. and Saranpää, P. 2001. Variation of non-structural carbohydrates in silver birch (*Betula pendula* Roth) wood. *Trees* **15**: 444–451.

Reid, C.D., Fiscus, E.L., and Burkey, K.O. 1998. Combined effects of chronic ozone and elevated CO₂ on rubisco activity and leaf components in soybean (*Glycine max*). *Journal of Experimental Botany* **49**: 1999–2011.

Rey, A. and Jarvis, P.G. 1998. Long-term photosynthetic acclimation to increased atmospheric CO₂ concentration in young birch (*Betula pendula*) trees. *Tree Physiology* **18**: 441–450.

Riikonen, J., Lindsberg, M.-M., Holopainen, T., Oksanen, E., Lappi, J., Peltonen, P., and Vapaavuori, E. 2004. Silver birch and climate change: variable growth and carbon

allocation responses to elevated concentrations of carbon dioxide and ozone. *Tree Physiology* **24**: 1227–1237.

Wurth, M.K.R., Winter, K., and Korner, C. 1998. Leaf carbohydrate responses to CO₂ enrichment at the top of a tropical forest. *Oecologia* **116**: 18–25.

2.27 Stomatal Density

2.27.1 Herbaceous Plants

- In addition to sequentially reducing the openness of their stomata to restrict unnecessary water loss via excessive transpiration as the air's CO₂ content rises, some plants also reduce the density (number per area) of stomates on their leaves, but only to a certain degree, beyond which this latter phenomenon would be counterproductive.

As the air's CO₂ content rises, many plants reduce their stomatal apertures, because with more CO₂ in the air they don't need to open their stomates as wide as they do at lower atmospheric CO₂ concentrations to allow for sufficient inward diffusion of CO₂ for use in photosynthesis. As a result, plants growing in CO₂-enriched air typically exhibit reduced rates of water loss via transpiration, smaller yield losses attributable to the indiscriminate uptake of air pollutants, and increased water-use efficiencies.

For much the same reason (and producing similar effects), many plants also reduce the density of stomates on the surfaces of their leaves at higher atmospheric CO₂ concentrations. This section reviews the findings of a few of the studies that have addressed this subject in non-woody herbaceous plants.

Case *et al.* (1998) collected 12 wild radish genotypes with a variety of stomatal indices and guard cell lengths in Maine (USA) and grew them to maturity in greenhouses maintained at atmospheric CO₂ concentrations of 370 and 680 ppm. They found the elevated CO₂ did not significantly affect stomatal index or guard cell length. Across all genotypes investigated, leaf surface characteristics essentially were unchanged by elevated CO₂.

In the case of C₄ maize plants grown for 30 days in plexiglass chambers maintained at ambient or triple-ambient concentrations of atmospheric CO₂, on the other hand, Maroco *et al.* (1999) determined the leaves of the CO₂-enriched plants displayed approximately 10% fewer stomates per unit leaf area than the leaves of control plants growing in ambient air.

Why one of these plants exhibited no change in stomatal density as the air's CO₂ content was increased above the current ambient value, while the other exhibited a decrease, may perhaps be explained by the results reported by Gray *et al.* (2000). They identified a gene of the small mustard plant *Arabidopsis thaliana* that prevents decreases in the number density of leaf stomata in response to atmospheric CO₂ enrichment above a certain critical value of atmospheric CO₂ concentration. It can readily be appreciated why this is so, because decreases in stomatal density and conductance in response to rising atmospheric CO₂ concentrations (which are typically beneficial) cannot go on indefinitely, for there would ultimately come a point (likely different for different species) where further decreases in these plant properties become counterproductive, leading to a situation where the enhanced air-to-leaf CO₂ concentration gradient could not overcome the increased resistance of CO₂ entry into the leaf, causing the plant to die of carbon starvation, or where transpiration is reduced so much that leaf evaporative cooling cannot prevent plant death due to increased thermal stress.

Viewed in this light, the difference between the stomatal density responses of wild radish and maize likely derives from genetically programmed species-specific differences in the critical value of atmospheric CO₂ concentration at which the decline in stomatal density with increasing atmospheric CO₂ concentration is genetically terminated. Serna and Fenoll (2000) note, "plants seem to be well armed to cope with a further enrichment in atmospheric CO₂," and genes such as the one discovered by Gray *et al.*—denoted HIC for high carbon dioxide—"should ensure that, at high CO₂ concentrations, changes in stomatal indices are kept to a minimum."

References

- Case, A.L., Curtis, P.S., and Snow, A.A. 1998. Heritable variation in stomatal responses to elevated CO₂ in wild radish, *Raphanus raphanistrum* (Brassicaceae). *American Journal of Botany* **85**: 253–258.
- Gray, J.E., Holroyd, G.H., van der Lee, F.M., Bahrami, A.R., Sijmons, P.C., Woodward, F.I., Schuch, W., and Hetherington, A.M. 2000. The HIC signaling pathway links CO₂ perception to stomatal development. *Nature* **408**: 713–716.
- Maroco, J.P., Edwards, G.E., and Ku, M.S.B. 1999. Photosynthetic acclimation of maize to growth under elevated levels of carbon dioxide. *Planta* **210**: 115–125.

Serna, L. and Fenoll, C. 2000. Coping with human CO₂ emissions. *Nature* **408**: 656–657.

2.27.2 Woody Plants

- As the air's CO₂ content rises, leaf stomatal densities (number per area) of woody plants range from no change at all to double-digit percentage decreases that cease after a few hundred ppm increase in CO₂, beyond which this phenomenon becomes counterproductive.

As the air's CO₂ content rises, many plants reduce their stomatal apertures, because with more CO₂ in the air they don't need to open their stomates as wide as they do at lower atmospheric CO₂ concentrations to allow for sufficient inward diffusion of CO₂ for use in photosynthesis. As a result, plants growing in CO₂-enriched air typically exhibit reduced rates of transpirational water loss, smaller productivity losses attributed to the uptake of aerial pollutants, and increased water use efficiency.

For much the same reason (and producing similar effects), many plants also reduce the density of stomates on their leaf surfaces at higher atmospheric CO₂ concentrations. This section reviews the findings of studies that addressed this subject in woody plants such as trees and shrubs.

Apple *et al.* (2000) grew two-year-old Douglas fir seedlings for three years in controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 350 or 550 ppm and ambient or elevated (ambient plus 4°C) air temperatures. They found neither elevated CO₂ nor elevated air temperature, acting alone or together, significantly affected needle stomatal density.

By contrast, in a study of the long-term effects of elevated CO₂ on various leaf properties of mature white oak trees growing at different distances from CO₂-emitting springs in central Italy, Paoletti *et al.* (1998) found elevated CO₂ significantly decreased leaf stomatal density by a factor of nearly 1.5 as the air's CO₂ concentration rose from 350 to 750 ppm. From that point on, however, there were no further reductions in stomatal density, even for CO₂ concentrations as great as 2600 ppm.

Evaluating the impact of a 350-to-750 ppm increase in the atmosphere's CO₂ concentration, Lin *et al.* (2001) grew seven-year-old Scots pine seedlings in the field in open-top chambers for four years, applying no additional nutrients or irrigation waters to the soils in which the young trees were rooted. After

the fourth year of their experiment, a detailed analysis of their data revealed the extra CO₂ reduced needle stomatal density by an average of 7.4%, indicating Scots pines may be better able to conserve water and cope with periods of drought and water stress in a high-CO₂ world of the future.

Beerling *et al.* (1998) grew one-year old *Ginkgo biloba* saplings in greenhouses maintained at atmospheric CO₂ concentrations of 350 and 560 ppm for three years. They found the leaves of plants grown at 560 ppm CO₂ exhibited significant reductions in both stomatal density (number of stomates per leaf area) and stomatal index (ratio of stomata to epidermal cells). Interestingly, the stomatal density of the CO₂-enriched leaves was similar to that measured on fossilized *Ginkgo* leaves dating back to the Triassic and Jurassic time periods, and because the CO₂-induced reductions in stomatal density and index did not impact rates of photosynthesis, it can be inferred the water-use efficiencies of ancient *Ginkgo* species were much higher than those of their modern counterparts. Consequently, as the CO₂ content of the air continues to rise, it may, as Beerling *et al.* remark, “contribute to restoring the function of this ‘living fossil’ species back to that more representative of its long geological history.”

Much like what has been learned about herbaceous plants, studies of the effects of atmospheric CO₂ enrichment on the leaf stomatal density of woody species reveal a wide range of responses, from no change at all to a double-digit percentage point decrease that ceases after a few hundred ppm increase in CO₂. These changes have been found to be beneficial to the species that exhibit them, including the cessation of the response at a species-specific critical atmospheric CO₂ concentration.

References

- Apple, M.E., Olszyk, D.M., Ormrod, D.P., Lewis, J., Southworth, D., and Tingey, D.T. 2000. Morphology and stomatal function of Douglas fir needles exposed to climate change: elevated CO₂ and temperature. *International Journal of Plant Science* **161**: 127–132.
- Beerling, D.J., McElwain, J.C., and Osborne, C.P. 1998. Stomatal responses of the ‘living fossil’ *Ginkgo biloba* L. to changes in atmospheric CO₂ concentrations. *Journal of Experimental Botany* **49**: 1603–1607.
- Lin, J., Jach, M.E., and Ceulemans, R. 2001. Stomatal density and needle anatomy of Scots pine (*Pinus sylvestris*) are affected by elevated CO₂. *New Phytologist* **150**: 665–674.

Paoletti, E., Nourrisson, G., Garrec, J.P., and Raschi, A. 1998. Modifications of the leaf surface structures of *Quercus ilex* L. in open, naturally CO₂-enriched environments. *Plant, Cell and Environment* **21**: 1071–1075.

2.28 Sugars

- Atmospheric CO₂ enrichment typically increases plants’ ability to produce greater amounts of various forms of sugar.

Plants grown in CO₂-enriched atmospheres nearly always exhibit increased photosynthetic rates, which typically lead to increased foliar concentrations of total nonstructural carbohydrates, including various sugars. Schortemeyer *et al.* (1999), for example, report significant increases in leaf total nonstructural carbohydrate contents in an Australian tree species exposed to twice-ambient atmospheric CO₂ concentrations for six weeks. Similarly, Wurth *et al.* (1998) found twice-ambient CO₂ levels increased leaf sugar concentrations by an average of 30% in four Panamanian tropical tree species. Just an eight-day exposure of apple seedlings to an atmospheric CO₂ concentration of 1,600 ppm led to a 38% increase in leaf sorbitol concentration.

In a study of *Pinus radiata* seedlings that had been growing for several years in open-top chambers maintained at atmospheric CO₂ concentrations of 360 and 650 ppm, Griffin *et al.* (2000) found needle sugar contents increased by 26%. Likewise, studying young spruce (*Picea abies*) seedlings for three years in growth chambers maintained at atmospheric CO₂ concentrations of 280, 420, and 560 ppm, Wiemken and Ineichen (2000) discovered that in late summer, fall, and winter, glucose concentrations in needles on the CO₂-enriched trees were 40 to 50% higher than those of needles on trees subjected to ambient and sub-ambient CO₂ concentrations (420 and 280 ppm, respectively).

Atmospheric CO₂ enrichment also has been documented to increase sugar contents in plant organs other than leaves. Lake and Hughes (1999), for example, found a doubling of the air’s CO₂ concentration produced a 2.4-fold increase in nectar production in nasturtium flowers. And in the early flowering stage of *Cucumis melo* melons, Dag and Eisikowitch (2000) observed in a sector of a greenhouse maintained at a CO₂ concentration of 1,000 ppm throughout the morning, 400 ppm between 1300 and 1500 hours, and then 600 ppm until the next morning, nectar volumes per flower were

Plant Characteristics

significantly higher than in the control sector of the greenhouse, sometimes by as much as 100%.

De Souza *et al.* (2008) grew sugarcane (*Saccharum officinarum* L.), one of Earth's most important sugar-producing plants, in pots within open-top chambers maintained at either ambient (~370 ppm) or elevated (~720 ppm) atmospheric CO₂ concentrations in the field under natural conditions at Sao Paulo, Brazil over a period of 50 weeks, during which time and at the end of the season, various plant physiological parameters and properties were measured. The plants grown in the elevated CO₂ chambers exhibited "an increase of about 30% in photosynthesis and 17% in height, and accumulated 40% more biomass in comparison with the plants grown at ambient CO₂," and the CO₂-enriched plants "also had lower stomatal conductance and transpiration rates (-37 and -32%, respectively), and higher water use efficiency (c.a. 62%)." In addition, the sucrose concentration in the sugarcane leaves rose from 2.18% in the ambient-treatment plants to 2.82% in the CO₂-enriched plants, for a CO₂-induced increase of 29%.

References

Dag, A. and Eisikowitch, D. 2000. The effect of carbon dioxide enrichment on nectar production in melons under greenhouse conditions. *Journal of Apicultural Research* **39**: 88–89.

De Souza, A.P., Gaspar, M., da Silva, E.A., Ulian, E.C., Waclawovsky, A.J., Nishiyama Jr., M.Y., dos Santos, R.V., Teixeira, M.M., Souza, G.M., and Buckeridge, M.S. 2008. Elevated CO₂ increases photosynthesis, biomass and productivity, and modifies gene expression in sugarcane. *Plant, Cell and Environment* **31**: 1116–1127.

Griffin, K.L., Tissue, D.T., Turnbull, M.H., and Whitehead, D. 2000. The onset of photosynthetic acclimation to elevated CO₂ partial pressure in field-grown *Pinus radiata* D. Don. after 4 years. *Plant, Cell and Environment* **23**: 1089–1098.

Lake, J.C. and Hughes, L. 1999. Nectar production and floral characteristics of *Tropaeolum majus* L. grown in ambient and elevated carbon dioxide. *Annals of Botany* **84**: 535–541.

Pan, Q., Wang, Z., and Quebedeaux, B. 1998. Responses of the apple plant to CO₂ enrichment: changes in photosynthesis, sorbitol, other soluble sugars, and starch. *Australian Journal of Plant Physiology* **25**: 293–297.

Schortemeyer, M., Atkin, O.K., McFarlane, N., and Evans, J.R. 1999. The impact of elevated atmospheric CO₂ and

nitrate supply on growth, biomass allocation, nitrogen partitioning and N₂ fixation of *Acacia melanoxylon*. *Australian Journal of Plant Physiology* **26**: 737–774.

Wiemken, V. and Ineichen, K. 2000. Seasonal fluctuations of the levels of soluble carbohydrates in spruce needles exposed to elevated CO₂ and nitrogen fertilization and glucose as a potential mediator of acclimation to elevated CO₂. *Journal of Plant Physiology* **156**: 746–750.

Wurth, M.K.R., Winter, K., and Korner, C. 1998. Leaf carbohydrate responses to CO₂ enrichment at the top of a tropical forest. *Oecologia* **116**: 18–25.

2.29 Tannins

Atmospheric CO₂ enrichment significantly enhances the condensed tannin concentrations of the vast majority of Earth's trees and grasses, giving them stronger defenses against various herbivores both above and below ground. And by causing less methane to be released to the atmosphere via ruminants browsing on tree leaves and grass, this phenomenon should reduce the rate of rise of the air's methane concentration and thereby decrease methane-induced global warming.

Condensed tannins are naturally occurring secondary carbon compounds produced in the leaves of a number of different plants that often act to deter herbivorous insects. In New Zealand, the Legume Lotus is a good source of these substances, and scientists with the country's AgResearch Grasslands institute have determined sheep and cattle feeding on forage containing this plant may reduce their methane emissions by as much as 16%.

This latter finding is of special importance to New Zealanders, because the methane expelled by cattle and sheep, which is a by-product of the fermentation of feed in the rumen of these animals, accounts for close to 90% of the country's methane emissions. A significant reduction in such a large national source of one of the atmosphere's most potent greenhouse gases would go a long way toward reducing emissions of climate-altering substances, which would be, according to the press release that described this development, "very welcome." The release also stated consumption of tannins has "a variety of other animal-related benefits, such as improved milk yield, increased liveweight gain, decreased internal parasite burden and reduced occurrence of bloat, dags and fly strike."

It is also important to note ruminants, as they are called, comprise a great group of animals in addition to sheep and cattle. They are four-footed, hoofed,

even-toed, cud-chewing mammals that have a stomach consisting of four divisions or chambers; the group includes antelope, bison, buffalo, camel, deer, giraffe, goat, llama, etc. These animals eat a number of other types of plants that may also experience increases in leaf tannin production as the air's CO₂ content rises. The following sections investigate this subject as it applies to other types of plants.

2.29.1 Aspen Trees

- Because the amount of methane expelled by ruminants is an inverse function of the amount of condensed tannins contained in the foliage they consume, the increased tannin concentrations likely to exist in aspen foliage in a high-CO₂ world of the future should result in less methane being released to the atmosphere via ruminants browsing on the trees' leaves. This should help decrease methane-induced global warming.

King *et al.* (2001) grew aspen (*Populus tremuloides*) seedlings for five months in open-top chambers maintained at atmospheric CO₂ concentrations of either 350 or 700 ppm; at the end of this period they collected and analyzed naturally senesced leaf litter. They found the elevated CO₂ of this particular study had no effect on the tannin concentration of leaf litter.

A substantially different result was obtained in an earlier study of aspen leaves conducted by McDonald *et al.* (1999), who grew aspen seedlings in controlled environment greenhouses maintained at either ambient (387 ppm) or elevated (696 ppm) CO₂ concentrations under conditions of either low or high light availability (half and full sunlight, respectively) for 31 days after the mean date of bud break. Under low light conditions the CO₂-enriched seedlings exhibited an approximate 15% increase in leaf condensed tannin concentration, and under high light conditions the CO₂-induced increase in leaf condensed tannin concentration was 175%.

In a much more complex study, Agrell *et al.* (2005) examined the effects of ambient and elevated concentrations of atmospheric CO₂ (360 and 560 ppm, respectively) and O₃ (35–60 ppb and 52–90 ppb, respectively) on the foliar chemistry of more mature aspen trees of two different genotypes (216 and 259) growing out-of-doors at the Aspen Free Air CO₂ Enrichment (FACE) facility near Rhinelander, Wisconsin (USA). They also studied the impacts of these effects on the host plant preferences of forest tent caterpillar larvae.

Agrell *et al.* report, “the only chemical component showing a somewhat consistent covariation with larval preferences was condensed tannins,” noting “the tree becoming relatively less preferred as a result of CO₂ or O₃ treatment was in general also the one for which average levels of condensed tannins were most positively (or least negatively) affected by that treatment.” The mean condensed tannin concentrations of the aspen 216 and 259 genotypes were 25% and 57% higher, respectively, under the elevated CO₂ and O₃ combination treatment compared to the ambient CO₂ and O₃ combination treatment.

In light of these findings, it is logical to presume that as atmospheric concentrations of CO₂ and O₃ continue to rise, the increase in condensed tannin concentration likely to occur in the foliage of aspen trees should lead to their leaves becoming less preferred for consumption by the forest tent caterpillar, which according to Agrell *et al.* is “an eruptive generalist defoliator in North American hardwood forests, causing extensive damage during outbreak years (Fitzgerald, 1995).” Also, because the amount of methane expelled by ruminants is an inverse function of the amount of condensed tannins in the foliage they consume, the increased aspen foliage tannin concentrations likely to exist in a high-CO₂ world of the future should result in less methane being released to the atmosphere via ruminants browsing on aspen foliage, thus decreasing an impetus for methane-induced global warming.

References

- Agrell, J., Kopper, B., McDonald, E.P., and Lindroth, R.L. 2005. CO₂ and O₃ effects on host plant preferences of the forest tent caterpillar (*Malacosoma disstria*). *Global Change Biology* 11: 588–599.
- Fitzgerald, T.D. 1995. *The Tent Caterpillars*. Comstock Publishing, Ithaca, New York, USA.
- King, J.S., Pregitzer, K.S., Zak, D.R., Kubiske, M.E., Ashby, J.A., and Holmes, W.E. 2001. Chemistry and decomposition of litter from *Populus tremuloides* Michaux grown at elevated atmospheric CO₂ and varying N availability. *Global Change Biology* 7: 65–74.
- McDonald, E.P., Agrell, J., and Lindroth, R.L. 1999. CO₂ and light effects on deciduous trees: growth, foliar chemistry, and insect performance. *Oecologia* 119: 389–399.

2.29.2 Birch Trees

- Elevated concentrations of atmospheric CO₂ tend to increase leaf and fine-root tannin concentrations of birch trees, which tends to protect the trees' foliage from predation by voracious insect herbivores, protect the trees' roots from soil-borne pathogens and herbivores, enhance the sequestration of carbon in forest soils, and reduce methane emissions from ruminants that might consume the trees' foliage.

This section reviews how condensed tannin concentrations in the leaves and roots of paper birch (*Betula papyrifera* Marsh.) and silver birch (*Betula pendula* Roth) trees respond to atmospheric CO₂ enrichment with and without concomitant increases in atmospheric temperature and ozone concentrations.

Peltonen *et al.* (2005) studied the effect of doubled atmospheric CO₂ and O₃ concentrations on the accumulation of 27 phenolic compounds, including soluble condensed tannins, in the leaves of two European silver birch clones in seven-year-old soil-grown trees in central Finland exposed in open-top chambers for three growing seasons to ambient and twice-ambient atmospheric CO₂ and O₃ concentrations singly and in combination. They found the elevated CO₂ increased the concentration of soluble condensed tannins in the leaves of the trees by 19% and protected the leaves from elevated O₃ because, as they describe it, "all the O₃-derived effects on the leaf phenolics and traits were prevented by elevated CO₂."

Kuokkanen *et al.* (2003) grew two-year-old silver birch seedlings in both ambient air of 350 ppm CO₂ and air enriched to a CO₂ concentration of 700 ppm under conditions of either ambient temperature or ambient temperature plus 3°C for one full growing season in the field in closed-top chambers at the Mekrijärvi Research Station of the University of Joensuu in eastern Finland. Then, during the middle of the summer, when carbon-based secondary compounds of birch leaves are fairly stable, they picked several leaves from each tree and determined their condensed tannin concentrations, along with the concentrations of a number of other physiologically important substances. The concentration of total phenolics, condensed tannins, and their derivatives significantly increased in the leaves produced in the CO₂-enriched air, as also was observed by Lavola and Julkunen-Titto (1994), Williams *et al.* (1994), Kinney *et al.* (1997), Bezemer and Jones (1998), and Kuokkanen *et al.* (2001). The extra 350 ppm of CO₂ nearly tripled condensed tannin concentrations in the

ambient-temperature air, while it increased their concentrations in the elevated-temperature air by a factor in excess of 3.5.

Parsons *et al.* (2003) grew two-year-old paper birch saplings in well-watered and fertilized 16-liter pots from early May until late August in glasshouse rooms maintained at either 400 or 700 ppm CO₂. They found the concentration of condensed tannins in the fine roots of the saplings was increased by 27% in the CO₂-enriched treatment. The researchers state, "the higher condensed tannin concentrations that were present in the birch fine roots may offer these tissues greater protection against soil-borne pathogens and herbivores."

Parsons *et al.* (2004) collected leaf litter samples from early September to mid-October beneath paper birch trees growing in ambient and CO₂-enriched (to 200 ppm above ambient) FACE plots in northern Wisconsin (USA), which also were maintained under ambient and O₃-enriched (to 19 ppb above ambient) conditions. Afterward, the leaf mass produced in each treatment was determined, sub-samples of the leaves were assessed for a number of chemical constituents (including nitrogen, which hastens leaf decay, and condensed tannins, which retard decay). The remaining leaves were placed in 1-mm-aperture litterbags made of fiberglass cloth and left to decay on the ground for the next 12 months under the same atmospheric conditions in which they were produced. At the conclusion of the one-year litter-exposure period, the researchers measured the mass of remaining litter and determined the time required to achieve 95% mass loss.

Under ambient O₃ conditions, the nitrogen concentrations of the leaves in the CO₂-enriched plots at the time of litterfall were 31% less than those of the leaves in the ambient-CO₂ plots, and condensed tannin concentrations were 64% greater in the CO₂-enriched plots. Similarly, under the O₃-enriched conditions, leaf nitrogen concentrations were 32% less, and concentrations of condensed tannins were 99% greater.

These observations suggest leaf decay rates in the CO₂-enriched plots should be lower than in the ambient-CO₂ plots, and the mass-loss rates determined at the end of the one-year exposure period bore out this expectation. Parsons *et al.* report, "for control litter, 5% of mass remained after 3.6 years, while CO₂-enriched litter took ~4.5 years to turn over 95% of its mass." Hence, it could take 25% more time (4.5 years / 3.6 years) to lose an equivalent percentage of paper birch leaf litter from CO₂-enriched forests, independent of the air's O₃ concentration. In addition,

the CO₂-enriched trees “attained greater size, and a greater degree of canopy closure, and contributed more litterfall to the development of [the] forest floor than did trees in the control rings,” making it clear the ongoing rise in the atmosphere’s CO₂ concentration should greatly augment the sequestration of carbon by paper birch tree stands as the air’s CO₂ content climbs.

Also working at the Wisconsin FACE site, Agrell *et al.* (2005) examined the effects of ambient and elevated concentrations of atmospheric CO₂ (360 and 560 ppm) and O₃ (35–60 ppb and 52–90 ppb) on the foliar chemistry of paper birch trees, as well as the impacts of these effects on the host plant preferences of forest tent caterpillar larvae. They found the mean condensed tannin concentration of the birch tree leaves was 18% greater in the elevated CO₂ and O₃ treatment than in the ambient CO₂ and O₃ treatment. In addition, “the only chemical component showing a somewhat consistent covariation with larval preferences was condensed tannins,” and “the tree becoming relatively less preferred as a result of CO₂ or O₃ treatment was in general also the one for which average levels of condensed tannins were most positively (or least negatively) affected by that treatment.”

In light of these findings, it is logical to presume the rising atmospheric concentrations of CO₂ and O₃ and consequent increase in condensed tannin concentration likely to occur in the foliage of birch trees should lead to their leaves becoming less preferred for consumption by the forest tent caterpillar, which according to Agrell *et al.* is “an eruptive generalist defoliator in North American hardwood forests, causing extensive damage during outbreak years (Fitzgerald, 1995).” Also, because the amount of methane expelled by ruminants is an inverse function of the condensed tannin concentration of the foliage they consume, the higher birch-foliage tannin concentrations likely to prevail in a high-CO₂ world of the future should result in less methane being released to the atmosphere via ruminants browsing on the foliage of birch trees, reducing that impetus for methane-induced global warming.

Elevated concentrations of atmospheric CO₂ tend to increase leaf and fine-root tannin concentrations of birch trees, which in turn tends to protect the trees’ foliage from predation by voracious insect herbivores, protect the trees’ roots from soil-borne pathogens and herbivores, enhance the sequestration of carbon in forest soils, and reduce methane emissions from ruminants that consume the trees’ foliage.

References

- Agrell, J., Kopper, B., McDonald, E.P., and Lindroth, R.L. 2005. CO₂ and O₃ effects on host plant preferences of the forest tent caterpillar (*Malacosoma disstria*). *Global Change Biology* **11**: 588–599.
- Bezemer, T.M. and Jones, T.H. 1998. Plant-insect herbivore interactions in elevated atmospheric CO₂, quantitative analyses and guild effects. *Oikos* **82**: 212–222.
- Fitzgerald, T.D. 1995. *The Tent Caterpillars*. Comstock Publishing, Ithaca, New York, USA.
- Kinney, K.K., Lindroth, R.L., Jung, S.M., and Nordheim, E.V. 1997. Effects of CO₂ and NO₃ availability on deciduous trees, phytochemistry and insect performance. *Ecology* **78**: 215–230.
- Kuokkanen, K., Julkunen-Titto, R., Keinänen, M., Niemela, P., and Tahvanainen, J. 2001. The effect of elevated CO₂ and temperature on the secondary chemistry of *Betula pendula* seedlings. *Trees* **15**: 378–384.
- Kuokkanen, K., Yan, S., and Niemela, P. 2003. Effects of elevated CO₂ and temperature on the leaf chemistry of birch *Betula pendula* (Roth) and the feeding behavior of the weevil *Phyllobius maculicornis*. *Agricultural and Forest Entomology* **5**: 209–217.
- Lavola, A. and Julkunen-Titto, R. 1994. The effect of elevated carbon dioxide and fertilization on primary and secondary metabolites in birch, *Betula pendula* (Roth). *Oecologia* **99**: 315–321.
- Parsons, W.F.J., Kopper, B.J., and Lindroth, R.L. 2003. Altered growth and fine root chemistry of *Betula papyrifera* and *Acer saccharum* under elevated CO₂. *Canadian Journal of Forest Research* **33**: 842–846.
- Parsons, W.F.J., Lindroth, R.L., and Bockheim, J.G. 2004. Decomposition of *Betula papyrifera* leaf litter under the independent and interactive effects of elevated CO₂ and O₃. *Global Change Biology* **10**: 1666–1677.
- Peltonen, P.A., Vapaavuori, E., and Julkunen-Tiitto, R. 2005. Accumulation of phenolic compounds in birch leaves is changed by elevated carbon dioxide and ozone. *Global Change Biology* **11**: 1305–1324.
- Williams, R.S., Lincoln, D.E., and Thomas, R.B. 1994. Loblolly pine grown under elevated CO₂ affects early instar pine sawfly performance. *Oecologia* **98**: 64–71.

2.29.3 Oak Trees

- The large increase of condensed tannin concentrations in oak tree foliage produced in CO₂-enriched air results in methane emissions

from ruminants feeding on such foliage being lower than methane emissions from ruminants feeding on foliage grown in non-CO₂-enriched air, and foliage better able to resist herbivore attacks.

This section examines how rising air temperatures and atmospheric CO₂ concentrations affect the leaf tannin concentrations of several oak tree species, including myrtle oak (*Quercus myrtifolia* Wild.), pedunculate oak (*Quercus robur* L.), sand live oak (*Quercus geminata* Small), and Chapman's oak (*Quercus chapmanii* Sargent).

Dury *et al.* (1998) grew four-year-old pedunculate oak trees in pots within greenhouses maintained at ambient and twice-ambient atmospheric CO₂ concentrations in combination with ambient and elevated (ambient plus 3°C) air temperatures for approximately one year. The elevated CO₂ concentration had only minor and contrasting direct effects on leaf palatability, including a temporary increase in foliar phenolic concentrations and decreases in leaf toughness and nitrogen content. The elevated temperature treatment, on the other hand, significantly reduced leaf palatability, because oak leaf toughness increased as a consequence of temperature-induced increases in condensed tannin concentrations. Hence the five researchers conclude, "a 3°C rise in temperature might be expected to result in prolonged larval development, increased food consumption, and reduced growth" for herbivores feeding on oak leaves in a CO₂-enriched and warmer world of the future.

Cornelissen *et al.* (2003) studied fluctuating asymmetry in the leaves of two species of sclerophyllous oaks—myrtle oak (*Quercus myrtifolia*) and sand live oak (*Quercus geminata*)—that dominate a native scrub-oak community at the Kennedy Space Center, Titusville, Florida (USA), which has served as the base of operations for a number of important open-top-chamber investigations of the effects of a 350-ppm increase in the air's CO₂ concentration on this unique ecosystem. Fluctuating asymmetry is the terminology used to describe small variations from perfect symmetry in otherwise bilaterally symmetrical characters in an organism (Moller and Swaddle, 1997); such asymmetry is believed to arise as a consequence of developmental instabilities experienced during ontogeny that may result from various stresses, including both genetic and environmental factors (Moller and Shykoff, 1999).

Based on measurements of distances from the leaf midrib to the left and right edges of the leaf at its

widest point and leaf areas on the left and right sides of the leaf midrib, Cornelissen *et al.* determined "asymmetric leaves were less frequent in elevated CO₂, and, when encountered, they were less asymmetric than leaves growing under ambient CO₂." In addition, they found "*Q. myrtifolia* leaves under elevated CO₂ were 15.0% larger than in ambient CO₂ and *Q. geminata* leaves were 38.0% larger in elevated CO₂ conditions." They also determined "elevated CO₂ significantly increased tannin concentration for both *Q. myrtifolia* and *Q. geminata* leaves" and "asymmetric leaves contained significantly lower concentrations of tannins than symmetric leaves for both *Q. geminata* and *Q. myrtifolia*."

Commenting on their two primary findings—reduced percentages of leaves experiencing asymmetry in the presence of elevated levels of atmospheric CO₂ and the lesser degree of asymmetry exhibited by affected leaves in the elevated CO₂ treatment—Cornelissen *et al.* write, "a possible explanation for this pattern is the fact that, in contrast to other environmental stresses, which can cause negative effects on plant growth, the predominant effect of elevated CO₂ on plants is to promote growth with consequent reallocation of resources (Docherty *et al.*, 1996)." Another possibility they discuss "is the fact that CO₂ acts as a plant fertilizer," and, as a result, "elevated CO₂ ameliorates plant stress compared with ambient levels of CO₂," which is one of the well-documented biological benefits of atmospheric CO₂ enrichment (Idso and Idso, 1994).

With respect to the ancillary finding of CO₂-induced increases in tannin concentrations in the leaves of both oak species (a mean increase of approximately 35% for *Q. myrtifolia* and 43% for *Q. geminata*), this phenomenon may provide the two species with greater protection against herbivores, and part of that protection may be associated with the observed CO₂-induced reductions in the amount and degree of asymmetry in the leaves of the CO₂-enriched trees. Consistent with this hypothesis, for example, Stiling *et al.* (1999, 2003) found higher abundances of leaf miners in the leaves of the trees in the ambient CO₂ chambers, where asymmetric leaves were more abundant, and in the current study it was determined leaf miners attacked asymmetric leaves more frequently than would be expected by chance alone in both CO₂ treatments.

In a subsequent study conducted at the Kennedy Space Center's scrub-oak community, Hall *et al.* (2005b) evaluated foliar quality and herbivore damage in three oaks (*Q. myrtifolia*, *Q. chapmanii*, and *Q. geminata*) plus the nitrogen-fixing legume

Galactia elliottii at three-month intervals from May 2001 to May 2003, at which times samples of undamaged leaves were removed from each of the four species in all chambers and analyzed for various chemical constituents, and 200 randomly selected leaves of each species in each chamber were scored for the presence of six types of herbivore damage. The data indicated for condensed tannins, hydrolyzable tannins, total phenolics and lignin, in all four species there were always greater concentrations of all four leaf constituents in the CO₂-enriched leaves, with across-species mean increases of 6.8% for condensed tannins, 6.1% for hydrolyzable tannins, 5.1% for total phenolics, and 4.3% for lignin. There also were large CO₂-induced decreases in all leaf damage categories among all species: chewing (-48%), mines (-37%), eye spot gall (-45%), leaf tier (-52%), leaf mite (-23%), and leaf gall (-16%). Hall *et al.* conclude the changes in leaf chemical constituents and herbivore damage “suggest that damage to plants may decline as atmospheric CO₂ levels continue to rise.”

Largely overlapping the investigation of Hall *et al.* (2005b), Hall *et al.* (2005a) evaluated the effects of the Kennedy Space Center experiment’s extra 350 ppm of CO₂ on litter quality and herbivore activity, and their interactions, over the three-year-period 2000–2002. They found “changes in litter chemistry from year to year were far larger than effects of CO₂ or insect damage, suggesting that these may have only minor effects on litter decomposition.” The one exception to this finding was “condensed tannin concentrations increased under elevated CO₂ regardless of species, herbivore damage, or growing season,” rising by 11% in 2000, 18% in 2001, and 41% in 2002 as a result of atmospheric CO₂ enrichment, as best as can be determined from the researchers’ bar graphs. The five scientists also report “lepidopteran larvae can exhibit slower growth rates when feeding on elevated CO₂ plants (Fajer *et al.*, 1991) and become more susceptible to pathogens, parasitoids, and predators (Lindroth, 1996; Stiling *et al.*, 1999),” noting further that at their field site, “which hosts the longest continuous study of the effects of elevated CO₂ on insects, herbivore populations decline markedly under elevated CO₂ (Stiling *et al.*, 1999, 2002, 2003; Hall *et al.*, 2005b).”

The evidence thus suggests the large and continuous enhancement of condensed tannin concentrations in oak tree foliage produced in CO₂-enriched air will help reduce greenhouse gas-induced global warming because methane emissions from ruminants feeding on foliage rich in condensed

tannins tend to be lower than when those ruminants feed on foliage of lower tannin concentration. In addition, the marked tannin-induced declines in herbivore populations observed in CO₂-enriched open-top-chamber studies indicate the ongoing increase in atmospheric CO₂ will improve plants’ resistance to herbivore attacks, a highly beneficial outcome.

References

- Cornelissen, T., Stiling, P., and Drake, B. 2003. Elevated CO₂ decreases leaf fluctuating asymmetry and herbivory by leaf miners on two oak species. *Global Change Biology* **10**: 27–36.
- Docherty, M., Hurst, D.K., and Holopainen, J.K., *et al.* 1996. Carbon dioxide-induced changes in beech foliage cause female beech weevil larvae to feed in a compensatory manner. *Global Change Biology* **2**: 335–341.
- Dury, S.J., Good, J.E.G., Perrins, C.M., Buse, A., and Kaye, T. 1998. The effects of increasing CO₂ and temperature on oak leaf palatability and the implications for herbivorous insects. *Global Change Biology* **4**: 55–61.
- Fajer, E.D., Bowers, M.D., and Bazzaz, F.A. 1991. The effects of enriched CO₂ atmospheres on the buckeye butterfly, *Junonia coenia*. *Ecology* **72**: 751–754.
- Hall, M.C., Stiling, P., Hungate, B.A., Drake, B.G., and Hunter, M.D. 2005a. Effects of elevated CO₂ and herbivore damage on litter quality in a scrub oak ecosystem. *Journal of Chemical Ecology* **31**: 2343–2356.
- Hall, M.C., Stiling, P., Moon, D.C., Drake, B.G., and Hunter, M.D. 2005b. Effects of elevated CO₂ on foliar quality and herbivore damage in a scrub oak ecosystem. *Journal of Chemical Ecology* **31**: 267–285.
- Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: a review of the past 10 years’ research. *Agricultural and Forest Meteorology* **69**: 153–203.
- Lindroth, R.L. 1996. CO₂-mediated changes in tree chemistry and tree-Lepidoptera interactions. In: Koch, G.W. and Mooney, H.A. (Eds.) *Carbon Dioxide and Terrestrial Ecosystems*. Academic Press, San Diego, California, USA, pp. 105–120.
- Moller, A.P. and Shykoff, P. 1999. Morphological developmental stability in plants: patterns and causes. *International Journal of Plant Sciences* **160**: S135–S146.
- Moller, A.P. and Swaddle, J.P. 1997. *Asymmetry, Developmental Stability and Evolution*. Oxford University Press, Oxford, UK.

Plant Characteristics

Stiling, P., Cattell, M., Moon, D.C., Rossi, A., Hungate, B.A., Hymus, G., and Drake, B.G. 2002. Elevated atmospheric CO₂ lowers herbivore abundance, but increases leaf abscission rates. *Global Change Biology* 8: 658–667.

Stiling, P., Moon, D.C., Hunter, M.D., Colson, J., Rossi, A.M., Hymus, G.J., and Drake, B.G. 2003. Elevated CO₂ lowers relative and absolute herbivore density across all species of a scrub-oak forest. *Oecologia* 134: 82–87.

Stiling, P., Rossi, A.M., Hungate, B., Dijkstra, P., Hinkle, C.R., Knot III, W.M., and Drake, B. 1999. Decreased leaf-miner abundance in elevated CO₂: Reduced leaf quality and increased parasitoid attack. *Ecological Applications* 9: 240–244.

2.29.4 Other

- Atmospheric CO₂ enrichment significantly enhances the concentrations of condensed tannins in the vast majority of the planet's trees and grasses, providing them with stronger defenses against various herbivores both above and below ground. Increasing atmospheric CO₂ levels also may be helping to reduce the rate-of-rise of the air's methane concentration.

Ruminants—sheep, cattle, antelope, bison, buffalo, camel, deer, giraffe, goat, llama, and more—eat a wide variety of plants, many of which undergo increases in leaf tannin production as the air's CO₂ content rises, as has been found to be true for a number of different species, including both deciduous and evergreen trees, as described by Lindroth *et al.* (1993, 1995), Traw *et al.* (1996), and Hattenschwiler and Schafellner (1999), and a number of species of grass, as described by (Goverde *et al.*, 2002).

With respect to how widespread CO₂-induced increases in foliar phenolics and tannins are, and the magnitudes of their increases, almost all relevant knowledge initially came from studies of temperate-region trees, the leaf phenolic concentrations of which had been shown to rise by 20–60% in response to a doubling of the air's CO₂ content (Koricheva *et al.*, 1998; Peñuelas and Estiarte, 1998; McDonald *et al.*, 1999; Agrell *et al.*, 2000; Hartley *et al.*, 2000). This knowledge base was vastly enhanced by the experiment of Coley *et al.* (2002), which focused on nine species of tropical trees. The trees were rooted in the ground and grown in their natural environment (near the Smithsonian Tropical Research Institute's experiment site in central Panama), rather than being planted in pots and grown in greenhouses. This point

is especially important because nonnatural environments can lead to results different from those obtained with open-top chambers or FACE facilities constructed around trees growing out-of-doors in the absence of artificial root restrictions (O'Neil and Norby, 1996).

Eight of the nine species studied in Coley *et al.*'s six-month open-top chamber experiment exhibited positive leaf phenolic/tannin responses to a doubling of the atmosphere's CO₂ content, the largest of which was a concentration increase of 119%. The single negative response was a 27% decline, and the mean response of all nine species was an increase of 48%. These results are comparable with those obtained for temperate-region trees, and they provide the basis for Coley *et al.*'s primary conclusion; i.e., that although “both temperate and tropical trees show large interspecific variation in the extent of their response to CO₂ ... the overwhelming pattern is for an increase in phenolics by approximately 50%.”

For four years, Kelly *et al.* (2010) grew six-year-old quaking aspen (*Populus tremuloides*) clones, two-year-old white willow (*Salix alba*) clones, and two-year-old sugar maple (*Acer saccharum*) siblings out-of-doors at the University of Michigan Biological Station in northern Michigan (USA) in open-bottom root boxes enclosed within clear-plastic-wall open-top chambers continuously supplied throughout the growing season (from May until leaf senescence in November) with either ambient-CO₂-air (360 ppm) or elevated-CO₂-air (720 ppm). At the conclusion of the four-year period, fallen leaves were collected, dried, and analyzed for simple phenolic and condensed tannin concentrations. Kelly *et al.*'s tabular results indicate the 360-ppm CO₂ increase boosted the simple phenolics concentrations of the aspen, maple, and willow leaves by 16, 30, and 22%, respectively, and it boosted their condensed tannin concentrations by 60, 85, and 26%, respectively. And because both foliar phenolics and condensed tannins often enhance plant resistance to herbivore and pathogen attack, plus the fact that ruminants browsing on foliage containing condensed tannins seem to have a tendency to expel less methane to the atmosphere, the increased concentrations of these substances in the leaves of the trees grown in CO₂-enriched air bodes well for the health of the trees themselves and for some amelioration of CO₂- and methane-induced global warming.

These findings suggest many wild and domesticated animals may be participating in this important natural “program” for reducing methane emissions to the atmosphere. They may also be at

least partially responsible for the reduced rate of rise of the atmosphere's methane concentration (as shown in Figure 2.29.4.1) over the past few decades. If so, one could expect to see more of the same as the air's CO₂ content continues to rise; for the biosphere appears to take care of its own, as demonstrated by this unique negative feedback phenomenon.

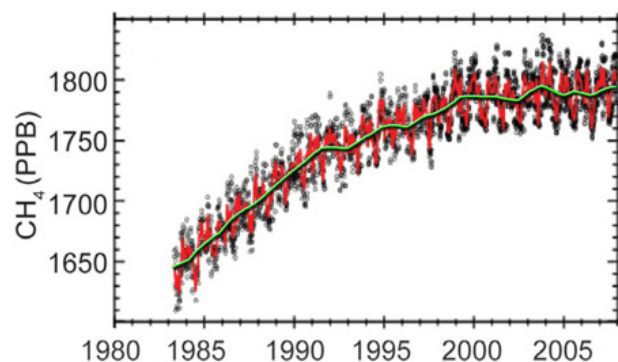


Figure 2.29.4.1. Trace gas mole fractions of methane (CH₄) as measured at Mauna Loa, Hawaii. Adapted from Schnell and Dlugokencky (2008).

References

- Agrell, J., McDonald, E.P., and Lindroth, R.L. 2000. Effects of CO₂ and light on tree phytochemistry and insect performance. *Oikos* **88**: 259–272.
- Coley, P.D., Massa, M., Lovelock, C.E., and Winter, K. 2002. Effect of elevated CO₂ on foliar chemistry of saplings of nine species of tropical tree. *Oecologia* **133**: 62–69.
- Freeman, C., Ostle, N., and Kang, H. 2001. An enzymic 'latch' on a global carbon store. *Nature* **409**: 149.
- Goverde, M., Bazin, A., Shykoff, J.A., and Erhardt, A. 1999. Influence of leaf chemistry of *Lotus corniculatus* (Fabaceae) on larval development of *Polyommatus icarus* (Lepidoptera, Lycaenidae): effects of elevated CO₂ and plant genotype. *Functional Ecology* **13**: 801–810.
- Goverde, M., Erhardt, A., and Niklaus, P.A. 2002. In situ development of a satyrid butterfly on calcareous grassland exposed to elevated carbon dioxide. *Ecology* **83**: 1399–1411.
- Hartley, S.E., Jones, C.G., Couper, G.C., and Jones, T.H. 2000. Biosynthesis of plant phenolic compounds in elevated atmospheric CO₂. *Global Change Biology* **6**: 497–506.
- Hattenschwiler, S. and Schafellner, C. 1999. Opposing effects of elevated CO₂ and N deposition on *Lymantria* *monacha* larvae feeding on spruce trees. *Oecologia* **118**: 210–217.
- Kelly, J.J., Bansal, A., Winkelman, J., Janus, L.R., Hell, S., Wencel, M., Belt, P., Kuehn, K.A., Rier, S.T., and Tuchman, N.C. 2010. Alteration of microbial communities colonizing leaf litter in a temperate woodland stream by growth of trees under conditions of elevated atmospheric CO₂. *Applied and Environmental Microbiology* **76**: 4950–4959.
- Koricheva, J., Larsson, S., Haukioja, E., and Keinänen, M. 1998. Regulation of woody plant metabolism by resource availability: hypothesis testing by means of a meta-analysis. *Oikos* **83**: 212–226.
- Lindroth, R.L., Arteel, G.E., and Kinney, K.K. 1995. Responses of three saturniid species to paper birch grown under enriched CO₂ atmospheres. *Functional Ecology* **9**: 306–311.
- Lindroth, R.L., Kinney, K.K., and Platz, C.L. 1993. Responses of deciduous trees to elevated atmospheric CO₂: Productivity, phytochemistry, and insect performance. *Ecology* **74**: 763–777.
- McDonald, E.P., Agrell, J., and Lindroth, R.L. 1999. CO₂ and light effects on deciduous trees: growth, foliar chemistry and insect performance. *Oecologia* **119**: 389–399.
- O'Neil, E.G. and Norby, R.J. 1996. Litter quality and decomposition rates of foliar litter produced under CO₂ enrichment. In: Koch, G.W. and Mooney, H.A. (Eds.) *Carbon Dioxide and Terrestrial Ecosystems*. Academic Press, San Diego, CA, pp. 87–103.
- Peñuelas, J. and Estiarte, M. 1998. Can elevated CO₂ affect secondary metabolism and ecosystem function? *Trends in Ecology and Evolution* **13**: 20–24.
- Peñuelas, J., Estiarte, M., and Llusia, J. 1997. Carbon-based secondary compounds at elevated CO₂. *Photosynthetica* **33**: 313–316.
- Schnell, R.C. and Dlugokencky, E. 2008. Methane. In: Levinson, D.H. and Lawrimore, J.H. (Eds.) *State of the Climate in 2007. Special Supplement to the Bulletin of the American Meteorological Society* **89**: S27.
- Traw, M.B., Lindroth, R.L., and Bazzaz, F.A. (1996) Decline in gypsy moth (*Lymantria dispar*) performance on an elevated CO₂ atmosphere depends upon host plant species. *Oecologia* **108**: 113–120.

2.30 Thylakoid Membranes

- Thylakoid membranes of chloroplasts perform a host of important functions that influence the process of carbon fixation in plants. In CO₂-

Plant Characteristics

enriched air, they generally perform these functions more efficiently, enabling plants to overcome some of the deleterious effects of a host of plant stresses, including insufficient soil moisture, abnormally cold temperatures, abnormally hot temperatures, and ozone pollution.

Nearly all plants respond positively to increases in the air's CO₂ content by increasing their rates of photosynthesis, partly as a consequence of decreases in photorespiration and increases in the operating efficiency of the primary carboxylating enzyme rubisco. Less research has addressed the direct effects of elevated CO₂ on thylakoid membranes, the membranes within chloroplasts that contain chlorophyll and other pigments that absorb sunlight, together with the specialized protein complexes of photosystem II that play an integral role in the light-dependent reactions of photosynthesis that convert sunlight into usable cellular energy. This section reviews the findings of papers investigating how elevated CO₂ may impact thylakoid membranes and thereby influence the overall process of carbon fixation in plants.

After growing alfalfa in open-top chambers at ambient (340 ppm) and enriched (600 ppm) atmospheric CO₂ concentrations with ample soil moisture for 25 days, followed by inadequate levels of soil moisture for five additional days, Sgherri *et al.* (1998) determined the plants grown in the elevated CO₂ treatment maintained greater leaf chlorophyll contents and lipid-to-protein ratios in their thylakoid membranes, especially under conditions of water stress. When water was withheld, for example, leaf chlorophyll content dropped by a mere 6% at 600 ppm CO₂, whereas it plummeted by approximately 30% at 340 ppm. Leaf lipid contents in the plants grown in the CO₂-enriched air were about 22 and 83% higher than those measured in the plants grown in the ambient air treatment during the periods of ample and insufficient soil moisture, respectively. In addition, in the high CO₂ treatment the average degree of unsaturation of the two most important thylakoid membrane lipids was approximately 20 and 37% greater than it was in plants grown at 340 ppm CO₂ during times of adequate and inadequate soil moisture, respectively.

With respect to the implications of these observations, it is generally believed that the greater concentrations of thylakoid lipids typically observed at elevated atmospheric CO₂ concentrations, plus their enhanced degree of unsaturation, may allow thylakoid

membranes to maintain a more fluid and stable environment, which is critical during periods of water stress in enabling plants to continue photosynthetic carbon uptake. These effects are so important, some researchers suggest adaptive plant responses such as these may allow plants to better cope with any altered environmental condition that produces stress.

The study of Tuba *et al.* (1998) provides a good example of this phenomenon as it pertains to extreme water stress. Detached leaves of *Xerophyta scabrida* (a woody shrub that grows in arid regions of east Africa) were rehydrated and regreened in air of 350 and 700 ppm CO₂, after which they were allowed to desiccate. The elevated CO₂ did not affect the amount of chlorophyll, the functioning of the thylakoid membranes, or the time to complete drying during desiccation. However, it allowed positive photosynthetic carbon gains in the shrub's leaves to continue three times longer than in leaves exposed to ambient air, which resulted in the CO₂-enriched leaves gaining more than 10 times the amount of carbon over the period of desiccation than was gained by the leaves exposed to normal air.

Tuba *et al.* also studied the effects of desiccation on the carbon balance of a moss and a lichen under the same two atmospheric CO₂ concentrations, observing similar response patterns in both plants. Positive photosynthetic carbon gains were maintained 14% longer with atmospheric CO₂ enrichment, and total assimilation during the dry-down in elevated CO₂ was increased by 52 and 69% in the lichen and moss, respectively.

Investigating responses to chilling, Hugly and Somerville (1992) worked with wild-type *Arabidopsis thaliana* and two mutants deficient in thylakoid lipid unsaturation. They found "chloroplast membrane lipid polyunsaturation contributes to the low-temperature fitness of the organism" and "is required for some aspect of chloroplast biogenesis." When lipid polyunsaturation was low, for example, they observed "dramatic reductions in chloroplast size, membrane content, and organization in developing leaves." Furthermore, they found a positive correlation "between the severity of chlorosis in the two mutants at low temperatures and the degree of reduction in polyunsaturated chloroplast lipid composition."

Kodama *et al.* (1994) demonstrated the low-temperature-induced suppression of tobacco leaf growth and concomitant induction of chlorosis observed in wild-type plants was much less evident in transgenic plants containing a gene that allowed for greater expression of unsaturation in the fatty acids of leaf lipids. They conclude substantially unsaturated

fatty acids “are undoubtedly an important factor contributing to cold tolerance.”

Moon *et al.* (1995) found heightened unsaturation of the membrane lipids of chloroplasts stabilized the photosynthetic machinery of transgenic tobacco plants against low-temperature photoinhibition “by accelerating the recovery of the photosystem II protein complex.” Also working with transgenic tobacco plants, Kodama *et al.* (1995) showed increased fatty acid desaturation is one of the prerequisites for normal leaf development at low, nonfreezing temperatures, and Ishizaki-Nishizawa *et al.* (1996) demonstrated transgenic tobacco plants with a reduced level of saturated fatty acids in most membrane lipids “exhibited a significant increase in chilling resistance.”

These observations are laden with significance for Earth’s agro-ecosystems because many economically important crops, such as rice, maize, and soybeans, are classified as chilling-sensitive; they experience injury or death at temperatures between 0 and 15°C (Lyons, 1973). But if atmospheric CO₂ enrichment enhances their production and degree-of-unsaturation of thylakoid lipids, as it does in alfalfa, a continuation of the ongoing rise in the air’s CO₂ content could increase the abilities of these critically important agricultural species to withstand periodic exposure to debilitating low temperatures. This phenomenon could provide the extra boost in food production that will be needed to sustain the planet’s increasing human population in the future (Wallace, 2000; Tilman *et al.*, 2001).

Earth’s natural ecosystems also would benefit from a CO₂-induced increase in thylakoid lipids containing more-highly-unsaturated fatty acids. Many plants of tropical origin, for example, suffer cold damage when temperatures fall below 20°C (Graham and Patterson, 1982), and with the improved lipid characteristics provided by the ongoing rise in the air’s CO₂ content, such plants would be able to expand their ranges both poleward and upward in a higher-CO₂ world, significantly increasing ecosystem biodiversity along the way.

At the other end of the biologically tolerable temperature spectrum is heat stress. Taub *et al.* (2000) note electron transport through photosystem II is the most heat-sensitive component of the photosynthetic process, and any reductions in electron transport through this thylakoid-membrane-bound protein complex invariably lead to reductions in photosynthetic carbon uptake and reduced growth potential. Hence, they conducted several experiments on herbaceous, woody, monocot, and dicot species (to

assess the degree of universality of any response that might be detected) in controlled environment chambers, greenhouses, and FACE plots to examine the photosynthetic responses of this wide array of plants to acute heat stress under ambient and elevated CO₂ concentrations ranging from 550 to 1,000 ppm.

Of the 16 plant species studied, all but one displayed greater photochemical efficiencies of photosystem II when growing in CO₂-enriched air as opposed to ambient air when exposed to high air temperatures. The air temperatures that caused a 50% reduction in the maximum efficiency of photosystem II were nearly one degree Celsius higher for plants grown in elevated CO₂ air than for plants grown in ambient air. In other words, elevated CO₂ almost universally allowed more electrons to flow through photosystem II, thereby laying the foundation for greater photosynthetic rates. In an extended experiment, rates of net photosynthesis measured at 40°C in CO₂-enriched cucumbers were 3.2 times greater than those exhibited by plants grown in ambient air and exposed to the same air temperature.

Another stress to which many plants are routinely exposed is elevated atmospheric ozone concentrations. Oksanen *et al.* (2001) grew aspen clones with varying degrees of ozone tolerance together with sugar maple and paper birch trees for three years in 30-m diameter FACE plots maintained at atmospheric CO₂ concentrations of 360 and 560 ppm with and without exposure to elevated ozone concentrations (1.5 times ambient) to study the interactive effects of these two trace gases on leaf ultrastructure.

In the birch trees, the negative effects of ozone on leaf ultrastructure were minor, and injuries to thylakoid membranes were partially ameliorated by exposure to elevated CO₂. In the aspen clones, ozone exposure caused more significant structural injuries to thylakoid membranes and the stromal compartment within chloroplasts, but these injuries also were largely ameliorated by atmospheric CO₂ enrichment. Leaf thickness, mesophyll tissue thickness, the amount of chloroplasts per unit cell area, and the amount of starch in chloroplasts all were lower in the high ozone treatment, but simultaneous exposure of the ozone-stressed trees to elevated CO₂ more than compensated for the ozone-induced problems. As tropospheric ozone concentrations continue to rise, therefore, they likely will pose a problem for regenerating aspen and birch trees by negatively affecting chloroplast ultrastructure at the site of carbon fixation, which likely will decrease their productivity and growth. However, if the atmospheric CO₂ concentration also continues to rise, these

negative effects will be either partly, completely, or more than completely ameliorated, thus stimulating productivity and growth to varying degrees within these species.

The studies reviewed above suggest atmospheric CO₂ enrichment may constitute a powerful remedy for all sorts of environmental ailments that afflict plants and have their origin in stress-induced problems associated with the functioning of the thylakoid membranes of the plants' chloroplasts.

References

Graham, D. and Patterson, B.D. 1982. Responses of plants to low, non-freezing temperatures: proteins, metabolism, and acclimation. *Annual Review of Plant Physiology* **33**: 347–372.

Hugly, S. and Somerville, C. 1992. A role for membrane lipid polyunsaturation in chloroplast biogenesis at low temperature. *Plant Physiology* **99**: 197–202.

Ishizaki-Nishizawa, O., Fujii, T., Azuma, M., Sekiguchi, K., Murata, N., Ohtani, T., and Toguri T. 1996. Low-temperature resistance of higher plants is significantly enhanced by a nonspecific cyanobacterial desaturase. *Nature Biotechnology* **14**: 1003–1006.

Kodama, H., Hamada, T., Horiguchi, G., Nishimura, M., and Iba, K. 1994. Genetic enhancement of cold tolerance by expression of a gene for chloroplast w-3 fatty acid desaturase in transgenic tobacco. *Plant Physiology* **105**: 601–605.

Kodama, H., Horiguchi, G., Nishiuchi, T., Nishimura, M., and Iba, K. 1995. Fatty acid desaturation during chilling acclimation is one of the factors involved in conferring low-temperature tolerance to young tobacco leaves. *Plant Physiology* **107**: 1177–1185.

Lyons, J.M. 1973. Chilling injury in plants. *Annual Review of Plant Physiology* **24**: 445–466.

Moon, B.Y., Higashi, S.-I., Gombos, Z., and Murata, N. 1995. Unsaturation of the membrane lipids of chloroplasts stabilizes the photosynthetic machinery against low-temperature photoinhibition in transgenic tobacco plants. *Proceedings of the National Academy of Sciences, USA* **92**: 6219–6223.

Oksanen, E., Sober, J., and Karnosky, D.F. 2001. Impacts of elevated CO₂ and/or O₃ on leaf ultrastructure of aspen (*Populus tremuloides*) and birch (*Betula papyrifera*) in the Aspen FACE experiment. *Environmental Pollution* **115**: 437–446.

Sgherri, C.L.M., Quartacci, M.F., Menconi, M., Raschi, A., and Navari-Izzo, F. 1998. Interactions between drought and elevated CO₂ on alfalfa plants. *Journal of Plant Physiology* **152**: 118–124.

Taub, D.R., Seeman, J.R., and Coleman, J.S. 2000. Growth in elevated CO₂ protects photosynthesis against high-temperature damage. *Plant, Cell and Environment* **23**: 649–656.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., and Swackhamer, D. 2001. Forecasting agriculturally driven global environmental change. *Science* **292**: 281–284.

Tuba, Z., Csintalan, Z., Szente, K., Nagy, Z., and Grace, J. 1998. Carbon gains by desiccation-tolerant plants at elevated CO₂. *Functional Ecology* **12**: 39–44.

Wallace, J.S. 2000. Increasing agricultural water use efficiency to meet future food production. *Agriculture, Ecosystems & Environment* **82**: 105–119.

2.31 Transpiration

2.31.1 Herbaceous Plants

If the atmosphere's CO₂ content continues to rise as it has over the past few decades, the world's farmers should be able to produce substantially more food on each hectare of land with little or no change in per-hectare water requirements. In the case of C₄ crops, higher yields may be produced with smaller amounts of water, even in the face of higher temperatures. And most herbaceous non-crop plants should respond to increases in the air's CO₂ concentration in like manner, leading to greater soil moisture content in CO₂-enriched ecosystems and a positive effect on plant growth.

2.31.1.1 Crops

- If the atmosphere's CO₂ content continues to rise as it has over the past few decades, the world's farmers should be able to produce substantially more food on each hectare of land with little or no change in per-hectare water requirements. Higher yields of C₄ crops may be produced with smaller amounts of water, even in higher temperatures.

Most plants respond to increases in the atmosphere's CO₂ content by reducing their leaf stomatal conductances, which typically leads to reduced rates of transpirational water loss. The resultant water savings, in turn, often lead to greater soil moisture content in CO₂-enriched ecosystems, with positive effects on plant water status and growth. This section

reviews the results of studies of both C₃ and C₄ crops that treat various aspects of this CO₂-induced multistage interaction.

Dong-Xiu *et al.* (2002) grew spring wheat in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm and three levels of soil moisture (40, 60, and 80% of field capacity). In addition to increasing rates of net photosynthesis by 48, 120, and 97% at low, medium, and high soil water contents, this doubling of the air's CO₂ concentration reduced rates of transpiration by 56, 53, and 63%, respectively, in the three soil water treatments.

De Costa *et al.* (2003) grew two crops of rice in the field in Sri Lanka—from January to March (the *maha* season) and from May to August (the *yala* season)—in open-top chambers maintained at either ambient or ambient plus 200 ppm CO₂. Leaf net photosynthetic rates were significantly higher in the CO₂-enriched chambers than in the ambient-air chambers: 51–75% greater in the *maha* season and 22–33% greater in the *yala* season. In addition, leaf stomatal conductances exhibited CO₂-induced reductions of 15–52% in the *maha* season and 13–19% in the *yala* season. However, because of the significantly greater leaf area in the CO₂-enriched chambers, total canopy transpiration rate per unit land area did not differ significantly between the two CO₂ treatments. Nevertheless, leaf water potentials were higher (less negative, and therefore more beneficial) in the CO₂-enriched chambers.

Vu (2005) grew peanuts from seed to maturity in greenhouses maintained at atmospheric CO₂ concentrations of 360 and 720 ppm and at air temperatures 1.5 and 6.0°C above outdoor air temperatures. Although rubisco protein content and activity were down-regulated by elevated CO₂, the rubisco photosynthetic efficiency of the elevated-CO₂ plants “was 1.3- to 1.9-fold greater than that of the ambient-CO₂ plants at both growth temperatures.” He also found “leaf soluble sugars and starch of plants grown at elevated CO₂ were 1.3- and 2-fold higher, respectively, than those of plants grown at ambient CO₂.” Finally, the leaf transpirational water loss of the elevated-CO₂ plants compared to that of the ambient-CO₂ plants was 12% less at near-ambient temperatures and 17% less in the higher temperature regime.

Malmstrom and Field (1997) grew individual oat plants for two months in pots placed within phytocells having atmospheric CO₂ concentrations of 350 and 700 ppm. One-third of the plants were infected with the barley yellow dwarf virus that plagues more than 150 plant species, including all major cereal crops.

The elevated CO₂ stimulated rates of net photosynthesis in all plants, with the greatest percentage increase occurring in diseased individuals (48% vs. 34%), and it decreased stomatal conductance by 50% in infected plants and 34% in healthy ones, thus reducing transpirational water losses. Together, these phenomena contributed to a CO₂-induced doubling of the instantaneous water use efficiency in healthy plants and a 2.7-fold increase in diseased plants.

Leakey *et al.* (2004) grew corn in their SoyFACE facility in the heart of the U.S. Corn Belt while exposing different parts of the field to atmospheric CO₂ concentrations of 354 and 549 ppm during a year of summer rainfall “very close to the 50-year average for this site, indicating that the year was not atypical or a drought year.” On five days during the growing season (11 and 22 July, 9 and 21 August, and 5 September), they measured diurnal patterns of photosynthesis, stomatal conductance, and micro-climatic conditions.

Contrary to what many people had long assumed would be the case for a C₄ crop such as corn growing under the best of natural conditions, Leakey *et al.* found “growth at elevated CO₂ significantly increased leaf photosynthetic CO₂ uptake rate by up to 41%.” The highest whole-day increase was 21% (11 July) followed by 11% (22 July), during a period of low rainfall. Thereafter, however, during a period of greater rainfall, there were no significant differences between the photosynthetic rates of the plants in the two CO₂ treatments. Over the entire growing season, the CO₂-induced increase in leaf photosynthesis averaged 10%.

Additionally, on all but the first day of measurements, stomatal conductance was significantly lower (–23% on average) in the elevated CO₂ treatment, which led to reduced transpiration rates in the CO₂-enriched plants. And since “low soil water availability and high evaporative demand can both generate water stress and inhibit leaf net CO₂ assimilation in C₄ plants,” as Leakey *et al.* note, they conclude the lower transpiration rates of the plants growing in the CO₂-enriched air “may have counteracted the development of water stress under elevated CO₂ and prevented the inhibition of leaf net CO₂ assimilation observed under ambient CO₂.”

Therefore, they write, “contrary to expectations, this US Corn Belt summer climate appeared to cause sufficient water stress under ambient CO₂ to allow the ameliorating effects of elevated CO₂ to significantly enhance leaf net CO₂ assimilation.” They conclude this response of corn to elevated CO₂ “indicates the potential for greater future crop biomass and harvest-

able yield across the US Corn Belt,” due largely to the amelioration of water stress by CO₂-induced decreases in transpirational water loss.

Grant *et al.* (2004) adjusted the crop growth and water relations model *ecosys* to represent the C₄ crop sorghum and ran it for two growing seasons (1 May 1998 to 31 October 1999) under both wet and dry irrigation regimes at two atmospheric CO₂ concentrations (approximately 368 and 561 ppm), using hourly meteorological data measured at a field south of Phoenix, Arizona (USA). They used these simulated energy balances and water relations—verified by measurements of energy flux and water potential—to infer the effects of free-air atmospheric CO₂ enrichment on various plant parameters and processes.

The 12 researchers report “model results, corroborated by field measurements, showed elevated CO₂ raised canopy water potential and lowered latent heat fluxes under high irrigation [both of which responses are beneficial] and delayed water stress under low irrigation [which is also beneficial].” As they described it elsewhere, the elevated CO₂ “reduced transpiration and hence improved water status of sorghum [and] lowered the vulnerability of sorghum CO₂ fixation to soil or atmospheric water deficits, even when irrigation was high.” Also, in applying their reality-tuned model to a scenario where the air’s CO₂ content was 50% higher and air temperature was 3°C greater, they calculated sorghum yields would rise by about 13%, and “current high sorghum yields could be achieved with ~120 mm or ~20% less irrigation water if these rises in temperature and CO₂ were to occur.”

The studies reviewed here suggest a continued rise of the atmosphere’s CO₂ content should allow production of substantially more food on each hectare of land with little or no change in per-hectare water requirements. In the case of C₄ crops, it appears higher yields may be produced with smaller amounts of water, even in the face of higher temperatures.

References

De Costa, W.A.J.M., Weerakoon, W.M.W., Abeywardena, R.M.I., and Herath, H.M.L.K. 2003. Response of photosynthesis and water relations of rice (*Oryza sativa*) to elevated atmospheric carbon dioxide in the subhumid zone of Sri Lanka. *Journal of Agronomy and Crop Science* **189**: 71–82.

Dong-Xiu, W., Gen-Xuan, W., Yong-Fei, B., Jian-Xiong, L., and Hong-Xu, R. 2002. Response of growth and water

use efficiency of spring wheat to whole season CO₂ enrichment and drought. *Acta Botanica Sinica* **44**: 1477–1483.

Grant, R.F., Kimball, B.A., Wall, G.W., Triggs, J.M., Brooks, T.J., Pinter Jr., P.J., Conley, M.M., Ottman, M.J., Lamorte, R.L., Leavitt, S.W., Thompson, T.L., and Matthias, A.D. 2004. Modeling elevated carbon dioxide effects on water relations, water use, and growth of irrigated sorghum. *Agronomy Journal* **96**: 1693–1705.

Leakey, A.D.B., Bernacchi, C.J., Dohleman, F.G., Ort, D.R., and Long, S.P. 2004. Will photosynthesis of maize (*Zea mays*) in the US Corn Belt increase in future [CO₂] rich atmospheres? An analysis of diurnal courses of CO₂ uptake under free-air concentration enrichment (FACE). *Global Change Biology* **10**: 951–962.

Malmstrom, C.M. and Field, C.B. 1997. Virus-induced differences in the response of oat plants to elevated carbon dioxide. *Plant, Cell and Environment* **20**: 178–188.

Vu, J.C.V. 2005. Acclimation of peanut (*Arachis hypogaea* L.) leaf photosynthesis to elevated growth CO₂ and temperature. *Environmental and Experimental Botany* **53**: 85–95.

2.31.1.2 Other Plants

- Most herbaceous non-crop plants respond to increases in the air’s CO₂ concentration by reducing their leaf stomatal conductances, which typically leads to reduced rates of evaporative water loss from them. The saved water, in turn, often leads to greater soil moisture content in CO₂-enriched ecosystems, with positive effects on plant growth.

This section examines the results of some studies of C₃ and C₄ grassland species that broach various aspects of this multifaceted subject.

Szente *et al.* (1998) grew four perennial C₃ plants (two grasses and two broad-leaved species) common to loess grasslands of Budapest in open-top chambers maintained at atmospheric CO₂ concentrations of 350 or 700 ppm for 231 days. They found this doubling of the air’s CO₂ content significantly enhanced rates of net photosynthesis in all species studied, with the two grasses and the two broad-leaved species exhibiting average increases of 136 and 486%, respectively. The extra CO₂ increased transpiration rates for one of the grasses and one of the broad-leaved species, but it did not affect the water loss rates of the remaining species. Nevertheless, the two grasses exhibited an average CO₂-induced increase in water use efficiency

of 72%, and the two broad-leaved species displayed an average increase of 366%. These large improvements should allow them to cope better with the hot and dry summers they characteristically experience in this part of Hungary.

Engloner *et al.* (2003) removed grassland monoliths with their original soils to a depth of 40 cm from a xeric loess grassland and relocated them to open-top chambers outside Budapest, where they were exposed for seven years to either ambient air or air enriched to a CO₂ concentration of 700 ppm. Measurements of leaf photosynthesis and transpiration rates of a dominant member of this ecosystem (couch-grass) were conducted throughout the experiment according to protocols described by Tuba *et al.* (1994, 1996), and measurements of starch and soluble sugars were made as described by Tuba *et al.* (1994). Rates of net photosynthesis increased by an average of 194% in response to the ~90% increase in atmospheric CO₂ concentration, leading to starch and soluble sugar increases of approximately 50 and 72%, respectively. Leaf transpiration rates declined by about 18%, leading to a 345% increase in water use efficiency, which for a xeric grassland species is like manna from heaven, greatly fortifying it against the rigors of its xeric environment.

Turning to C₄ plants, Seneweera *et al.* (1998) grew a drought-resistant perennial grass (*Panicum coloratum*) for five weeks in controlled environment chambers having atmospheric CO₂ concentrations of 350 or 1,000 ppm and different vapor pressure deficits (VPDs) maintained by keeping the relative humidity of the air at either 50 or 80%. The plants were watered daily to 65, 80, or 100% of their potting soils' field capacities. Under favorable environmental conditions, characterized by a low VPD and high soil moisture (100% field capacity), atmospheric CO₂ enrichment failed to cause any significant increases in leaf or stem dry weight. However, when water-stressed conditions prevailed, due to either a high VPD, low field capacities of 65 or 80%, or combinations of both parameters, elevated CO₂ caused large, significant increases in growth. At the high VPD, for example, the percentage increases in leaf dry weight at field capacities of 65 and 80% were 117 and 112%, respectively, and the growth responses for stems under these conditions were 50 and 57%.

These growth increases resulted in part from the ability of elevated CO₂ to ameliorate the negative effects of water stress on growth. Under the most extreme water-stressed condition, for example, leaf water potential values were about 3.5 times more negative, i.e., more stressful, for plants grown in air

of 350 ppm CO₂ than for plants grown in air of 1,000 ppm, because transpirational water loss was always less for plants grown in elevated CO₂. For the most water-stressed condition investigated, which resulted from a high VPD and a field capacity of 65%, the transpiration rates of plants grown in ambient CO₂ were about 2.5 times greater than those of plants grown in elevated CO₂. Consequently, higher concentrations of atmospheric CO₂ likely will allow C₄ grasses to maintain better internal water relations by reducing transpirational water losses, resulting in greater water-use efficiencies and the likely expansion of the plants into hot and arid regions commonly subjected to drought.

In an extension of this work, Seneweera *et al.* (2001) grew *P. coloratum* in controlled environment chambers maintained at atmospheric CO₂ concentrations of 360 and 1,000 ppm for three weeks before withholding water from half the plants for 10 days, after which the plants were rewatered for five days to promote recovery. At the onset of water stress, shoot dry mass in the CO₂-enriched plants was 33% greater than in the plants grown in ambient air. Although water stress reduced shoot dry mass, the reductions were less severe for CO₂-enriched than ambiently grown plants. During the water stress treatment, leaf water potentials and leaf relative water contents dropped at much slower rates and to lesser degrees in the CO₂-enriched plants than in the ambiently grown plants. Similarly, transpiration rates of the CO₂-enriched plants were much less than those of plants growing in ambient air, and this phenomenon helped contribute to the greater soil moisture contents that were always present beneath the CO₂-enriched plants. At final harvest, the CO₂-induced enhancement of shoot dry mass was 44 and 70% for plants that had been subjected to well-watered and water-stressed treatments, respectively.

In a two-year experiment in an annual-dominated California grassland, Zavaleta *et al.* (2003) delivered extra heating to a number of FACE plots (enriched with an extra 300 ppm of CO₂) via IR heat lamps that warmed the surface of the soil beneath them by 0.8–1.0°C. The individual effects of atmospheric CO₂ enrichment and soil warming were of similar magnitude, and acting together they enhanced mean spring soil moisture content by about 15% over that of the control plots. The effect of CO₂ was produced primarily as a consequence of its ability to cause partial stomatal closure and thereby reduce season-long plant water loss via transpiration. With warming, there was an acceleration of canopy senescence that further increased soil moisture by reducing the period

Plant Characteristics

of time (the length of the growing season) over which transpiration losses occur, all without any decrease in total plant production.

The six researchers note their findings “illustrate the potential for organism-environment interactions to modify the direction as well as the magnitude of global change effects on ecosystem functioning.” Whereas for the past several years there have been multiple predictions of vast reaches of agricultural land drying up and being lost to profitable production in a CO₂-enriched and warmed world of the future, this study suggests just the opposite could occur. As Zavaleta *et al.* describe it, “we suggest that in at least some ecosystems, declines in plant transpiration mediated by changes in phenology can offset direct increases in evaporative water losses under future warming.”

For both C₃ and C₄ grassland plants, the reductions in leaf transpirational water loss that result from increases in the air’s CO₂ concentration should significantly enhance their ability to withstand the rigors of periodic severe water stress in arid and semi-arid parts of the globe—even in the face of significant warming, which may induce its own beneficial feedback—while enhancing their productivities and thereby providing more forage for the various forms of animal life that inhabit these regions. In addition, these plants may reclaim great tracts of desert as their water use efficiencies rise to levels not experienced for millions of years.

References

- Engloner, A.I., Kovacs, D., Balogh, J., and Tuba, Z. 2003. Anatomical and eco-physiological changes in leaves of couch-grass (*Elymus repens* L.), a temperate loess grassland species, after 7 years growth under elevated CO₂ concentration. *Photosynthetica* **41**: 185–189.
- Seneweera, S.P., Ghannoum, O., and Conroy, J. 1998. High vapor pressure deficit and low soil water availability enhance shoot growth responses of a C₄ grass (*Panicum coloratum* cv. Bambatsi) to CO₂ enrichment. *Australian Journal of Plant Physiology* **25**: 287–292.
- Seneweera, S., Ghannoum, O., and Conroy, J.P. 2001. Root and shoot factors contribute to the effect of drought on photosynthesis and growth of the C₄ grass *Panicum coloratum* at elevated CO₂ partial pressures. *Australian Journal of Plant Physiology* **28**: 451–460.
- Szente, K., Nagy, Z., and Tuba, Z. 1998. Enhanced water use efficiency in dry loess grassland species grown at elevated air CO₂ concentration. *Photosynthetica* **35**: 637–640.
- Tuba, Z., Szente, K., and Koch, J. 1994. Response of photosynthesis, stomatal conductance, water use efficiency and production to long-term elevated CO₂ in winter wheat. *Journal of Plant Physiology* **144**: 651–668.
- Tuba, Z., Szente, K., Nagy, Z., Csintalan, Z., and Koch, J. 1996. Responses of CO₂ assimilation, transpiration and water use efficiency to long-term elevated CO₂ in perennial C₃ xeric loess steppe species. *Journal of Plant Physiology* **148**: 356–361.
- Zavaleta, E.S., Thomas, B.D., Chiariello, N.R., Asner, G.P., Shaw, M.R., and Field, C.B. 2003. Plants reverse warming effect on ecosystem water balance. *Proceedings of the National Academy of Science USA* **100**: 9892–9893.

2.31.2 Woody Plants

As the air’s CO₂ content rises, the water use efficiencies (amount of carbon gain per unit of water loss) of coniferous trees and dryland shrubs tend to rise as well. The same is true of most deciduous trees, enabling them to cope more effectively with the increased water stress they would otherwise experience in stressful conditions and locations.

2.31.2.1 Conifers

- As the air’s CO₂ content rises, conifer water use efficiency (the amount of carbon gain at the needle level per unit of water loss) tends to rise as well.

Apple *et al.* (2000) grew two-year-old Douglas fir seedlings for three additional years in controlled environment chambers maintained at atmospheric CO₂ concentrations of either 350 or 550 ppm and ambient or elevated (ambient plus 4°C) air temperature. They found the 200-ppm increase in the air’s CO₂ concentration and the 4°C increase in air temperature, when applied together, did not significantly affect seedling transpiration. When applied alone, however, the extra CO₂ reduced transpiration by 12%, and the elevated air temperature increased it by 66%.

After a one-year continuation of the same experiment, Lewis *et al.* (2002) report results obtained over its final 21 months. Once again, the extra CO₂ decreased transpiration by 12%, but the elevated air temperature increased it by 37%, considerably less than the 66% increase report by Apple *et al.* Adding more confusion, the combination of the identical CO₂ effect and a weaker temperature

effect yielded a 19% increase in transpiration, whereas in the first three years of the study the identical CO₂ effect and a stronger temperature effect produced no change in transpiration.

In a one-year study in which closed-top chambers were constructed around 30-year-old Scots pine trees growing in Finland, Kellomaki and Wang (1998) applied doubled CO₂ to half the trees while studying the effect of a 4°C increase in air temperature. The elevated CO₂ reduced cumulative sap flow (a measure of transpiration) by 14% in the trees maintained at ambient temperatures, but when both air temperature and CO₂ concentration were increased together, cumulative sap flow exhibited no change.

In the studies cited above, atmospheric CO₂ enrichment consistently produced a small reduction in tree transpiration rates at ambient air temperatures, and the added effect of warming was inconsistent and confusing. Hence, it is instructive to consider the study of Saurer *et al.* (2004), who measured carbon isotope ratios in the rings of coniferous trees of northern Eurasia (including the genera *Larix*, *Picea* and *Pinus*) across a longitudinal transect that covered the entire supercontinent in the latitude range 59–71°N. Between the two 30-year periods 1861–1890 and 1961–1990, when air temperature and CO₂ concentration both rose significantly, they found intrinsic water use efficiency (Wi, the amount of carbon gain at the needle level per unit of water loss) rose significantly, such that “125 out of 126 trees showed increasing Wi from 1861–1890 to 1961–1990, with an average improvement of $19.2 \pm 0.9\%$.”

The three Swiss scientists say their results suggest the trees they studied “are able to produce the same biomass today [as they did 100 years ago] but with lower costs in terms of transpiration.” This finding is very important because, they write, recent warming in other longitudinal segments of the same latitude belt “may be accompanied by increased drought stress (Lloyd and Fastie, 2002)” and the ongoing rise in the air’s CO₂ content may be helping the trees in those areas to better cope with this environmental challenge, even in the face of increasing air temperatures.

References

Apple, M.E., Olszyk, D.M., Ormrod, D.P., Lewis, J., Southworth, D., and Tingey, D.T. 2000. Morphology and stomatal function of Douglas fir needles exposed to climate change: elevated CO₂ and temperature. *International Journal of Plant Science* **161**: 127–132.

Kellomaki, S. and Wang, K.-Y. 1998. Sap flow in Scots pines growing under conditions of year-round carbon dioxide enrichment and temperature elevation. *Plant, Cell and Environment* **21**: 969–981.

Lewis, J.D., Lucash, M., Olszyk, D.M., and Tingey, D.T. 2002. Stomatal responses of Douglas-fir seedlings to elevated carbon dioxide and temperature during the third and fourth years of exposure. *Plant, Cell and Environment* **25**: 1411–1421.

Lloyd, A.H. and Fastie, C.L. 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change* **52**: 481–509.

Saurer, M., Siegwolf, R.T.W., and Schweingruber, F.H. 2004. Carbon isotope discrimination indicates improving water use efficiency of trees in northern Eurasia over the last 100 years. *Global Change Biology* **10**: 2109–2120.

2.31.2.2 Dryland Plants

- As the air’s CO₂ content rises, the water-use efficiencies of Earth’s dryland plants usually tend to rise as well.

In a FACE experiment conducted in a chaparral region of southern California, Roberts *et al.* (1998) exposed *Adenostoma fasciculatum* shrubs to atmospheric CO₂ concentrations of 360 and 550 ppm. After six months of treatment, it was clear the elevated CO₂ had reduced the stomatal conductances of the shrubs’ leaves and decreased their rates of evaporative water loss. The CO₂-enriched shrubs exhibited leaf water potentials significantly more positive (less stressful) than those of the plants growing in ambient air. This enhancement of internal water status should help this woody perennial better withstand the periods of drought that commonly occur throughout its southern California range.

Dugas *et al.* (2001) studied the response of whole-plant transpiration to atmospheric CO₂ enrichment in the woody legume *Acacia farnesiana*, which occurs throughout the south-central United States and is one of the most aggressive woody-plant invaders of grasslands worldwide. Plants of this species were grown for a full year in greenhouse bays continuously maintained at atmospheric CO₂ concentrations of either 385 or 980 ppm, and at the end of this time whole-plant transpiration was assessed via sap flow measurements. The mean transpiration rate of the plants grown at an atmospheric CO₂ concentration of 980 ppm was only about one-fourth of that exhibited by the plants grown at a concentration of 385 ppm.

Plant Characteristics

The increase in water use efficiency implied by this result could explain *A. farnesiana*'s increasing ascendancy over dryland grasses as the air's CO₂ content has risen over the past century or more.

Peterson and Neofotis (2004) sprouted and grew velvet mesquite plants in small pots within controlled environment chambers maintained at atmospheric CO₂ concentrations of either 380 or 760 ppm. Although they did not see a large CO₂-induced increase in plant growth, by the end of their six-week study there was a highly significant 41% reduction in the volume of water transpired by the mesquite seedlings in the CO₂-enriched treatment. "This large reduction in whole-plant water use," they write, "occurred because the reduction in transpiration per unit leaf area at elevated CO₂ was not offset by a proportional increase in total leaf area."

The pair of scientists from the Biosphere 2 Center near Oracle, Arizona, state their findings suggest in a future high-CO₂ world, mesquite seedlings "may deplete soil moisture at a slower rate than they do currently," and "this could facilitate seedling survival between intermittent rain events." They also note their work "corroborates the conclusions of Polley *et al.* (1994, 1999, 2003) that increasing levels of atmospheric CO₂ may facilitate the establishment of mesquite seedlings through a reduction in soil water depletion." Peterson and Neofotis note "mesquites and other woody species in the semiarid southwestern United States have shown substantial increases in population density and geographic range since Anglo-American settlement of the region approximately 120 years ago," citing Van Auken and Bush (1990), Gibbens *et al.* (1992), Bahre and Shelton (1993), Archer (1995), Boutton *et al.* (1999), Van Auken (2000), Ansley *et al.* (2001), Wilson *et al.* (2001), and Biggs *et al.* (2002).

Just as nonagricultural herbaceous plants are encroaching on Earth's deserts as the air's CO₂ content rises, so too are woody dryland shrubs following in their "rootsteps," as the greening of Earth continues.

References

Ansley, R.J., Ben Wu, X., and Kramp, B.A. 2001. Observation: long-term increases in mesquite canopy cover in a north Texas savanna. *Journal of Range Management* **54**: 171–176.

Archer, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* **2**: 83–99.

Bahre, C.J. and Shelton, M.L. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *Journal of Biogeography* **20**: 489–504.

Biggs, T.H., Quade, J., and Webb, R.H. 2002. $\delta^{13}\text{C}$ values of soil organic matter in semiarid grassland with mesquite (*Prosopis*) encroachment in southeastern Arizona. *Geoderma* **110**: 109–130.

Boutton, T.W., Archer, S.R., and Midwood, A.J. 1999. Stable isotopes in ecosystem science: structure, function and dynamics of a subtropical savanna. *Rapid Communications in Mass Spectrometry* **13**: 1263–1277.

Dugas, W.A., Polley, H.W., Mayeux, H.S., and Johnson, H.B. 2001. Acclimation of whole-plant *Acacia farnesiana* transpiration to carbon dioxide concentration. *Tree Physiology* **21**: 771–773.

Gibbens, R.P., Beck, R.F., McNeely, R.P., and Herbel, C.H. 1992. Recent rates of mesquite establishment in the northern Chihuahuan desert. *Journal of Range Management* **45**: 585–588.

Peterson, A.G. and Neofotis, P.G. 2004. A hierarchical analysis of the interactive effects of elevated CO₂ and water availability on the nitrogen and transpiration productivities of velvet mesquite seedlings. *Oecologia* **141**: 629–640.

Polley, H.W., Johnson, H.B., and Mayeux, H.S. 1994. Increasing CO₂: comparative responses of the C₄ grass *Schizachyrium* and grassland invader *Prosopis*. *Ecology* **75**: 976–988.

Polley, H.W., Johnson, H.B., and Tischler, C.R. 2003. Woody invasion of grasslands: evidence that CO₂ enrichment indirectly promotes establishment of *Prosopis glandulosa*. *Plant Ecology* **164**: 85–94.

Polley, H.W., Tischler, C.R., Johnson, H.B., and Pennington, R.E. 1999. Growth, water relations, and survival of drought-exposed seedlings from six maternal families of honey mesquite (*Prosopis glandulosa*): responses to CO₂ enrichment. *Tree Physiology* **19**: 359–366.

Roberts, S.W., Oechel, W.C., Bryant, P.J., Hastings, S.J., Major, J., and Nosov, V. 1988. A field fumigation system for elevated carbon dioxide exposure in chaparral shrubs. *Functional Ecology* **12**: 708–719.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecological Systems* **31**: 197–215.

Van Auken, O.W. and Bush, J.K. 1990. Importance of grass density and time of planting on *Prosopis glandulosa* seedling growth. *Southwest Naturalist* **35**: 411–415.

Wilson, T.B., Webb, R.H., and Thompson, T.L. 2001. *Mechanisms of Range Expansion and Removal of Mesquite*

in *Desert Grasslands of the Southwestern United States*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

2.31.2.3 Deciduous Trees

- Most deciduous trees exhibit modest reductions in transpirational water loss in CO₂-enriched air, enabling them to cope more effectively with the increased water stress they otherwise would experience under water-limiting conditions.

Wayne *et al.* (1998) grew yellow birch seedlings in controlled environment chambers maintained at atmospheric CO₂ concentrations of either 400 or 800 ppm and day/night air temperatures of either 26/21 or 31/26°C for two months. They determined the elevated CO₂ treatment stimulated net photosynthesis by 48% at both temperatures, and it increased seedling biomass by 60% and 227% at normal and high air temperatures, respectively. In addition, because the extra CO₂ reduced transpiration by 25 and 36% at the normal and high air temperatures, plant water use efficiency rose by 52 and 94% in these two situations, which suggests yellow birch may someday be able to expand into regions where high summer temperatures and limited rainfall currently discourage its presence.

In a FACE study established within a 10-year-old stand of sweetgum trees growing on a nutrient-rich soil in Tennessee (USA), Wullschleger and Norby (2001) measured CO₂-induced sap-flow reductions that averaged 13% over the growing season. The elevated CO₂ (540 vs. 390 ppm) also reduced growing-season transpiration rates by about the same amount, leading to a 28% increase in stand-level water use efficiency in the CO₂-enriched trees. In a second year of measurements, Wullschleger *et al.* (2002) found the CO₂-enriched air reduced the stomatal conductances of individual leaves by an average of 23% across the growing season. When extrapolated to the entire canopy, however, the reduction fell to 14%, and there was a 7% reduction in stand evapotranspiration.

Tognetti *et al.* (1998) studied the effects of naturally occurring elevated CO₂ concentrations (500 to 1,000 ppm) near a CO₂-emitting spring in central Italy on summer water relations of mature oak trees by measuring leaf stomatal conductances and trunk sap flow rates (a measure of transpiration) over a period of two years and comparing the results with

those obtained from similar-age oaks (15 to 25 years old) growing in air of ambient CO₂ concentration at a site about three kilometers away. As both summers were characterized by severe drought, rates of water loss were relatively high in both sets of trees. Leaf stomatal conductances, however, were significantly lower in the trees growing near the CO₂ springs, as were trunk sap velocities. These findings suggest the trees near the CO₂-emitting springs experienced less water loss and maintained a more favorable internal water status than those growing in non-CO₂-enriched ambient air.

Tognetti *et al.* also determined the trees growing near the CO₂-emitting springs possessed less foliage area than the control trees, and this reduction in transpirational surface area allowed the CO₂-enriched trees to maintain a better internal water status than the control trees during periods of drought. The researchers state the reduction in foliage area was “equally, if not more, effective than stomatal closure in reducing transpiration and plant water use under elevated CO₂.” Thus if drought situations continue to recur during future Italian summers, the rising CO₂ content of the atmosphere should provide oak, and perhaps other trees, with at least two different mechanisms for sustaining their growth during protracted periods of reduced water availability.

In a more broad-ranging study, Cech *et al.* (2003) enriched the air’s CO₂ content within the canopy of a 30-meter-tall species-rich forest just south of Basel, Switzerland, using the web-FACE technique of Pepin and Korner (2002), to a mean value of 520 ppm for an entire growing season to test, they write, “whether elevated CO₂ reduces water use in mature forest trees.” They took sap flow measurements of 14 broadleaved trees (three *Fagus*, four *Quercus*, four *Carpinus*, one *Tilia*, one *Acer*, and one *Prunus*) and their ambient-treatment counterparts via the constant heat-flow technique of Granier (1985, 1987) from 5 June to 1 October 2001.

Over the growing season, the extra 150 ppm of CO₂ reduced mean daily sap flow across all species by an average of 10.7%. At one end of the spectrum, the reductions were high (22%) when the evaporative demand of the air was low (mean daily vapor pressure deficits less than 5 hPa); but they were small (2%) at the other end, when the evaporative demand of the air was high (mean daily vapor pressure deficits greater than 10 hPa). The researchers conclude the “daily water savings by CO₂-enriched trees may have accumulated to [produce] a significantly improved water status by the time when control trees were short of soil moisture,” so “CO₂-enriched trees would enter

drier periods with a higher soil moisture capital, permitting prolonged gas exchange (for a few days)."

In light of these several experimental observations, it would appear most deciduous trees exhibit modest reductions in transpirational water loss in CO₂-enriched air. Consequently, if the planet continues to warm and experience increased dryness in some regions, Earth's deciduous trees may more effectively deal with the increased water stress they otherwise would experience in these places, if the air's CO₂ content continues to rise as well.

References

Cech, P.G., Pepin, S., and Korner, C. 2003. Elevated CO₂ reduces sap flux in mature deciduous forest trees. *Oecologia* **137**: 258–268.

Granier, A. 1985. A new method of sap flow measurement in tree stems. *Annales Des Sciences Forestieres* **42**: 193–200.

Granier, A. 1987. Evaluation of transpiration in a Douglas fir stand by means of sap flow measurements. *Tree Physiology* **3**: 309–320.

Pepin, S. and Korner, C. 2002. web-FACE: a new canopy free-air CO₂ enrichment system for tall trees in mature forests. *Oecologia* **133**: 1–9.

Tognetti, R., Longobucco, A., Miglietta, F., and Raschi, A. 1998. Transpiration and stomatal behaviour of *Quercus ilex* plants during the summer in a Mediterranean carbon dioxide spring. *Plant, Cell and Environment* **21**: 613–622.

Wayne, P.M., Reekie, E.G., and Bazzaz, F.A. 1998. Elevated CO₂ ameliorates birch response to high temperature and frost stress: implications for modeling climate-induced geographic range shifts. *Oecologia* **114**: 335–342.

Wullschlegel, S.D., Gunderson, C.A., Hanson, P.J., Wilson, K.B., and Norby, R.J. 2002. Sensitivity of stomatal and canopy conductance to elevated CO₂ concentration—interacting variables and perspectives of scale. *New Phytologist* **153**: 485–496.

Wullschlegel, S.D. and Norby, R.J. 2001. Sap velocity and canopy transpiration in a sweetgum stand exposed to free-air CO₂ enrichment (FACE). *New Phytologist* **150**: 489–498.

2.32 Vegetative Storage Proteins

- Atmospheric CO₂ enrichment appears to enhance the between-cuttings savings of vegetative storage proteins (VSPs) in the roots of alfalfa crops, as well as the between-years storage of

VSPs in the leaves of sour orange trees (and possibly other citrus species), giving first flush of foliage a tremendous head start when the next crop's or tree's growing season begins.

Maier *et al.* (2008) described how a soil nitrogen fertilizer application affected upper-canopy needle morphology and gas exchange in 20-meter-tall loblolly pine (*Pinus taeda* L.) trees previously exposed to elevated atmospheric CO₂ concentrations (200 ppm above ambient) for nine years at the Duke Forest FACE facility in Orange County, North Carolina (USA). During the tenth year of exposure to elevated CO₂, there was a strong enhancement (greater than 50%) of light-saturated net photosynthesis across all age classes of needles, and the stimulation was 28% greater in current-year foliage than in one-year-old foliage. In addition, current-year foliage incorporated the added nitrogen into photosynthetic components that increased the photosynthetic capacity of the current-year foliage, but the one-year-old foliage tended to simply store extra nitrogen, which subsequently served as "an important source of nitrogen for the development of current-year foliage" via "efficient retranslocation of nitrogen from senescing one-year-old foliage to developing foliage."

These findings echo those observed several years earlier in sour orange tree (*Citrus aurantium* L.) foliage in an open-top chamber experiment conducted at Phoenix, Arizona (USA) by Idso *et al.* (2001), where half the trees they studied had been grown from the seedling stage for the prior six years in air continuously enriched with an extra 300 ppm of CO₂. In the seventh year of that study, the Arizona researchers identified three putative vegetative storage proteins located within amorphous material in the vacuoles of leaf mesophyll cells that was rerouted, "starting at about day 25 of the new year, into developing foliage on the new branch buds of the CO₂-enriched trees." They speculate this phenomenon may have been "the key that allows the CO₂-enriched trees to temporarily stockpile the unusually large pool of nitrogen that is needed to support the large CO₂-induced increase in new-branch growth that is observed in the spring," citing Idso *et al.* (2000), who previously found 24 days after new-branch emergence in the spring, "the new branches of the CO₂-enriched trees were, on average, 4.4 times more massive than the new branches of the trees growing in ambient air," and "the total new-branch tissue produced on the CO₂-enriched trees to that point in time was over six times greater than that produced on

the ambient-treatment trees.”

If there is a common mechanism that links the results of the two groups, it could revolve around the hypothesized vacuolar storage proteins Idso *et al.* (2001) identified in the sour orange tree foliage, since they detected immunologically related proteins in a variety of other citrus species, but not in 20 different grasses, shrubs, and trees growing in the Biosphere 2 facility near Oracle, Arizona. This possibility merits further study because if it is found to have merit, Idso *et al.* (2001) further speculate the proteins in question “could possibly be genetically exploited to enhance the responses of other plant species to atmospheric CO₂ enrichment.” This could prove to be a valuable property of agriculturally important plants in a high-CO₂ world of the future.

Erice *et al.* (2007) studied 30-day-old nodulated alfalfa (*Medicago sativa* L.) plants grown in two temperature-gradient greenhouses (one maintained at an atmospheric CO₂ concentration of 350 ppm and the other at a concentration of 700 ppm) in pots recessed into the ground in an alfalfa field under conditions of ambient temperature (TA) and elevated temperature (TE = TA + 4°C) and well-watered (to field capacity) and water-stressed (50% field capacity) conditions for one month, after which a first cutting took place, and for one additional month, after which a second cutting took place. After each cutting, the scientists determined plant dry matter production and analyzed taproots for vegetative storage protein contents.

At the time of first cutting, the alfalfa plants had had their dry matter production boosted by an average of about 30% in the well-watered treatment (averaged across both temperature treatments) over the first growth period, but by only about 10% in the water-stressed treatment. At the time of the second cutting, however, the well-watered plants had experienced an average dry matter production increase on the order of 20% over the second growth period, and the plants in the water-stressed treatment displayed a mean increase of fully 40%. In addition, Erice *et al.* report over the first growth period “taproot vegetative storage protein content increased in response to drought and elevated CO₂.”

The researchers thus state, “it has been demonstrated that nitrogen pools in alfalfa taproot, especially vegetative storage proteins, condition new regrowing shoots,” and that appears to be what happened in their study. At the end of the first growth period, for example, the enhanced taproot vegetative storage protein content in the water-stressed and CO₂-enriched treatment may have been the reason the elevated CO₂ was so effective in stimulating biomass

production in the water-stressed treatment over the second growth period.

This finding is somewhat analogous to the observation of Idso *et al.* (2001), who found nitrogen reabsorbed from second-year leaves of sour orange trees (which hold most of their leaves for two years) during the process of senescence in the fall was stored over winter in much greater amounts in putative vegetative storage proteins in first-year leaves of CO₂-enriched trees than in first-year leaves of trees growing in ambient air. When the stored nitrogen was released in the spring to produce a flush of new leaves on the trees, leaf production on the CO₂-enriched trees vastly outpaced the production of new leaves on trees growing in ambient air. Taken together, these observations indicate yet another of the manifold benefits of atmospheric CO₂ enrichment.

References

Erice, G., Irigoyen, J.J., Sanchez-Diaz, M., Avice, J.-C., and Ourry, A. 2007. Effect of drought, elevated CO₂ and temperature on accumulation of N and vegetative storage proteins (VSP) in taproot of nodulated alfalfa before and after cutting. *Plant Science* **172**: 903–912.

Idso, C.D., Idso, S.B., Kimball, B.A., Park, H.-S., Hooper, J.K., and Balling Jr., R.C. 2000. Ultra-enhanced spring branch growth in CO₂-enriched trees: can it alter the phase of the atmosphere’s seasonal CO₂ cycle? *Environmental and Experimental Botany* **43**: 91–100.

Idso, K.E., Hooper, J.K., Idso, S.B., Wall, G.W., and Kimball, B.A. 2001. Atmospheric CO₂ enrichment influences the synthesis and mobilization of putative vacuolar storage proteins in sour orange tree leaves. *Environmental and Experimental Botany* **48**: 199–211.

Maier, C.A., Palmroth, S., and Ward, E. 2008. Short-term effects of fertilization on photosynthesis and leaf morphology of field-grown loblolly pine following long-term exposure to elevated CO₂ concentration. *Tree Physiology* **28**: 597–606.

2.33 Water Use Efficiency

As the atmosphere’s CO₂ concentration rises, most plants tend to exhibit increased rates of net photosynthesis and biomass production, and on a per-unit-leaf-area basis, plants exposed to elevated CO₂ concentrations are likely to lose less water via transpiration because they tend to exhibit lower stomatal conductances. Therefore, the amount of carbon gained per unit of water lost per unit leaf

area—or water use efficiency—should increase significantly as the air's CO₂ content rises. The following three sub-sections present evidence for this phenomenon in agricultural crops, grasslands, and trees.

2.33.1 Agricultural Species

- As the CO₂ content of the air continues to rise, nearly all agricultural plants will respond favorably by exhibiting increases in water use efficiency. It is also thus likely food and fiber production will increase on a worldwide basis, even in areas where productivity is currently severely restricted by limited availability of soil moisture.

Serraj *et al.* (1999) found soybeans grown at 700 ppm CO₂ displayed 10 to 25% reductions in total water loss while simultaneously exhibiting dry weight increases of as much as 33%. Thus, elevated CO₂ significantly increased the water-use efficiencies of the plants. Likewise, Garcia *et al.* (1998) determined spring wheat grown at 550 ppm CO₂ exhibited a water use efficiency about one-third greater than that of plants grown at 370 ppm CO₂. Similarly, Hakala *et al.* (1999) report twice-ambient CO₂ concentrations increased the water use efficiency of spring wheat by 70 to 100%, depending on experimental air temperature. In addition, Hunsaker *et al.* (2000) report CO₂-induced increases in water use efficiency for field-grown wheat 20 and 10% higher than those displayed by ambiently grown wheat subjected to high and low soil nitrogen regimes, respectively. Also, pea plants grown for two months in growth chambers maintained at CO₂ concentrations of 700 ppm displayed an average water use efficiency 27% greater than that exhibited by ambiently grown control plants (Gavito *et al.*, 2000).

In some cases, the water use efficiency increases caused by atmospheric CO₂ enrichment are spectacularly high. De Luis *et al.* (1999), for example, demonstrated alfalfa plants subjected to atmospheric CO₂ concentrations of 700 ppm had water-use efficiencies 2.6 and 4.1 times greater than those of control plants growing at 400 ppm CO₂ under water-stressed and well-watered conditions, respectively. Also, when grown at an atmospheric CO₂ concentration of 700 ppm, a 2.7-fold increase in water use efficiency was reported by Malmstrom and Field (1997) for oats infected with the barley yellow dwarf virus.

In addition to enhancing the water-use efficiencies of agricultural C₃ crops, elevated CO₂ also enhances the water-use efficiencies of crops possessing alternate carbon fixation pathways. Maroco *et al.* (1999), for example, demonstrated maize—a C₄ crop—grown for 30 days at an atmospheric CO₂ concentration of 1,100 ppm exhibited an intrinsic water use efficiency 225% higher than that of plants grown at 350 ppm CO₂. In addition, Conley *et al.* (2001) report a 200-ppm increase in the air's CO₂ content boosted the water use efficiency of field-grown sorghum by 9 and 19% under well-watered and water-stressed conditions, respectively. Also, Zhu *et al.* (1999) report pineapple—a CAM plant—grown at 700 ppm CO₂ exhibited water-use efficiencies always significantly greater than those of control plants grown at 350 ppm CO₂ over a wide range of growth temperatures.

Olivo *et al.* (2002) grew two potato species (*Solanum curtilobum* cv. Ugro Shiri, from high altitude, and *S. tuberosum* cv. Baronesa, from low altitude) in pots placed within open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm for 30 days following the onset of reproductive growth, to study the effects of elevated CO₂ on gas exchange and biomass production in these two species in the first-ever study of the CO₂ responsiveness of the high-altitude-adapted *Solanum curtilobum*, which is economically important in the highlands of the South American Andes. The elevated CO₂ treatment increased rates of net photosynthesis by 56 and 53% in the high- and low-altitude potato species, respectively, while reducing their stomatal conductances by 55 and 59% and thereby increasing their water-use efficiencies by 90 and 80%, respectively. Tuber dry mass production was increased by 85 and 40% in the high- and low-altitude potato species, respectively.

Dong-Xiu *et al.* (2002) grew spring wheat (*Triticum aestivum* L. cv. Gaoyuan 602) in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm and three levels of soil moisture (40, 60, and 80% of field capacity), to study the interactive effects of these environmental variables on the productivity and growth of this variety of wheat. The elevated CO₂ treatment increased rates of net photosynthesis by 48, 120, and 97% at low, medium, and high soil water capacities, respectively, and it reduced rates of transpiration by 56, 53, and 63% in the same order. These changes led to CO₂-induced increases in plant water use efficiency of approximately 25, 15, and 30% under low, medium, and high soil moisture conditions,

respectively.

Agrawal and Deepak (2003) grew two other cultivars of wheat (*Triticum aestivum* L. cv. Malviya 234 and HP1209) in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 600 ppm alone and in combination with 60 ppb of sulfur dioxide (SO₂), to study the interactive effects of elevated CO₂ and this major air pollutant on the growth and yield of this important crop. They found exposure to elevated CO₂ significantly increased photosynthetic rates by 58 and 48% in M234 and HP1209, respectively, and fumigation with elevated SO₂ did not significantly impact rates of photosynthesis in either cultivar. However, plants grown in the combined treatment of elevated CO₂ and elevated SO₂ displayed photosynthetic rates significantly less-enhanced to values of 42 and 38% greater than those measured in control plants for M234 and HP1209, respectively.

Of more significance to the topic of this review, however, plants grown in elevated CO₂ also displayed an approximate 20% reduction in stomatal conductance, and those grown in elevated SO₂ exhibited an average increase of 15%. But when exposed simultaneously to both gases, the plants displayed an average 11% reduction in stomatal conductance, which resulted in a 32% increase in water use efficiency, whereas plants exposed to elevated SO₂ alone displayed an average decrease in water use efficiency of 16%.

Working with a very different type of crop, Kyei-Boahen *et al.* (2003) grew well-watered and well-fertilized plants of four carrot (*Daucus carota* var. sativus L.) cultivars (Cascade, Caro Choice, Oranza, and Red Core Chantenay) from seed in 15-cm-diameter plastic pots in a controlled environment facility for 30 days past emergence. Leaf net photosynthetic rate (PN), stomatal conductance (Gs), and transpiration rate (E) were then measured at 100-ppm intervals of short-term (five-minute) atmospheric CO₂ enrichment yielding absolute CO₂ concentrations (Ca) stretching from 50 to 1,050 ppm. The five researchers found “an increase in Ca from 50 to 350 ppm produced a 100-fold increase in PN and the value increased by 43% when Ca was elevated from 350 to 650 ppm,” but “only [a] 7% increase in PN was observed when Ca was increased from 650 to 1050 ppm.”

They also found “increasing Ca from 50 to 350 ppm increased Gs to a maximum and thereafter Gs declined by 17% when Ca was increased to 650 ppm,” and “a three-fold increase in Ca from 350 to 1050 ppm decreased Gs by 53%.” They further

report, “E reached maximum values (0.9–1.1 mmol m⁻² s⁻¹) at 350 ppm followed by a decline to 0.40–0.60 mmol m⁻² s⁻¹ when Ca was increased to 1050 ppm.” Finally, “water use efficiency increased linearly with Ca due to increases in PN in addition to the decline in E at high Ca,” so “increasing Ca from 350 to 650 ppm improved water use efficiency by 76%, whereas a three-fold increase in Ca from 350–1050 ppm resulted in a three-fold increase in water use efficiency” They conclude, “future enrichment in the atmospheric CO₂ may lead to adjustments in PN and Gs, which could improve carrot productivity and water utilization.”

Triggs *et al.* (2004) grew sorghum (*Sorghum bicolor* (L.) Moench, a C₄ grain crop) for two full seasons in control CO₂ plots (about 370 ppm) and FACE plots (Control + 200 ppm) under both well-watered (Wet) and water-stressed (Dry, less than half the total water received by the Wet treatment via rainfall and irrigation) conditions near Maricopa, Arizona (USA), assessing evapotranspiration (ET) on a continuous basis by means of micrometeorological measurements designed to allow the calculation of all of the other elements (net radiation, sensible heat flux, and soil surface heat flux) of the energy balance of the crop-soil interface with the atmosphere.

Triggs *et al.* report, “In the Wet treatments, a reduction in ET of about 19%, combined with only a slight increase in total biomass (+4%), resulted in a 28% increase in WUE in elevated CO₂ conditions,” and “in the Dry treatments, the relatively large increase in total biomass (+16% for both years) more than compensated for the approximate 5% increase in total ET, giving the FACE-Dry treatments an increase in WUE of 16% over both seasons.” Based on these results, Triggs *et al.* conclude, “even if future climate change results in less water available for agriculture, higher atmospheric CO₂ concentrations will still benefit C₄ crops,” but they note, “in regions with ample precipitation or irrigation, C₃ crops with higher growth responses may be preferable.”

Grant *et al.* (2004) adjusted the crop growth and water relations model *ecosys* to represent sorghum (*Sorghum bicolor* (L.) Moench) and run for two growing seasons (1 May 1998 to 31 October 1999) under both wet and dry irrigation schedules at two atmospheric CO₂ concentrations (approximately 368 and 561 ppm) using hourly meteorological data measured at a field south of Phoenix, Arizona (USA), after which the crop’s simulated energy balances and water relations—verified by measurements of energy flux and water potential—were used to infer the effects of free-air atmospheric CO₂ enrichment on various plant parameters and processes.

Plant Characteristics

The 12 researchers write, “model results, corroborated by field measurements, showed that elevated CO₂ raised canopy water potential and lowered latent heat fluxes under high irrigation [both of which responses are beneficial] and delayed water stress under low irrigation [which is also beneficial],” such that the elevated CO₂ “reduced transpiration and hence improved water status of sorghum [and] lowered the vulnerability of sorghum CO₂ fixation to soil or atmospheric water deficits, even when irrigation was high.” In applying their reality-tuned model to a scenario where the air’s CO₂ content was 50% higher and air temperature was 3°C greater, they calculated that sorghum yields would rise by about 13%, and “current high sorghum yields could be achieved with ~120 mm or ~20% less irrigation water if these rises in temperature and CO₂ were to occur.” Their real-world data and their analysis of those data indicate rising atmospheric CO₂ concentrations, even in the face of rising air temperatures, should be good for both sorghum and the people who grow it, in terms of both the higher yields that can be produced under these conditions and the smaller amounts of water required to produce them.

Yoshimoto *et al.* (2005) grew rice (*Oryza sativa* L. cv. Akita-Komachi) from hand-transplanting to harvest (May to September) under normal paddy culture near Shizukuishi, Iwate (Japan) within FACE rings maintained at either ambient or ambient + 200 ppm CO₂ for 24 hours per day. Over this period they measured a number of micrometeorological parameters and plant characteristics that enabled them to calculate both the amount of water lost directly from the paddy-water surface and that lost by plant transpiration, which together with the plant biomass data they obtained at harvest enabled them to calculate total growing-season crop water use efficiency.

Yoshimoto *et al.* determined “elevated CO₂ reduced stomatal conductance by 13% in upper leaves and by 40% in lower leaves at the panicle initiation stage,” but the reduction declined thereafter. In addition, “stomata closed more in the elevated CO₂ plot as vapor pressure deficit increased,” i.e., during drier conditions. In more common terms, and averaged over the entire growing season, the Japanese researchers determined the total water used by the crop was 268.7 mm in the ambient CO₂ treatment and 246.7 mm in the elevated CO₂ treatment. Combining this CO₂-induced reduction in total evaporative water loss (8.2%) with the CO₂-induced increase in total plant biomass that was observed (9.1%) indicated season-long crop water use efficiency rose by about

19% in response to the approximate 54% increase in atmospheric CO₂ concentration provided by the FACE apparatus. Thus, as world population continues to grow, the increase in rice-crop water use efficiency provided by the concomitant increase in the atmosphere’s CO₂ concentration should be a great asset in helping to produce the extra food that will be needed to feed the planet’s many newcomers, while sparing some of the precious water that will be needed to slake their thirst.

Kim *et al.* (2006) grew well-watered and fertilized maize (*Zea mays* L. cv. Pioneer 3733) plants from seed to developmental stage R3 (milky ripe stage, 70 days after planting) in sunlit soil-plant-atmosphere research (SPAR) chambers maintained at either 370 (ambient) or 750 (elevated) ppm CO₂ concentrations, while periodically measuring a number of plant physiological parameters. They discovered that at saturating photosynthetically active radiation (PAR, 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$), rates of leaf net photosynthesis in the elevated CO₂ chambers were only 4% greater than those in the ambient CO₂ chambers. However, upper-canopy leaves grown at elevated CO₂ exhibited reductions in excess of 50% in both leaf stomatal conductance and transpiration, and as a result of these changes, instantaneous leaf water use efficiency was more than doubled in the high-CO₂ treatment. Because of shading within the canopy, and because the difference in stomatal conductance between ambient and elevated CO₂ declines as PAR drops, the CO₂-induced reduction in canopy evapotranspiration was only a little over 20%.

Commenting on their findings, the seven scientists write, “although several previous studies report CO₂ enrichment enhanced the growth of maize under well watered and fertilized conditions,” in their study “there was little evidence of increased biomass accumulation.” On the other hand, they state the sizable CO₂-induced reduction in canopy evapotranspiration “is comparable to findings from other studies of C₄ plants.” Although the maize plants of their study were somewhat anomalous in not undergoing a significant boost in growth in response to atmospheric CO₂ enrichment, their more characteristic transpiration response enabled them to produce their slightly enhanced biomass with a considerably smaller consumption of water than that of the plants growing in ambient air.

Cunniff *et al.* (2008) note, “early agriculture was characterized by sets of primary domesticates or ‘founder crops’ that were adopted in several independent centers of origin,” all at about the same time; and they speculate, “this synchronicity suggests

the involvement of a global trigger.” Further noting Sage (1995) saw a causal link between this development and the rise in atmospheric CO₂ concentration that followed deglaciation (a jump from about 180 to 270 ppm), they hypothesize the aerial fertilization effect caused by the rise in CO₂ combined with its transpiration-reducing effect led to a large increase in the water use efficiencies of the world’s major C₄ founder crops, and this development was the global trigger that launched the agricultural enterprise. To test this hypothesis, they designed “a controlled environment experiment using five modern day representatives of wild C₄ crop progenitors, all ‘founder crops’ from a variety of independent centers.”

The five crops employed in their study were *Setaria viridis* (L.) P. Beauv., *Panicum miliaceum* var. *ruderales* (Kitag.), *Pennisetum violaceum* (Lam.) Rich., *Sorghum arundinaceum* (Desv.), and *Zea mays* subsp. *parviglumis* H.H. Iltis & Doebley. Each was grown individually in 6-cm x 6-cm x 6-cm pots filled with a 1:1 mix of washed sand and vermiculite for 40–50 days within growth chambers maintained at atmospheric CO₂ concentrations of 180, 280, and 380 ppm, characteristic of glacial, post-glacial, and modern times, respectively. The scientists found the “increase in CO₂ from glacial to postglacial levels [180 to 280 ppm] caused a significant gain in vegetative biomass of up to 40%,” together with “a reduction in the transpiration rate via decreases in stomatal conductance of ~35%,” which led to “a 70% increase in water use efficiency, and a much greater productivity potential in water-limited conditions.”

The five researchers conclude, “these key physiological changes could have greatly enhanced the productivity of wild crop progenitors after deglaciation ... improving the productivity and survival of these wild C₄ crop progenitors in early agricultural systems.” They note, “the lowered water requirements of C₄ crop progenitors under increased CO₂ would have been particularly beneficial in the arid climatic regions where these plants were domesticated.”

For comparative purposes, the researchers also had included one C₃ species in their study—*Hordeum spontaneum* K. Koch—and they report it “showed a near-doubling in biomass compared with [the] 40% increase in the C₄ species under growth treatments equivalent to the postglacial CO₂ rise.”

The civilizations of the past, which could not have existed without agriculture, were largely made possible by the increase in the air’s CO₂ content that accompanied deglaciation. The peoples of Earth today

are likewise indebted to this phenomenon, as well as to the additional 100 ppm of CO₂ the atmosphere has subsequently acquired. The ongoing rise in the air’s CO₂ content is likely to play a pivotal role in enabling society to grow the food needed to sustain the still-expanding global population without usurping all the planet’s remaining freshwater resources and much of its untapped arable land.

Morison *et al.* (2007) discuss at length the water use challenge, noting “agriculture accounts for 80–90% of all freshwater used by humans,” “most of that is in crop production,” and “in many areas, this water use is unsustainable.” They also note “farmers in many countries are now faced with legislative restrictions on use of water,” indicating the Chinese government has “set a target of a reduction of 20% in water use in agriculture by the year 2020,” but “if food security for the region is not to be threatened, this must be achieved without a loss in production.” How is this global food and water crisis to be overcome?

In their many pages of discussion of the subject, the four UK researchers examine underlying relationships that connect crop carbon uptake, growth, and water loss, noting “much effort is being made to reduce water use by crops and produce ‘more crop per drop.’” Some of the topics they examine in the course of this discussion were designed to alter various crop characteristics that might increase their water use efficiency, such as genetic engineering, and others deal with crop management strategies, such as how and when to apply irrigation water. As reported by the studies discussed above, and additional studies discussed below, water use efficiencies driven by increasing levels of atmospheric CO₂ will help address the problem.

Fleisher *et al.* (2008) grew potato (*Solanum tuberosum* cv. Kennebec) plants from “seed tubers” in soil-plant-atmosphere research (SPAR) chambers maintained at daytime atmospheric CO₂ concentrations of either 370 or 740 ppm in a 75/25 mix of coarse sand and vermiculite at well-watered and progressively water-stressed conditions until they were harvested when canopy photosynthetic rates dropped to below 50% of their seasonal peak values, before and after which they measured a variety of plant physical properties and physiological parameters.

They write, “elevated CO₂ plants maintained a higher daily net assimilation rate throughout most of the growing season,” and “at moderate and more severe levels of water stress, CO₂ enrichment appeared to encourage shifting of assimilate into

Plant Characteristics

tubers as opposed to additional vegetative growth.” Hence, “total biomass, yield and water use efficiency increased under elevated CO₂, with the largest percent increases occurring at irrigations that induced the most water stress,” and “water use efficiency was nearly doubled under enriched CO₂ when expressed on a tuber fresh weight basis.” Overall, “the results indicate that increases in potato gas exchange, dry matter production and yield with elevated CO₂ are consistent at various levels of water stress as compared with ambient CO₂.”

Ceusters *et al.* (2008) measured gas exchange and diel metabolite (e.g. malate, soluble sugars, starch) dynamics in the youngest fully expanded leaves of well-watered and well-fertilized CAM bromeliad *Aechmea* ‘Maya’ plants—a spineless cultivar resulting from a cross between *A. tessmannii* and *A. fasciata*—after exposure of half of the original seven-month-old plants to 700 ppm CO₂ for five more months in one of two controlled-environment compartments of a greenhouse, and the other compartment was maintained at the original atmospheric CO₂ concentration of 380 ppm. They report, “there was a 60% increase in 24-hour carbon gain under elevated CO₂ due to a stimulation of daytime C₃ and C₄ carboxylation,” and they note water use efficiency was twofold higher during the night under elevated CO₂ and three- to four-fold higher during the day.

The six scientists state the great increase they observed in plant water use efficiency “could be a major physiological advantage to growth under elevated CO₂ in this CAM bromeliad,” and this fact further suggests CAM species should “be considered in an agronomic context as potential sources of biomass production on arid, marginal lands.”

Sanchez-Guerrero (2009) grew cucumber plants from seed to maturity in standard perlite bags within climate-controlled greenhouses at Almeria, Spain, and the plants were “fertigated” (fertilized and irrigated) via a nutrient-solution drip system regulated to maintain the same electrical conductivity in the leached solution draining from the perlite bags of each greenhouse. One of the greenhouses was supplied with extra CO₂ during daylight hours (through outlets below each plant) when the greenhouse side vents were closed or when the roof vent was less than 20% of full opening, resulting in a mean daytime concentration of about 450 ppm around the plants, approximately 100 ppm more than the CO₂ concentration around the plants in the other greenhouse.

The total season-long yield of the CO₂-enriched cucumber crop was increased by 19% by the extra

100 ppm of CO₂ supplied to it during daylight hours, and the overall water use efficiency of the CO₂-enriched plants, based on the amount of water supplied to them, was about 40% higher. The five Spanish scientists conclude their study “confirms the potential interest of using moderate CO₂ enrichment strategies in greenhouses located in areas such as the Mediterranean basin, where the agricultural sector is facing scarce and declining water resources, and needs to drastically reduce the contamination due to fertilizer emission to ensure the sustainability of greenhouse production.”

Shimono *et al.* (2010) write, “by 2050, the world’s population will have increased by about 37%, from the current level of 6.7 billion to an estimated 9.2 billion (UN, 2009), with a corresponding increase in global food demand.” They also note “about 0.6 billion Mg of rice is produced annually from an area of 1.5 million km², making rice one of the most important crops for supporting human life,” especially, as noted by Pritchard and Amthor (2005), since it supplies the planet’s human population with an estimated 20% of its energy needs (on a caloric basis) and 14% of its protein requirements (on a weight basis).

The six scientists further note “rice production depends heavily on water availability,” stating “irrigated lowlands account for 55% of the total area of harvested rice and typically produce two to three times the crop yield of rice grown under non-irrigated conditions (IRRI, 2002).” And because mankind’s demand for ever-greater quantities of water will continue to rise, due to the need to adequately feed the world’s growing numbers, they conclude, “efficient use of water will thus be essential for future rice production.”

To determine how the ongoing rise in the air’s CO₂ content may impact agriculture in this regard, the Japanese researchers conducted a two-year free-air CO₂ enrichment (FACE) study in fields at Shizukuishi, Iwate (Japan) to learn how elevated CO₂ may reduce crop water use via its impact on the leaf stomatal conductances (*gs*) of three varieties of rice (*Oryza sativa* L.): early maturing Kirara397, intermediate-maturing Akitakomachi, and latest-maturing Hitomebore.

In response to the 53% increase in daytime atmospheric CO₂ concentration employed in their experiments, Shimono *et al.* determined “the reduction in *gs* due to elevated CO₂ was similar across measurements, averaging around 20% in the morning, 24% around noon and 23% in the afternoon across all growth stages.” In addition, “there was no

significant CO₂ x cultivar interaction.” Therefore, with the concomitant increase in grain yield that results from atmospheric CO₂ enrichment, a continuation of the historical and still-ongoing rise in the air’s CO₂ content will play a major role in enabling the world to meet its food needs without having to lay claim to all of the planet’s remaining freshwater resources and much of its undeveloped land.

Expanding on this thesis, Fereres *et al.* (2011) write, “forecasts on population growth and economic development indicate that there will be substantial increases in food demand for the forthcoming decades,” and as a result, “food security has not only moved to the forefront of agricultural research, but is now perceived as an important topic for more fundamental research,” citing numerous items published in *Nature* (2010) and *Science* (2010). They add, “the question of whether there will be enough food in the future should immediately be followed by the question: Will there be enough water to produce sufficient food?” They state, “given the competition for water faced by the agricultural sector, and the uncertainties associated with climate change, improving the efficiency of water use in both rain-fed and irrigated systems is the main avenue to face the challenge.”

As to developing new sources of water, or transferring water from one place to another, in order to increase food production where water shortages exist, the three Spanish researchers state such measures have “limited potential in some areas” but are “no longer possible in other world regions.” They do note, however, many agriculturalists have significantly increased crop water use efficiency “by reducing water losses (and some of the water consumed in evaporation from soil) through improved agronomy and engineering of irrigation systems.” But they lament the fact, as they put it, “science has been much less successful so far in reducing the water consumed in transpiration.”

Fortunately, mankind has had a measurable amount of success in this area, albeit unintentionally and unknowingly. The extraction of fossil fuels from the crust of the Earth has provided coal, gas, and oil to fuel the engines of industry, and the carbon dioxide emitted to the air in the combustion process has raised the atmosphere’s CO₂ concentration by some 40% since the inception of the Industrial Revolution. That phenomenon has had two major effects on man’s production of food: It has increased significantly the leaf photosynthetic rates of crops, and it has reduced significantly their transpiration rates, which has led to

significant increases in leaf water use efficiency, the amount of biomass produced per unit of water transpired in the process.

In spite of these well-documented facts, to quote Morgan *et al.* (2011), “many believe that CO₂-induced reductions in transpiration at the leaf level will be largely offset at the canopy level by increases in leaf area,” and “global warming is predicted to induce desiccation in many world regions through increases in evaporative demand.”

In a real-world test of these two potentially negative phenomena in a prairie heating and CO₂ enrichment (PHACE) experiment conducted in a native mixed-grass prairie in Wyoming (USA), Morgan *et al.* found the positive effects of elevated CO₂ prevailed, indicating, they write, “in a warmer, CO₂-enriched world, both soil water content and productivity in semi-arid grasslands may be higher than previously expected,” providing what Baldocchi (2011) described as “one of the first and best views of how a mixed-grass ecosystem growing in a semi-arid climate will respond to future CO₂ and climatic conditions.”

A full decade earlier, Robock *et al.* (2000) had already developed a massive collection of soil moisture data from more than 600 stations spread across a variety of climatic regimes, including the former Soviet Union, China, Mongolia, India, and the United States. In analyzing those observations, they determined, “in contrast to predictions of summer desiccation with increasing temperatures, for the stations with the longest records, summer soil moisture in the top one meter has increased while temperatures have risen.”

Allen *et al.* (2011) write, “plants of the C₄ photosynthetic pathway have a CO₂-concentrating mechanism that overcomes limitations of low atmospheric CO₂” and thereby provides them with “a near-saturating photosynthetic capability at current atmospheric CO₂.” In this circumstance, they note, “a rise in atmospheric CO₂ will theoretically have a limited direct impact on C₄ photosynthesis.” However, “a number of C₄ crop plants express a positive response to elevated growth CO₂, although to a smaller extent compared to C₃ plants,” citing the analyses of Kimball (1993) and Poorter *et al.* (1996).

To test plants’ reaction to drought stress, the four researchers planted seeds of maize (*Zea mays* L. cv. Saturn Yellow) and grain sorghum (*Sorghum bicolor* L. cv. DeKalb 28E) in pots and grew them for 39 days in sunlit controlled-environment chambers at 360 and 720 ppm CO₂ concentrations. Throughout this period, canopy net photosynthesis and evapotranspiration

Plant Characteristics

were measured and summarized daily from 0800 to 1700 hours. Irrigation was withheld from matched pairs of treatments starting 26 days after sowing, and biomass determinations were made at 34 and 39 days after sowing for maize and grain sorghum, respectively.

The four researchers found for both maize and grain sorghum, there was a “maintenance of relatively high canopy photosynthetic rates in the face of decreased transpiration rates [that] resulted in enhanced water use efficiency when these plants were grown at elevated CO₂ of 720 ppm, but not at 360 ppm.” Thus they demonstrated “both plants maintained growth better at double-ambient CO₂ than their counterparts at ambient CO₂ in the presence of drought,” such that reductions in total above-ground biomass due to drought were 42% for maize and 36% for sorghum at ambient CO₂, but only 18% for maize and 14% for sorghum at double-ambient CO₂. In discussing their findings, Allen *et al.* state they “agree with Leakey (2009) that drought stress in C₄ crop plants can be ameliorated at elevated CO₂ as a result of lower stomatal conductance and sustained intercellular CO₂.”

As the CO₂ content of the air continues to rise, nearly all agricultural plants will respond favorably by exhibiting increases in water use efficiency. It is thus likely food and fiber production will increase on a worldwide basis, even in areas where productivity is severely restricted by limited availability of soil moisture. Global agricultural productivity should rise in tandem with future increases in the atmosphere’s CO₂ concentration.

References

- Agrawal, M. and Deepak, S.S. 2003. Physiological and biochemical responses of two cultivars of wheat to elevated levels of CO₂ and SO₂, singly and in combination. *Environmental Pollution* **121**: 189–197.
- Allen Jr., L.H., Kakani, V.G., Vu, J.C.V., and Boote, K.J. 2011. Elevated CO₂ increases water use efficiency by sustaining photosynthesis of water-limited maize and sorghum. *Journal of Plant Physiology* **168**: 1909–1918.
- Baldocchi, D. 2011. The grass response. *Nature* **476**: 160–161.
- Ceusters, J., Borland, A.M., Londers, E., Verdoodt, V., Godts, C., and de Proft, M.P. 2008. Diel shifts in carboxylation pathway and metabolite dynamics in the CAM Bromeliad *Aechmea* ‘Maya’ in response to elevated CO₂. *Annals of Botany* **102**: 389–397.
- Conley, M.M., Kimball, B.A., Brooks, T.J., Pinter Jr., P.J., Hunsaker, D.J., Wall, G.W., Adams, N.R., LaMorte, R.L., Matthias, A.D., Thompson, T.L., Leavitt, S.W., Ottman, M.J., Cousins, A.B., and Triggs, J.M. 2001. CO₂ enrichment increases water use efficiency in sorghum. *New Phytologist* **151**: 407–412.
- Cunniff, J., Osborne, C.P., Ripley, B.S., Charles, M., and Jones, G. 2008. Response of wild C₄ crop progenitors to subambient CO₂ highlights a possible role in the origin of agriculture. *Global Change Biology* **14**: 576–587.
- De Luis, J., Irigoyen, J.J., and Sanchez-Diaz, M. 1999. Elevated CO₂ enhances plant growth in droughted N₂-fixing alfalfa without improving water stress. *Physiologia Plantarum* **107**: 84–89.
- Dong-Xiu, W., Gen-Xuan, W., Yong-Fei, B., Jian-Xiong, L., and Hong-Xu, R. 2002. Response of growth and water use efficiency of spring wheat to whole season CO₂ enrichment and drought. *Acta Botanica Sinica* **44**: 1477–1483.
- Fereres, E., Orgaz, F., and Gonzalez-Dugo, V. 2011. Reflections on food security under water scarcity. *Journal of Experimental Botany* **62**: 4079–4086.
- Fleisher, D.H., Timlin, D.J., and Reddy, V.R. 2008. Elevated carbon dioxide and water stress effects on potato canopy gas exchange, water use, and productivity. *Agricultural and Forest Meteorology* **148**: 1109–1122.
- Garcia, R.L., Long, S.P., Wall, G.W., Osborne, C.P., Kimball, B.A., Nie, G.Y., Pinter Jr., P.J., LaMorte, R.L., and Wechsung, F. 1998. Photosynthesis and conductance of spring-wheat leaves: field response to continuous free-air atmospheric CO₂ enrichment. *Plant, Cell and Environment* **21**: 659–669.
- Gavito, M.E., Curtis, P.S., Mikkelsen, T.N., and Jakobsen, I. 2000. Atmospheric CO₂ and mycorrhiza effects on biomass allocation and nutrient uptake of nodulated pea (*Pisum sativum* L.) plants. *Journal of Experimental Botany* **52**: 1931–1938.
- Grant, R.F., Kimball, B.A., Wall, G.W., Triggs, J.M., Brooks, T.J., Pinter Jr., P.J., Conley, M.M., Ottman, M.J., Lamorte, R.L., Leavitt, S.W., Thompson, T.L., and Matthias, A.D. 2004. Modeling elevated carbon dioxide effects on water relations, water use, and growth of irrigated sorghum. *Agronomy Journal* **96**: 1693–1705.
- Hakala, K., Helio, R., Tuhkanen, E., and Kaukoranta, T. 1999. Photosynthesis and Rubisco kinetics in spring wheat and meadow fescue under conditions of simulated climate change with elevated CO₂ and increased temperatures. *Agricultural and Food Science in Finland* **8**: 441–457.
- Hunsaker, D.J., Kimball, B.A., Pinter Jr., P.J., Wall, G.W., LaMorte, R.L., Adamsen, F.J., Leavitt, S.W., Thompson,

Climate Change Reconsidered II: Biological Impacts

- T.L., Matthias, A.D., and Brooks, T.J. 2000. CO₂ enrichment and soil nitrogen effects on wheat evapotranspiration and water use efficiency. *Agricultural and Forest Meteorology* **104**: 85–105.
- IRRI (International Rice Research Institute). 2002. *Rice Almanac: Source Book for the Most Important Economic Activity on Earth*. CABI Publishing, Oxnon, United Kingdom.
- Kim, S.-H., Sicher, R.C., Bae, H., Gitz, D.C., Baker, J.T., Timlin, D.J., and Reddy, V.R. 2006. Canopy photosynthesis, evapotranspiration, leaf nitrogen, and transcription profiles of maize in response to CO₂ enrichment. *Global Change Biology* **12**: 588–600.
- Kimball, B.A. 1993. Effects of elevated CO₂ and climate variables on plants. *Journal of Soil and Water Conservation* **48**: 9–14.
- Kyei-Boahen, S., Astatkie, T., Lada, R., Gordon, R., and Caldwell, C. 2003. Gas exchange of carrot leaves in response to elevated CO₂ concentration. *Photosynthetica* **41**: 597–603.
- Leakey, A.D.B. 2009. Rising atmospheric carbon dioxide concentration and the future of C₄ crops for food and fuel. *Proceedings of the Royal Society B* **276**: 2333–2343.
- Malmstrom, C.M. and Field, C.B. 1997. Virus-induced differences in the response of oat plants to elevated carbon dioxide. *Plant, Cell and Environment* **20**: 178–188.
- Maroco, J.P., Edwards, G.E., and Ku, M.S.B. 1999. Photosynthetic acclimation of maize to growth under elevated levels of carbon dioxide. *Planta* **210**: 115–125.
- Morgan, J.A., LeCain, D.R., Pendall, E., Blumenthal, D.M., Kimball, B.A., Carrillo, Y., Williams, D.G., Heisler-White, J., Dijkstra, F.A., and West, M. 2011. C₄ grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature* **476**: 202–205.
- Morison, J.I.L., Baker, N.R., Mullineaux, P.M., and Davies, W.J. 2007. Improving water use in crop production. *Philosophical Transactions of the Royal Society B* **363**: 639–658.
- Nature. 2010. Can science feed the world? <http://www.nature.com/news/specials/food/index.html>.
- Olivo, N., Martinez, C.A., and Oliva, M.A. 2002. The photosynthetic response to elevated CO₂ in high altitude potato species (*Solanum curtilobum*). *Photosynthetica* **40**: 309–313.
- Ottman, M.J., Kimball, B.A., Pinter Jr., P.J., Wall, G.W., Vanderlip, R.L., Leavitt, S.W., LaMorte, R.L., Matthias, A.D., and Brooks, T.J. 2001. Elevated CO₂ increases sorghum biomass under drought conditions. *New Phytologist* **150**: 261–273.
- Poorter, H., Roumet, C., and Campbell, B.D. 1996. Interspecific variation in the growth response of plants to elevated CO₂: a search for functional types. In: Korner, C. and Bazzaz, F.A. (Eds.) *Carbon Dioxide, Populations, and Communities*. Academic Press, New York, New York, USA, pl 375–412.
- Pritchard, S.G. and Amthor, J.S. 2005. *Crops and Environmental Change*. Food Production Press, New York, New York, USA.
- Robock, A., Vinnikov, K.Y., Srinivasan, G., Entin, J.K., Hollinger, S.E., Speranskaya, N.A., Liu, S., and Namkhai, A. 2000. The global soil moisture data bank. *Bulletin of the American Meteorological Society* **81**: 1281–1299.
- Sage, R.F. 1995. Was low atmospheric CO₂ during the Pleistocene a limiting factor for the origin of agriculture? *Global Change Biology* **1**: 93–106.
- Sanchez-Guerrero, M.C., Lorenzo, P., Medrano, E., Baille, A., and Castilla, N. 2009. Effects of EC-based irrigation scheduling and CO₂ enrichment on water use efficiency of a greenhouse cucumber crop. *Agricultural Water Management* **96**: 429–436.
- Science. 2010. Food security. <http://www.sciencemag.org/site/special/foodsecurity/>.
- Serraj, R., Allen Jr., L.H., Sinclair, T.R. 1999. Soybean leaf growth and gas exchange response to drought under carbon dioxide enrichment. *Global Change Biology* **5**: 283–291.
- Shimono, H., Okada, M., Inoue, M., Nakamura, H., Kobayashi, K., and Hasegawa, T. 2010. Diurnal and seasonal variations in stomatal conductance of rice at elevated atmospheric CO₂ under fully open-air conditions. *Plant, Cell and Environment* **33**: 322–331.
- Triggs, J.M., Kimball, B.A., Pinter Jr., P.J., Wall, G.W., Conley, M.M., Brooks, T.J., LaMorte, R.L., Adam, N.R., Ottman, M.J., Matthias, A.D., Leavitt, S.W., and Cervený, R.S. 2004. Free-air CO₂ enrichment effects on the energy balance and evapotranspiration of sorghum. *Agricultural and Forest Meteorology* **124**: 63–79.
- UN (United Nations). 2009. *The 2006 World Population Prospects. The 2008 Revision Population Database*. United Nations, New York, New Your, USA. <http://esa.un.org/unpp/>.
- Yoshimoto, M., Oue, H., and Kobayashi, K. 2005. Energy balance and water use efficiency of rice canopies under free-air CO₂ enrichment. *Agricultural and Forest Meteorology* **133**: 226–246.
- Zhu, J., Goldstein, G., and Bartholomew, D.P. 1999. Gas exchange and carbon isotope composition of *Ananas comosus* in response to elevated CO₂ and temperature. *Plant, Cell and Environment* **22**: 999–1007.

2.33.2 Grasslands

- As the air's CO₂ content continues to rise, nearly all of Earth's grassland species likely will experience increases in both productivity and water use efficiency, even if available moisture decreases. The CO₂-induced increases in water use efficiency likely will allow grassland species to expand their ranges into desert areas where they previously could not survive due to lack of sufficient moisture, thereby contributing to a greater "greening of the globe."

As the air's CO₂ content rises, most plants exhibit increased rates of net photosynthesis and biomass production. Moreover, on a per-unit-leaf-area basis, they often lose less water via transpiration, as they tend to display lower stomatal conductances at elevated CO₂. Hence, the amount of carbon gained per unit of water lost per unit leaf area—water use efficiency—should increase dramatically as the air's CO₂ content continues to rise. This section summarizes the results of recent studies of this phenomenon in grassland species.

Grunzweig and Korner (2001) grew model grasslands representative of the semi-arid Negev of Israel for five months at atmospheric CO₂ concentrations of 440 and 600 ppm. The grasslands exhibited cumulative water-use efficiencies 17 and 28% greater, respectively, than control communities grown at 280 ppm CO₂. Similarly, Szente *et al.* (1998) report a doubling of the atmospheric CO₂ concentration increased the water use efficiency two C₃ grasses and two broad-leaved species common to the loess grasslands of Budapest by 72 and 266%, respectively. Leymarie *et al.* (1999) calculated twice-ambient CO₂ concentrations increased the water use efficiency of the herbaceous weedy species *Arabidopsis thaliana* by 41 and 120% under well-watered and water-stressed conditions, respectively. Other CO₂-induced increases in C₃ plant water use efficiency were documented by Clark *et al.* (1999) for several New Zealand pasture species and by Roumet *et al.* (2000) for various Mediterranean herbs.

Elevated CO₂ also has been shown to increase the water use efficiency of C₄ grassland species. Adams *et al.* (2000), for example, report twice-ambient CO₂ concentrations enhanced the daily water use efficiency of a C₄ tallgrass prairie in Kansas (USA) dominated by *Andropogon gerardii*. LeCain and Morgan (1998) also documented enhanced water-use efficiencies for six C₄ grasses grown with twice-ambient CO₂ concentrations. Seneweera *et al.* (1998)

report a 650-ppm increase in the air's CO₂ content dramatically increased the water use efficiency of the perennial C₄ grass *Panicum coloratum*.

As the air's CO₂ content continues to rise, nearly all of Earth's grassland species—including both C₃ and C₄ plants—likely will experience increases in water use efficiency. The productivity of the world's grasslands also should increase, even if available moisture decreases in certain areas. Such CO₂-induced increases in water use efficiency likely will allow grassland species to expand their ranges into desert areas where they previously could not survive due to lack of sufficient moisture, contributing to a greater "greening of the globe."

References

- Adams, N.R., Owensby, C.E., and Ham, J.M. 2000. The effect of CO₂ enrichment on leaf photosynthetic rates and instantaneous water use efficiency of *Andropogon gerardii* in the tallgrass prairie. *Photosynthesis Research* **65**: 121–129.
- Clark, H., Newton, P.C.D., and Barker, D.J. 1999. Physiological and morphological responses to elevated CO₂ and a soil moisture deficit of temperate pasture species growing in an established plant community. *Journal of Experimental Botany* **50**: 233–242.
- Grunzweig, J.M. and Korner, C. 2001. Growth, water and nitrogen relations in grassland model ecosystems of the semi-arid Negev of Israel exposed to elevated CO₂. *Oecologia* **128**: 251–262.
- LeCain, D.R. and Morgan, J.A. 1998. Growth, gas exchange, leaf nitrogen and carbohydrate concentrations in NAD-ME and NADP-ME C₄ grasses grown in elevated CO₂. *Physiologia Plantarum* **102**: 297–306.
- Leymarie, J., Lasceve, G., and Vavasseur, A. 1999. Elevated CO₂ enhances stomatal responses to osmotic stress and abscisic acid in *Arabidopsis thaliana*. *Plant, Cell and Environment* **22**: 301–308.
- Roumet, C., Garnier, E., Suzor, H., Salager, J.-L., and Roy, J. 2000. Short and long-term responses of whole-plant gas exchange to elevated CO₂ in four herbaceous species. *Environmental and Experimental Botany* **43**: 155–169.
- Seneweera, S.P., Ghannoum, O., and Conroy, J. 1998. High vapor pressure deficit and low soil water availability enhance shoot growth responses of a C₄ grass (*Panicum coloratum* cv. Bambatsi) to CO₂ enrichment. *Australian Journal of Plant Physiology* **25**: 287–292.
- Szente, K., Nagy, Z., and Tuba, Z. 1998. Enhanced water use efficiency in dry loess grassland species grown at elevated air CO₂ concentration. *Photosynthetica* **35**: 637–640.

2.33.3 Trees

- As the air's CO₂ content continues to rise, nearly all the planet's trees will exhibit increases in water use efficiency, enabling them to expand into areas where they previously could not grow due to insufficient available moisture. Earth will gradually acquire a much greener terrestrial cover with a significantly greater carbon sequestering capacity over time.

When the atmosphere's CO₂ concentration is increased, most plants exhibit increased rates of net photosynthesis and biomass production. In addition, they often lose less water via transpiration, as they tend to exhibit lower leaf stomatal conductances. Therefore, the amount of carbon they gain per unit of water lost per unit leaf area—water use efficiency—should increase significantly as the air's CO₂ content rises, as is described in this review of experimental results pertaining to this phenomenon in trees.

The effect of elevated atmospheric CO₂ concentrations on the water use efficiencies of trees is clearly positive, having been documented in numerous single-species studies of longleaf pine (Runion *et al.*, 1999), red oak (Anderson and Tomlinson, 1998), scrub oak (Lodge *et al.*, 2001), silver birch (Rey and Jarvis, 1998), beech (Bucher-Wallin *et al.*, 2000; Egli *et al.*, 1998), sweetgum (Gunderson *et al.*, 2002; Wullschlegel and Norby, 2001), and spruce (Robermtz and Stockfors, 1998). In a multispecies study performed by Tjoelker *et al.* (1998), seedlings of quaking aspen, paper birch, tamarack, black spruce, and jack pine, grown at 580 ppm CO₂ for three months, displayed water use efficiencies 40 to 80% larger than those exhibited by their respective controls grown at 370 ppm CO₂.

Similar results also have been obtained when trees were exposed to different environmental stresses. In a study conducted by Centritto *et al.* (1999), for example, cherry seedlings grown at twice-ambient levels of atmospheric CO₂ displayed water use efficiencies 50% greater than their ambient controls, regardless of soil moisture status. In the study of Wayne *et al.* (1998), yellow birch seedlings grown at 800 ppm CO₂ had water use efficiencies 52 and 94% greater than their respective controls when subjected to uncharacteristically low and high air temperature regimes, respectively.

In some parts of the world, perennial woody species have been exposed to elevated atmospheric CO₂ concentrations for decades, due to their proximity to CO₂-emitting springs and vents in the

Earth, allowing scientists to assess the long-term effects of this phenomenon. In Venezuela, for example, the water use efficiency of a common tree exposed to a lifetime atmospheric CO₂ concentration of approximately 1,000 ppm rose twofold and 19-fold during the local wet and dry seasons, respectively (Fernandez *et al.*, 1998). Similarly, Bartak *et al.* (1999) report 30-year-old *Arbutus unedo* trees growing in central Italy at a lifetime aerial CO₂ concentration around 465 ppm exhibited water use efficiencies 100% greater than control trees growing at a lifetime CO₂ concentration of 355 ppm. Also, two species of oak in central Italy that had been growing for 15 to 25 years at an atmospheric CO₂ concentration ranging from 500 to 1,000 ppm displayed “such marked increases in water use efficiency under elevated CO₂,” the scientists who studied them declare, this phenomenon “might be of great importance in Mediterranean environments in the perspective of global climate change.” The work of Blaschke *et al.* (2001) and Tognetti *et al.* (1998) suggest similar conclusions.

Some scientists also have looked to the past and determined the positive impact the historic rise in the air's CO₂ content already has had on plant water use efficiency. Duquesnay *et al.* (1998), for example, examined tree-ring data derived from beech trees and found the water use efficiency of such trees in north-eastern France increased by about 33% over the past century. Similarly, Feng (1999) used tree-ring chronologies from trees in western North America to calculate a 10 to 25% increase in tree water use efficiency from 1750 to 1970, during which time the atmospheric CO₂ concentration rose by approximately 16%.

Knapp *et al.* (2001) developed tree-ring chronologies from western juniper stands located in Oregon (USA) for the past century, determining growth recovery from drought was much greater in the latter third of their chronologies (1964–1998) than in the first third (1896–1930). The researchers suggest the greater atmospheric CO₂ concentrations of the latter period allowed the trees to recover more quickly from water stress. Beerling *et al.* (1998) grew *Ginkgo* saplings at 350 and 650 ppm CO₂ for three years and found elevated atmospheric CO₂ concentrations reduced leaf stomatal densities to values comparable to those measured on fossilized *Ginkgo* leaves dating back to the Triassic and Jurassic periods, implying greater water use efficiencies for those times too.

Tognetti *et al.* (2001) grew five-year-old seedlings of two olive cultivars in pots placed within free-air CO₂ enrichment (FACE) arrays maintained at

Plant Characteristics

atmospheric CO₂ concentrations of 360 and 560 ppm for seven to eight months in a study designed to evaluate the effects of elevated CO₂ on gas exchange in this economically important tree species. The elevated CO₂ enhanced rates of net photosynthesis by an average of 38% in both cultivars while reducing stomatal conductances by an average of 30%. Instantaneous water use efficiency rose by approximately 80% in both cultivars, suggesting that as the air's CO₂ content continues to rise, olive trees growing in semi-arid Mediterranean-type climates should be able to cope with recurring drought conditions that are common in such areas.

Centritto *et al.* (2002) grew peach (*Prunus persica*) seedlings at atmospheric CO₂ concentrations of 350 and 700 ppm for one full year in two "growth tunnels," then transferred them to pots and placed them in open-top chambers having the same CO₂ concentrations for an additional three months, during the final four weeks of which half of the seedlings in each CO₂ treatment were allowed to "dry-down." This enabled the three researchers to investigate the interactive effects of elevated CO₂ and water stress on both photosynthesis and growth.

The elevated CO₂ stimulated net photosynthesis rates by about 60% in the well-watered seedlings. Under drought conditions, however, the relative photosynthetic stimulation increased to as much as 180%, ameliorating the negative effect of water stress. In addition, elevated CO₂ increased whole-plant water use efficiency by 51 and 63% in the well-watered and water-stressed seedlings, respectively. Thus, as the air's CO₂ content increases, peach seedlings likely will exhibit increased rates of both net photosynthesis and biomass production. In addition, they likely will be better able to deal with intermittent periods of water shortage without compromising overall productivity and growth. Peach production can be expected to increase as the atmospheric CO₂ concentration continues to rise.

Arnth *et al.* (2002) describe how they developed 20 tree-ring ¹³C/¹²C chronologies from *Pinus sylvestris* (Scots pine) trees at five locations along a 1,000-km north-south transect running through central Siberia they converted into plant isotopic discrimination ($\delta^{13}\text{C}_c$) values. Based on these data, they conclude in 17 of the 20 samples the trees' $\delta^{13}\text{C}_c$ had declined during the past 150 years, "particularly so during the second half of the twentieth century." Based on a model of stomatal behavior combined with a process-oriented photosynthesis model, they deduce "this trend indicates a long-term decrease in canopy stomatal conductance, probably in

response to increasing atmospheric CO₂ concentrations." They conclude their observations suggest "increased water use efficiency for Scots pine in central Siberia over the last century."

Centritto (2002) grew peach seedlings for two years in pots placed within open-top chambers of either ambient or CO₂-enriched air (350 or 700 ppm, respectively) located inside a glasshouse, where they were continuously maintained at optimum soil fertility and, for the entire first growing season, at optimum soil water availability. In the second growing season, water was withheld from half the seedlings for four weeks.

At the end of the study, there were no CO₂-induced differences in the basal diameters of the seedlings. In terms of total dry weight, however, the elevated CO₂ treatment enhanced the growth of the water-stressed seedlings by 30% and the growth of the well-watered seedlings by 35%, which was largely a consequence of increased height growth. In addition, Centritto found no evidence of any downward acclimation of photosynthesis in the seedlings grown at elevated CO₂, nor was there any downward acclimation in rubisco carboxylation efficiency nor in the maximum RuBP regeneration capacity mediated by electron transport. There were also no significant effects of elevated CO₂ on stomatal conductance in either of the two water treatments. But the CO₂-induced increase in plant growth brought a complementary increase in seedling water use efficiency, even though there was no difference in total water uptake between the two CO₂ treatments. In a world of the future where atmospheric CO₂ concentration is approximately doubled, young peach trees likely will produce about a third more growth on the same amount of water as they did at the turn of the century.

As part of the long-term (November 1987 to January 2005) sour orange tree study conducted at the U.S. Water Conservation Laboratory in Phoenix, Arizona (Idso and Kimball, 2001; Kimball *et al.*, 2007), Leavitt *et al.* (2003) report the results of a multifaceted investigation of a phenomenon never before assessed in this long-term experiment: the effects of a 75% increase in the air's CO₂ content on the efficiency with which well-watered and well-fertilized sour orange trees utilize water. It was based, as the six scientists noted, "on the conceptual framework developed by Farquhar *et al.* (1982), who defined intrinsic water use efficiency (iWUE) as the ratio of the photosynthetic uptake of CO₂ through leaf stomata to the simultaneous transpirational loss of water vapor through the same [stomatal] openings."

This ratio may be experimentally evaluated by measuring stable-carbon isotopes of various plant tissues and the air to which those tissues were exposed during their development. In this study, the plant materials utilized were leaves that had been collected every two months throughout 1992 and on three occasions in 1994–95, plus wood samples extracted five years later from north-south- and east-west-oriented wood cores that passed through the centers of each of the eight trees' trunks at a height of 45 cm above the ground. The average result of these measurements, evaluated within the context described by Farquhar *et al.*, was, as Leavitt *et al.* report, "an 80% increase in [water use efficiency] in response to the [75%] increase in atmospheric CO₂ concentration employed in the study."

This result is interesting for a number of reasons. First, it suggests a doubling of the air's CO₂ content likely would bring more than a doubling of the trees' water use efficiency. Second, as the six scientists note, "this increase in sour orange tree iWUE is identical to the long-term CO₂-induced increase in the trees' production of wood and fruit biomass," as documented by Idso and Kimball (2001), suggesting a doubling of the air's CO₂ content should produce more than a doubling of the trees' total productivity, which further suggests the carbon sequestration potential of land planted to sour orange trees, and perhaps many other tree species, will increase dramatically in a CO₂-enriched world.

Third, Leavitt *et al.* note the CO₂-induced increase in sour orange tree water use efficiency is also identical "to the increase in the mean iWUE reported for 23 groups of naturally occurring trees scattered across western North America that was caused by the historical rise in the air's CO₂ content that occurred between 1800 and 1985," as documented by Feng (1999), who further noted these iWUE trends in trees "are largely caused by the anthropogenic increase of the atmospheric CO₂ concentration," concluding this phenomenon "would have caused natural trees in arid environments to grow more rapidly, acting as a carbon sink for anthropogenic CO₂." In addition, Leavitt *et al.* note "even greater water use efficiency responses have been observed in European tree-ring studies," citing Bert *et al.* (1997) with white fir and Hemming (1998) with beech, oak, and pine trees. With respect to what these observations portend for the decades ahead, Leavitt *et al.* state, "the ongoing rise in the air's CO₂ content could continue to do the same for Earth's trees in the future," dramatically increasing their productivity and the efficiency with which they utilize

water to achieve vastly enhanced growth rates.

As for how general this phenomenon could be expected to be, Saxe *et al.* (1998) determined in a comprehensive review of the scientific literature, "close to a doubling" of the air's CO₂ concentration leads to an approximate 50% increase in the biomass production of angiosperm trees and a 130% increase in the biomass production of coniferous species. With sour orange trees projected to experience just slightly more than a 100% increase in wood and fruit production in response to a doubling of the air's CO₂ concentration, the results of the Phoenix study fall well within the mid-range results typical of most other trees that have been similarly studied.

In light of these many empirical observations, one can confidently expect the growth rates of Earth's trees to increase dramatically as the air's CO₂ content continues to climb; this phenomenon, in turn, should enable them to sequester increasingly greater amounts of carbon. In addition, as the planet's trees become increasingly efficient at utilizing water, one could expect to see them rapidly expand into areas that are currently too dry to support their growth and reproduction, and this phenomenon also should increase the magnitude of carbon sequestration by Earth's trees. Hence, as time progresses, the planet's trees, if not destroyed by mankind's cutting and burning them, should provide an ever-increasing brake upon the rate of rise of the air's CO₂ content.

Waterhouse *et al.* (2004) determined the intrinsic water use efficiency (iWUE) responses of three tree species growing across northern Europe—pedunculate oak (*Quercus robur* L.), common beech (*Fagus sylvatica* L.), and Scots pine (*Pinus sylvestris* L.)—to the increase in the air's CO₂ concentration experienced between 1895 and 1994, using parameters derived from measurements of stable carbon isotope ratios of trunk cellulose. They report, "all species at all the sites show a long-term increase in their values of iWUE during the past century," and "the main cause of this common behavior is likely to be the increase in atmospheric CO₂ concentration."

Linearly extrapolating these responses, which occurred over a period of time when the air's CO₂ concentration rose by approximately 65 ppm, to what would be expected for the more common 300-ppm increase employed in the majority of atmospheric CO₂ enrichment experiments, the iWUE increases they derived amount to +158 ± 14% for the oak trees (mean ± standard error for the five sites studied), +195% for the pine trees, and +220% for the beech trees, as best as can be determined from the graphs of their results. These responses are huge and probably

Plant Characteristics

not due to rising CO₂ alone, but to the positive synergism that occurs when the air's CO₂ content and temperature rise together, as these parameters have done over the past century or so.

Peterson and Neofotis (2004) grew velvet mesquite (*Prosopis velutina* Woot.) seedlings for six weeks from their time of planting (as seeds) in small pots within environmentally controlled growth chambers maintained at atmospheric CO₂ concentrations of 380 and 760 ppm and two levels of water availability (high and low). Although they did not see a significant CO₂-induced increase in plant growth, they report by the end of their six-week study there was a highly significant reduction of approximately 41% in the volume of water transpired by *P. velutina* in response to the experimental doubling of the air's CO₂ content. "This large reduction in whole-plant water use," they write, "occurred because the reduction in transpiration per unit leaf area at elevated CO₂ was not offset by a proportional increase in total leaf area."

The two scientists from the Biosphere 2 Center near Oracle, Arizona (USA) state their findings suggest "under a future [high-CO₂] scenario, seedlings may deplete soil moisture at a slower rate than they do currently," and "this could facilitate seedling survival between intermittent rain events," noting their work "corroborates the conclusions of Polley *et al.* (1994, 1999, 2003) that increasing levels of atmospheric CO₂ may facilitate the establishment of mesquite seedlings through a reduction in soil water depletion." Peterson and Neofotis note, "mesquites and other woody species in the semiarid southwestern United States have shown substantial increases in population density and geographic range since Anglo-American settlement of the region approximately 120 years ago," citing Van Auken and Bush (1990), Gibbens *et al.* (1992), Bahre and Shelton (1993), Archer (1995), Boutton *et al.* (1999), Van Auken (2000), Ansley *et al.* (2001), Wilson *et al.* (2001), and Biggs *et al.* (2002).

Saurer *et al.* (2004), measured carbon isotope ratios in the rings of coniferous trees from northern Eurasia—including the three genera *Larix*, *Picea* and *Pinus*—across a longitudinal transect covering the entire super-continent in the latitude range from 59 to 71°N, to determine the change in intrinsic water use efficiency (Wi, the amount of water loss at the needle level per unit of carbon gain) experienced by the trees between the two 30-year periods 1861–1890 and 1961–1990.

They found the "increasing CO₂ in the atmosphere resulted in improved intrinsic water use

efficiency," such that "125 out of 126 trees showed increasing Wi from 1861–1890 to 1961–1990, with an average improvement of $19.2 \pm 0.9\%$." The three Swiss scientists state their results suggest the trees they studied "are able to produce the same biomass today [as they did 100 years ago] but with lower costs in terms of transpiration." This finding is highly significant, because some data had indicated recent warming in other longitudinal segments of the same latitude belt "may be accompanied by increased drought stress (Lloyd and Fastie, 2002)." The historical increase in the air's CO₂ content may have been helping those trees better cope with the newly established drought conditions.

Syvertsen and Levy (2005) reviewed what was known about salinity stress in citrus trees and how it may be modified by atmospheric CO₂ enrichment. They note, for example, rapidly growing plants almost always use more water than slower growing plants, and "in citrus, many vigorous rootstocks that produce fast-growing trees also tend to have poor salt tolerance (Castle *et al.*, 1993)," possibly because they accumulate more salt in their tissues because of their greater uptake of water. When growing plants in CO₂-enriched air, however, plant stomatal conductance and water use often are decreased at the same time net photosynthesis and growth are increased, so, "elevated CO₂ almost always leads to higher water use efficiency as it disconnects rapid tree growth from high water use." Consequently, the two scientists explain, "if salt uptake is coupled with water uptake, then leaves grown at elevated CO₂ should have lower salt concentrations than leaves grown at ambient CO₂ (Ball and Munns, 1992)."

"As expected," Syvertsen and Levy write, "all citrus rootstock species studied increased growth and water use efficiency in response to elevated CO₂ that was twice ambient," and generally, but not always, "the salinity-induced accumulation of sodium (Na⁺) in leaves was less when seedlings were grown at elevated CO₂ than at ambient CO₂." One exception, where Na⁺ accumulation was not affected by elevated CO₂, was Rangpur lime (*Citrus reticulata*); the scientists note this citrus variety is relatively salt-tolerant and another variety of the same species (Cleopatra mandarin) had lower leaf chloride (Cl⁻) concentrations in CO₂-enriched air than in ambient air.

All the citrus trees tested to that point in time had exhibited increased growth rates and water use efficiencies when growing in CO₂-enriched air. In addition, they generally experienced less salinity stress than when grown in lower-CO₂ ambient air. As

a result, the ongoing rise in the atmosphere's CO₂ concentration bodes well for the future vitality and productivity of the many varieties of citrus trees, which in turn bodes well for humanity.

Hietz *et al.* (2005) collected samples of wood from 37 tropical cedar (*Cedrela odorata* L.) trees that were between 11 and 151 years old in 2001 and from 16 big-leaf mahogany (*Swietenia macrophylla* King) trees that were between 48 and 126 years old at that time, from a rain forest in Aripuana, Brazil. They measured the wood samples' cellulose $\delta^{13}\text{C}$ in 10-year growth increments. They found the cellulose $\delta^{13}\text{C}$ decreased by 1.3 per mil in *Cedrela* and by 1.1 per mill in *Swietenia* over the past century, with the largest changes occurring during the last 50 years. Based on these data and known trends in atmospheric CO₂ and $\delta^{13}\text{C}$, they calculated the intrinsic water use efficiency of the trees increased by 34% in *Cedrela* and by 52% in *Swietenia* over this period, which they state is about the same as what had been deduced from similar measurements of the wood of temperate trees (Freyer, 1979; Bert *et al.*, 1997; Feng, 1999).

The three researchers note, since "water is probably not a strong limiting factor in tropical rain forest trees," the increase in water use efficiency they discovered likely "translates mostly to increased carbon assimilation, which may explain the observed increase in tree growth and turnover (Phillips, 1996; Laurance *et al.*, 2004)" in such forests.

Defining intrinsic water use efficiency (iWUE) as the ratio of the photosynthetic uptake of CO₂ through leaf stomata to the simultaneous transpirational loss of water vapor through the stomata, Liu *et al.* (2007) evaluated this parameter based on $\delta^{13}\text{C}$ measurements of cellulose extracted from the wood of tree-ring cores taken from living Qilian juniper (*Sabina przewalskii* Kom.) and Qinghai spruce (*Picea crassifolia* Kom.) trees, focusing on the period AD 1850–2000 at time resolutions of three years for juniper from the semi-arid Qilian Mountains, two years for juniper from the arid Qaidam Basin, and one year for spruce from both of the northwest China sites.

Overall, and based on means for the first and last decades of the study period, the seven Chinese researchers found "the iWUE values of the two species both showed long-term increases, by 33.6 and 37.4% for spruce in the arid and semi-arid areas, respectively, and by increases of 24.7 and 22.5% for juniper," noting "the main cause of this behavior is likely to be an increase in atmospheric CO₂ concentration," which for the start and end decades of

the study period rose from approximately 285 ppm to 362 ppm, about 27%.

Increases in the water use efficiencies of trees in arid and semi-arid regions must be considered a significant benefit. And in the case of the two species studied by Liu *et al.*, they note Qinghai spruce, in particular, "plays an important role in preventing soil erosion, regulating climate, and retaining ecological stability," citing Zhou and Li (1990) in this regard. This phenomenon is undoubtedly one of the chief reasons for the concomitant "greening of the Earth" that has been so evident in many historical studies of China and other parts of Asia.

Leal *et al.* (2008) obtained cores from eight to 20 black pine (*Pinus nigra*) trees growing at each of 28 sites within the Vienna basin of Austria in the European Eastern Alps during the summers of 1996 and 1997, focusing on trees possessing umbrella-like crowns (indicating water-limited conditions) growing on shallow and poor soils, in order to maximize their ring-width response to moisture availability. They discovered "a very clear change in the sensitivity of the growth rate of tree stems to water availability in the late 20th century," noting "trees previously sensitive to spring-summer drought show a lack of response to this climatic parameter in recent decades." Hence, they write, "tree-ring indices were larger in the second half of the 20th century than predicted given prevailing spring-summer drought conditions and the previous sensitivity of growth to these conditions." In addition, they found "a decrease in correspondence between the occurrence of extreme events in precipitation and rate of change of growth," such that "in the second half of the century this correspondence was not significant," and "recent extreme droughts did not result in the formation of very narrow rings, which means the droughts were not as limiting to tree growth as they had been in the past."

The five researchers suggest the greater atmospheric CO₂ concentrations of the latter decades of the twentieth century "induced improved water use efficiency enabling *P. nigra* growing in the Vienna basin to avoid the impact of recurrent dry conditions." This phenomenon also has been observed in many other parts of the world in a number of tree species.

Describing *Araucaria angustifolia* as "an indigenous conifer tree restricted to the southern region of South America that plays a key role in the dynamics of regional ecosystems where forest expansion over grasslands has been observed," Silva *et al.* (2009) studied various types of tree-ring data obtained from *A. angustifolia* trees growing in both

forest and grassland sites of southern Brazil. They compared changes in iWUE with historical changes in temperature, precipitation, and atmospheric CO₂ concentration over the past century.

During the past several decades, they write, “iWUE increased over 30% in both habitats [forests and grasslands],” and “this increase was highly correlated with increasing levels of CO₂ in the atmosphere.” However, tree growth remained rather stable over this latter period, due to lower-than-normal precipitation and higher-than-normal temperatures, which would normally tend to depress the growth of this species, as Katinas and Crisci (2008) described *A. angustifolia* as being “intolerant of dry seasons and requiring cool temperatures.” Therefore, Silva *et al.* conclude, “climatic fluctuations during the past few decades,” which normally would be expected to have been deleterious to the growth of *A. angustifolia*, seem to have had their growth-retarding effects “compensated by increases in atmospheric CO₂ and changes [i.e., increases] in iWUE.”

Wyckoff and Bowers (2010) note, “with continued increases in global greenhouse gas emissions, climate models predict that, by the end of the 21st century, Minnesota [USA] summer temperature will increase by 4–9°C and summer precipitation will slightly decrease,” citing Kling *et al.* (2003) and Christensen *et al.* (2007). They further note certain “forest models and extrapolations from the paleoecological record suggest that, in response to increased temperature and/or drought, forests may retreat to the extreme north-eastern parts of the state,” citing Pastor and Post (1998), Hamilton and Johnson (2002), and Galatowitsch *et al.* (2009).

Working with bur oak (*Quercus macrocarpa*) trees, Wyckoff and Bowers explored the likelihood of the latter of these two projections coming to pass by “(i) using tree rings to establish the relationship between drought and *Q. macrocarpa* growth for three sites along Minnesota’s prairie-forest border, (ii) calculating the current relationship between growth and mortality for adult *Q. macrocarpa* and (iii) using the distributions of current growth rates for *Q. macrocarpa* to predict the susceptibility of current populations to droughts of varying strength.” They also looked for “temporal trends in the correlation between *Q. macrocarpa* growth and climate, hypothesizing increases in CO₂ may lead to weaker relationships between drought and tree growth over time,” because atmospheric CO₂ enrichment typically leads to increases in plant water use efficiency, which generally makes them less susceptible to the deleterious impact of drought on growth.

The two University of Minnesota researchers discovered “the sensitivity of annual growth rates to drought has steadily declined over time as evidenced by increasing growth residuals and higher growth rates for a given PDSI [Palmer Drought Severity Index] value after 1950 [when the atmosphere’s CO₂ concentration rose by 57 ppm from 1950 to 2000] compared with the first half of the century [when the CO₂ increase was only 10 ppm].” Thus, they conclude, “for *Q. macrocarpa*, declining sensitivity of growth to drought translates into lower predicted mortality rates at all sites,” and “at one site, declining moisture sensitivity yields a 49% lower predicted mortality from a severe drought (PDSI = -8, on a par with the worst 1930s ‘American Dust Bowl’ droughts).” Hence, “the decreasing drought sensitivity of established trees may act as a buffer and delay the movement of the prairie-forest ecotone for many decades even in the face of climate change.”

Brienen *et al.* (2011) note water use efficiency is the ratio of photosynthesis (A) to transpiration (E), or the amount of carbon gained per unit of water used in the process of acquiring the carbon. They also define A/gs—where gs is stomatal conductance—to be intrinsic water use efficiency (Wi), and state, “an increase in Wi in response to increasing CO₂ since the industrial revolution has been found in nearly all temperate trees that have been studied,” citing Feng (1999), Saurer *et al.* (2004), and Nock *et al.* (2010). They decided to see if this is true also for tropical trees.

Noting “increases in Wi have been observed in short-term experiments of tree responses to elevated CO₂ (Norby *et al.*, 1999), and over long-time periods using records of $\delta^{13}\text{C}$ in tree rings that reflect the global increase in atmospheric CO₂ (Feng, 1999; Waterhouse *et al.*, 2004),” Brienen *et al.* “analyzed carbon isotope ratios over the last 40 years in tree rings of *Mimosa acantholoba*, a tropical dry forest pioneer species,” in a study conducted “on the Pacific slope of the isthmus of Tehuantepec, close to the village of Nizanda in the state of Oaxaca, South Mexico (16°39’N, 95°00’W).” The three researchers, representing Austria, Mexico, and the United Kingdom, report the dry-forest tropical *M. acantholoba* trees “responded strongly to the increase in atmospheric CO₂ over the last four decades,” as their “Wi increased dramatically by 40%.”

Chen *et al.* (2011) write “Idso (1998) suggested that elevated CO₂ affects plant growth dependent upon plant water status: it has less effect on plants in the well-watered optimal growth phase, but exerts more effect under non-lethal dry conditions, and is

most beneficial to plants under severe drought conditions.” In a further assessment of this phenomenon, Chen *et al.* measured leaf transpiration rate (E) and net photosynthetic rate (PN) in *Populus euphratica* trees growing just within the northern edge of the Taklimakan Desert in Xinjiang, northwestern China, where the riparian trees dominate the indigenous vegetation because of their tolerance of severe drought and the high salinity and alkalinity of the region’s soils. They did so in four locations, where mean soil water contents at groundwater depths of 4.12, 4.74, 5.54, and 7.74 meters were 10.9, 9.5, 3.5, and 1.3%, respectively, making their measurements at atmospheric CO_2 concentrations of either 360 or 720 ppm. They then calculated the trees’ water use efficiencies ($WUE = PN/E$) when measured under the two atmospheric CO_2 concentrations.

In the case of each CO_2 concentration, the researchers found no statistical difference between the leaf water use efficiencies of the first three groundwater depths; but the mean WUE at the higher of the two CO_2 concentrations was 44% greater than the mean measured at the lower CO_2 concentration. The WUE of the lowest and driest of the four groundwater depths was statistically different from the WUEs of the other three groundwater depths, and the mean WUE of the trees growing under this most stressful condition when measured at the higher of the two CO_2 concentrations was 86% greater than the mean measured at the lower CO_2 concentration. Chen *et al.* conclude, with respect to the plant water use efficiency of *Populus euphratica* trees, those growing “under a mild water stress show a weak responsiveness, and those under a moderate drought stress display a strong responsiveness to CO_2 enrichment.”

Soule and Knapp (2011) note, “in 2008, atmospheric CO_2 concentrations from the Mauna Loa, Hawaii, Observatory records exceeded 385 ppm, representing a 22% increase since 1959,” and “as CO_2 has increased, most tree species have been able to use water more efficiently,” as their “leaf stomatal apertures narrow during photosynthesis,” resulting in “less transpirational water loss per biomass gained.” The two researchers studied changes in and relationships among radial growth rates and the iWUE of ponderosa pine (*Pinus ponderosa*) trees, climate, and atmospheric CO_2 concentration in the western United States since the mid-nineteenth century, developing tree-ring chronologies for eight sites in three climate regions and using carbon isotope data to calculate pentadal values of iWUE. They examined relationships among radial growth, climate,

iWUE, and CO_2 via correlation and regression analyses.

Soule and Knapp report finding significant upward trends in iWUE at all sites, and they state, “despite an absence of climate changes that would favor growth,” upward radial growth trends occurred at five sites. In addition, they discovered the highest iWUE values “were recorded in the last pentad at six of eight sites and follow a positive quadratic progression at all sites, suggesting that future increases in iWUE are likely for ponderosa pine within our study regions as CO_2 levels increase.” They found “significant improvements in radial growth rates during drought years after 1950,” when the air’s CO_2 content rose at an accelerating rate.

The two U.S. researchers suggest “increased iWUE associated with rising CO_2 can positively impact tree growth rates in the western United States and are thus an evolving component of forest ecosystem processes.” They conclude, “if potential climate changes lead to increasing aridity in the western United States, additional increases in iWUE associated with future increases in CO_2 might ameliorate growth declines associated with drought conditions.”

Wang *et al.* (2012) introduce their treatment of the subject by noting iWUE “represents the ratio of photosynthetic assimilation (A) to stomatal conductance (g_w),” and “higher iWUE can result from reducing g_w , increasing A , or a combination of the two responses.” They also state, “empirical evidence from lab studies with a controlled CO_2 concentration and from free-air CO_2 enrichment (FACE) experiments have revealed significantly increased iWUE in response to rising CO_2 ,” as demonstrated by the studies of Luo *et al.* (1996), Ainsworth and Rogers (2007), and Niu *et al.* (2011). They also note “tree-ring stable carbon isotope ratios ($\delta^{13}C$) have proven to be an effective tool for evaluating variations in iWUE around the world,” citing Farquhar *et al.* (1989), Saurer *et al.* (2004), Liu *et al.* (2007), and Andreu *et al.* (2011). In addition, they report “during the past 100–200 years, most of the sampled forests demonstrated a trend of increasing iWUE, which paralleled the increasing atmospheric CO_2 ,” citing Peñuelas *et al.* (2011) and references therein.

In November 2009, Wang *et al.* extracted two cores from the trunks of each of 17 dominant living Qinghai spruce (*Picea crassifolia*) trees at a site in the Xinglong Mountains in the eastern part of northwestern China (35°40’N, 104°02’E), obtaining from those cores precise ring-width measurements

they used to calculate yearly mean basal area growth increments. They used subsamples of the cores to conduct the stable carbon isotope analyses needed to obtain the $\delta^{13}\text{C}$ data required to calculate iWUE over the course of their study period: 1800–2009. By calibrating the $\delta^{13}\text{C}$ data against climatic data obtained at the nearest weather station over the period 1954–2009, they were able to extend the histories of major meteorological parameters back to 1800. And by comparing these weather data with the tree growth and water use efficiency data, they were able to interpret the impacts of climate change and atmospheric CO_2 enrichment on spruce tree growth and water use efficiency.

For the arid region of northwestern China in which the spruce trees they studied were growing, Wang *et al.* found iWUE increased by approximately 40% between 1800 and 2009, rising very slowly for the first 150 years but then more rapidly to about 1975, and then faster still until 1998, when it leveled off for the remaining 11 years of the record. Commenting on the main cause of the increasing trend in iWUE from 1800 to 1998, they state it “is likely to be the increase in atmospheric CO_2 ,” because “regression analysis suggested that increasing atmospheric CO_2 explained 83.0% of the variation in iWUE from 1800 to 1998 ($p < 0.001$).” Thereafter, they note, a substantial drought at the end of the record is probably what caused the leveling off of iWUE, which was also strong enough to cause a decline in yearly basal area growth increment, much like what occurred between 1923 and 1934, which they describe as “the most severe drought since 1800,” citing Fang *et al.* (2009).

Wang *et al.*’s study suggests the historical increase in the air’s CO_2 content over the course of the Industrial Revolution gradually but greatly enhanced the intrinsic water use efficiency of Qinghai spruce trees in northwest China, as well as their growth rates. During times of very severe drought stress, even this added help can fall short of what is needed to keep the trees from maintaining an exemplary rate of growth. Rising atmospheric CO_2 concentrations see them through the times of severe stress to where they can once again grow exceedingly well once the drought is past.

Battipaglia *et al.* (2013) combined tree ring analyses with carbon and oxygen isotope measurements made at three free-air CO_2 enrichment (FACE) sites—POP-EUROFACE in Italy, Duke FACE in North Carolina (USA), and ORNL in Tennessee (USA)—“to cover the entire life of the trees,” which they accomplished by using $\delta^{13}\text{C}$ to assess carbon

isotope discrimination and changes in water use efficiency, while direct CO_2 effects on stomatal conductance were explored using $\delta^{18}\text{O}$ as a proxy.

The seven scientists report, “across all the sites, elevated CO_2 increased ^{13}C -derived water use efficiency on average by 73% for *Liquidambar styraciflua* [POP-EUROFACE, +200 ppm CO_2], 77% for *Pinus taeda* [Duke FACE, +200 ppm CO_2] and 75% for *Populus sp.* [ORNL, +153 ppm CO_2], but through different ecophysiological mechanisms.” They state their findings provide “a robust means of predicting water use efficiency responses from a variety of tree species exposed to variable environmental conditions over time, and species-specific relationships that can help modeling elevated CO_2 and climate impacts on forest productivity, carbon and water balances.”

As the CO_2 content of the air continues to rise, nearly all Earth’s trees will respond favorably through increases in water use efficiency. Woody species are likely to expand into areas where they previously could not exist due to limiting amounts of available moisture. One can expect Earth to become a greener biospheric body with greater carbon-sequestering capacity as the air’s CO_2 concentration continues to rise.

References

- Ainsworth, E.A. and Rogers, A. 2007. The response of photosynthesis and stomatal conductance to rising $[\text{CO}_2]$: mechanisms and environmental interactions. *Plant, Cell and Environment* **30**: 258–270.
- Anderson, P.D. and Tomlinson, P.T. 1998. Ontogeny affects response of northern red oak seedlings to elevated CO_2 and water stress. I. Carbon assimilation and biomass production. *New Phytologist* **140**: 477–491.
- Andreu, L., Planells, O., Gutierrez, E., Muntan, E., Helle, G., Anchukaitis, K.J., and Schleser, G.H. 2011. Long tree-ring chronologies reveal 20th century increases in water use efficiency but no enhancement of tree growth at five Iberian pine forests. *Global Change Biology* **17**: 2095–2112.
- Ansley, R.J., Ben Wu, X., and Kramp, B.A. 2001. Observation: long-term increases in mesquite canopy cover in a north Texas savanna. *Journal of Range Management* **54**: 171–176.
- Archer, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* **2**: 83–99.
- Arneth, A., Lloyd, J., Santruckova, H., Bird, M.,

Climate Change Reconsidered II: Biological Impacts

- Grigoryev, S., Kalaschnikov, Y.N., Gleixner, G., and Schulze, E.-D. 2002. Response of central Siberian Scots pine to soil water deficit and long-term trends in atmospheric CO₂ concentration. *Global Biogeochemical Cycles* **16**: 10.1029/2000GB001374.
- Bahre, C.J. and Shelton, M.L. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *Journal of Biogeography* **20**: 489–504.
- Ball, M.C. and Munns, R. 1992. Plant responses to salinity under elevated atmospheric concentrations of CO₂. *Australian Journal of Botany* **40**: 515–525.
- Bartak, M., Raschi, A., and Tognetti, R. 1999. Photosynthetic characteristics of Sun and shade leaves in the canopy of *Arbutus unedo* L. trees exposed to *in situ* long-term elevated CO₂. *Photosynthetica* **37**: 1–16.
- Battipaglia, G., Saurer, M., Cherubini, P., Calfapietra, C., McCarthy, H.R., Norby, R.J., and Cotrufo, M.F. 2013. Elevated CO₂ increases tree-level intrinsic water use efficiency: insights from carbon and oxygen isotope analyses in tree rings across three forest FACE sites. *New Phytologist* **197**: 544–554.
- Beerling, D.J., McElwain, J.C., and Osborne, C.P. 1998. Stomatal responses of the ‘living fossil’ *Ginkgo biloba* L. to changes in atmospheric CO₂ concentrations. *Journal of Experimental Botany* **49**: 1603–1607.
- Bert, D., Leavitt, S.W., and Dupouey, J.-L. 1997. Variations in wood δ¹³C and water use efficiency of *Abies alba* during the last century. *Ecology* **78**: 1588–1595.
- Biggs, T.H., Quade, J., and Webb, R.H. 2002. δ¹³C values of soil organic matter in semiarid grassland with mesquite (*Prosopis*) encroachment in southeastern Arizona. *Geoderma* **110**: 109–130.
- Blaschke, L., Schulte, M., Raschi, A., Slee, N., Rennenberg, H., and Polle, A. 2001. Photosynthesis, soluble and structural carbon compounds in two Mediterranean oak species (*Quercus pubescens* and *Q. ilex*) after lifetime growth at naturally elevated CO₂ concentrations. *Plant Biology* **3**: 288–298.
- Boutton, T.W., Archer, S.R., and Midwood, A.J. 1999. Stable isotopes in ecosystem science: structure, function and dynamics of a subtropical savanna. *Rapid Communications in Mass Spectrometry* **13**: 1263–1277.
- Brienen, R.J.W., Wanek, W., and Hietz, P. 2011. Stable carbon isotopes in tree rings indicate improved water use efficiency and drought responses of a tropical dry forest tree species. *Trees* **25**: 103–113.
- Bucher-Wallin, I.K., Sonnleitner, M.A., Egli, P., Gunthardt-Goerg, M.S., Tarjan, D., Schulin, R., and Bucher, J.B. 2000. Effects of elevated CO₂, increased nitrogen deposition and soil on evapotranspiration and water use efficiency of spruce-beech model ecosystems. *Phyton* **40**: 49–60.
- Castle, W.S., Tucker, D.P.H., Krezdorn, A.H., and Youtsey, C.O. 1993. *Rootstocks for Florida Citrus: Rootstock Selection, the First Step to Success*. University of Florida, Institute of Food and Agricultural Science, Gainesville, Florida, USA.
- Centritto, M. 2002. The effects of elevated [CO₂] and water availability on growth and physiology of peach (*Prunus persica*) plants. *Plant Biosystems* **136**: 177–188.
- Centritto, M., Lee, H.S.J., and Jarvis, P.G. 1999. Interactive effects of elevated [CO₂] and drought on cherry (*Prunus avium*) seedlings. I. Growth, whole-plant water use efficiency and water loss. *New Phytologist* **141**: 129–140.
- Centritto, M., Lucas, M.E., and Jarvis, P.G. 2002. Gas exchange, biomass, whole-plant water use efficiency and water uptake of peach (*Prunus persica*) seedlings in response to elevated carbon dioxide concentration and water availability. *Tree Physiology* **22**: 699–706.
- Chen, Y., Chen, Y., Xu, C., and Li, W. 2011. Photosynthesis and water use efficiency of *Populus euphratica* in response to changing groundwater depth and CO₂ concentration. *Environmental Earth Sciences* **62**: 119–125.
- Christensen, J.H., Hewitson, B., Bisuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.-T., Laprise, R., Magana-Rueda, V., Mearns, L., Menendez, C.G., Raisanen, J., Rinke, A., Saar, A., and Whetton, P. 2007. Regional climate projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Avery, K.B., Tignor, M., and Miller, H.L. (Eds.) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge University Press, Cambridge, UK/New York, New York, USA, pp. 847–940.
- Duquesnay, A., Breda, N., Stievenard, M., and Dupouey, J.L. 1998. Changes of tree-ring δ¹³C and water use efficiency of beech (*Fagus sylvatica* L.) in north-eastern France during the past century. *Plant, Cell and Environment* **21**: 565–572.
- Egli, P., Maurer, S., Gunthardt-Goerg, M.S., and Korner, C. 1998. Effects of elevated CO₂ and soil quality on leaf gas exchange and aboveground growth in beech-spruce model ecosystems. *New Phytologist* **140**: 185–196.
- Fang, K., Gou, X., Chen, F., Yang, M., Li, J., He, M., Zhang, Y., Tian, Q., and Peng, J. 2009. Drought variations in the eastern part of Northwest China over the past two centuries: evidence from tree rings. *Climate Research* **38**: 129–135.
- Farquhar, G.D., Ehleringer, J.R., and Hubick, K.T. 1989.

Plant Characteristics

- Carbon isotope discrimination and photosynthesis. *Annual Reviews of Plant Physiology and Plant Molecular Biology* **40**: 503–537.
- Farquhar, G.D., O’Leary, M.H., and Baxter, J.A. 1982. On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology* **9**: 121–137.
- Feng, X. 1999. Trends in intrinsic water use efficiency of natural trees for the past 100–200 years: A response to atmospheric CO₂ concentration. *Geochimica et Cosmochimica Acta* **63**: 1891–1903.
- Fernandez, M.D., Pieters, A., Donoso, C., Tezara, W., Azuke, M., Herrera, C., Rengifo, E., and Herrera, A. 1998. Effects of a natural source of very high CO₂ concentration on the leaf gas exchange, xylem water potential and stomatal characteristics of plants of *Spatiphyllum cannifolium* and *Bauhinia multinervia*. *New Phytologist* **138**: 689–697.
- Galatowitsch, S., Frelich, L., and Phillips-Mao, L. 2009. Regional climate change adaptation strategies for biodiversity conservation in a mid-continental region of North America. *Biological Conservation* **142**: 2012–2022.
- Gibbens, R.P., Beck, R.F., Mcneely, R.P., and Herbel, C.H. 1992. Recent rates of mesquite establishment in the northern Chihuahuan desert. *Journal of Range Management* **45**: 585–588.
- Gunderson, C.A., Sholtis, J.D., Wullschleger, S.D., Tissue, D.T., Hanson, P.J., and Norby, R.J. 2002. Environmental and stomatal control of photosynthetic enhancement in the canopy of a sweetgum (*Liquidambar styraciflua* L.) plantation during 3 years of CO₂ enrichment. *Plant, Cell and Environment* **25**: 379–393.
- Hamilton, J.D. and Johnson, S. 2002. *Playing with Fire: Climate Change in Minnesota*. Minnesotans for an Energy-Efficient Economy. St Paul, Minnesota, USA.
- Hemming, D.L. 1998. Stable Isotopes in Tree Rings: Biosensors of Climate and Atmospheric Carbon-Dioxide Variations. Ph.D. Dissertation. University of Cambridge, Cambridge, UK.
- Idso, S.B. 1998. Three phases of plant response to atmospheric CO₂ enrichment. *Plant Physiology* **87**: 5–7.
- Idso, S.B. and Kimball, B.A. 2001. CO₂ enrichment of sour orange trees: 13 years and counting. *Environmental and Experimental Botany* **46**: 147–153.
- Katinas, L. and Crisci, J.V. 2008. Reconstructing the biogeographical history of two plant genera with different dispersion capabilities. *Journal of Biogeography* **35**: 1374–1384.
- Kimball, B.A., Idso, S.B., Johnson, S., and Rillig, M.C. 2007. Seventeen years of carbon dioxide enrichment of sour orange trees: final results. *Global Change Biology* **13**: 2171–2183.
- Kling, G.W., Hayhoe, K., Johnson, L.B., Magnuson, J.J., Polasky, S., Robinson, S.K., Shuter, B.J., Wander, M.M., Wuebbles, D.J., and Zak, D.R. 2003. *Confronting Climate Change in the Great Lakes Region: Impacts on our Communities and Ecosystems*. Union of Concerned Scientists and Ecological Society of America, Washington, DC, USA.
- Knapp, P.A., Soule, P.T., and Grissino-Mayer, H.D. 2001. Post-drought growth responses of western juniper (*Junipers occidentalis* var. *occidentalis*) in central Oregon. *Geophysical Research Letters* **28**: 2657–2660.
- Leal, S., Eamus, D., Grabner, M., Wimmer, R., and Cherubini, P. 2008. Tree rings of *Pinus nigra* from the Vienna basin region (Austria) show evidence of change in climatic sensitivity in the late 20th century. *Canadian Journal of Forest Research* **38**: 744–759.
- Leavitt, S.W., Idso, S.B., Kimball, B.A., Burns, J.M., Sinha, A., and Stott, L. 2003. The effect of long-term atmospheric CO₂ enrichment on the intrinsic water use efficiency of sour orange trees. *Chemosphere* **50**: 217–222.
- Liu, X., Shao, X., Liang, E., Zhao, L., Chen, T., Qin, D., and Ren J. 2007. Species-dependent responses of juniper and spruce to increasing CO₂ concentration and to climate in semi-arid and arid areas of northwestern China. *Plant Ecology* **193**: 195–209.
- Lloyd, A.H. and Fastie, C.L. 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change* **52**: 481–509.
- Lodge, R.J., Dijkstra, P., Drake, B.G., and Morison, J.I.L. 2001. Stomatal acclimation to increased CO₂ concentration in a Florida scrub oak species *Quercus myrtifolia* Willd. *Plant, Cell and Environment* **24**: 77–88.
- Luo, Y., Sims, D.A., Thomas, R.B., Tissue, D.T., and Ball, J.T. 1996. Sensitivity of leaf photosynthesis to CO₂ concentration is an invariant function for C₃ plants: a test with experimental data and global applications. *Global Biogeochemical Cycles* **10**: 209–222.
- Niu, S., Xing, X., Zhang, Z., Xia, J., Zhou, X., Song, B., Li, L., and Wan, S. 2011. Water use efficiency in response to climate change: from leaf to ecosystem in a temperate steppe. *Global Change Biology* **17**: 1073–1082.
- Nock, C.A., Baker, P.J., Wanek, W., Leis, A., Grabner, M., Bunyavejchewin, S., and Hietz, P. 2010. Long-term increases in intrinsic water use efficiency do not lead to increased stem growth in a tropical monsoon forest in western Thailand. *Global Change Biology* **17**: 1049–1063.
- Norby, R.J., Wullschleger, S.D., Gunderson, C.A., Johnson, D.W., and Ceulemans, R. 1999. Tree responses to

Climate Change Reconsidered II: Biological Impacts

rising CO₂ in field experiments: implications for the future forest. *Plant, Cell and Environment* **22**: 683–714.

Pastor, J. and Post, W.M. 1988. Response of northern forests to CO₂-induced climate change. *Nature* **334**: 55–58.

Peñuelas, J., Canadell, J.G., and Ogaya, R. 2011. Increased water use efficiency during the 20th century did not translate into enhanced tree growth. *Global Ecology and Biogeography* **20**: 597–608.

Peterson, A.G. and Neofotis, P.G. 2004. A hierarchical analysis of the interactive effects of elevated CO₂ and water availability on the nitrogen and transpiration productivities of velvet mesquite seedlings. *Oecologia* **141**: 629–640.

Polley, H.W., Johnson, H.B., and Mayeux, H.S. 1994. Increasing CO₂: comparative responses of the C₄ grass *Schizachyrium* and grassland invader *Prosopis*. *Ecology* **75**: 976–988.

Polley, H.W., Johnson, H.B., and Tischler, C.R. 2003. Woody invasion of grasslands: evidence that CO₂ enrichment indirectly promotes establishment of *Prosopis glandulosa*. *Plant Ecology* **164**: 85–94.

Polley, H.W., Tischler, C.R., Johnson, H.B., and Pennington, R.E. 1999. Growth, water relations, and survival of drought-exposed seedlings from six maternal families of honey mesquite (*Prosopis glandulosa*): responses to CO₂ enrichment. *Tree Physiology* **19**: 359–366.

Rey, A. and Jarvis, P.G. 1998. Long-term photosynthetic acclimation to increased atmospheric CO₂ concentration in young birch (*Betula pendula*) trees. *Tree Physiology* **18**: 441–450.

Roberntz, P. and Stockfors, J. 1998. Effects of elevated CO₂ concentration and nutrition on net photosynthesis, stomatal conductance and needle respiration of field-grown Norway spruce trees. *Tree Physiology* **18**: 233–241.

Runion, G.B., Mitchell, R.J., Green, T.H., Prior, S.A., Rogers, H.H., and Gjerstad, D.H. 1999. Longleaf pine photosynthetic response to soil resource availability and elevated atmospheric carbon dioxide. *Journal of Environmental Quality* **28**: 880–887.

Saurer, M., Siegwolf, R.T.W., and Schweingruber, F.H. 2004. Carbon isotope discrimination indicates improving water use efficiency of trees in northern Eurasia over the last 100 years. *Global Change Biology* **10**: 2109–2120.

Saxe, H., Ellsworth, D.S., and Heath, J. 1998. Tree and forest functioning in an enriched CO₂ atmosphere. *New Phytologist* **139**: 395–436.

Silva, L.C.R., Anand, M., Oliveira, J.M., and Pillar, V.D. 2009. Past century changes in *Araucaria angustifolia*

(Bertol.) Kuntze water use efficiency and growth in forest and grassland ecosystems of southern Brazil: implications for forest expansion. *Global Change Biology* **15**: 2387–2396.

Soule, P.T. and Knapp, P.A. 2011. Radial growth and increased water use efficiency for ponderosa pine trees in three regions in the western United States. *The Professional Geographer* **63**: 370–391.

Syvrtsen, J. and Levy, Y. 2005. Salinity interactions with other abiotic and biotic stresses in citrus. *HortTechnology* **15**: 100–103.

Tjoelker, M.G., Oleksyn, J., and Reich, P.B. 1998. Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO₂ and temperature. *Tree Physiology* **18**: 715–726.

Tognetti, R., Johnson, J.D., Michelozzi, M., and Raschi, A. 1998. Response of foliar metabolism in mature trees of *Quercus pubescens* and *Quercus ilex* to long-term elevated CO₂. *Environmental and Experimental Botany* **39**: 233–245.

Tognetti, R., Sebastiani, L., Vitagliano, C., Raschi, A., and Minnocci, A. 2001. Responses of two olive tree (*Olea europaea* L.) cultivars to elevated CO₂ concentration in the field. *Photosynthetica* **39**: 403–410.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecological Systems* **31**: 197–215.

Van Auken, O.W. and Bush, J.K. 1990. Importance of grass density and time of planting on *Prosopis glandulosa* seedling growth. *Southwest Naturalist* **35**: 411–415.

Wang, W., Liu, X., An, W., Xu, G., and Zeng, X. 2012. Increased intrinsic water use efficiency during a period with persistent decreased tree radial growth in northwestern China: Causes and implications. *Forest Ecology and Management* **275**: 14–22.

Waterhouse, J.S., Switsur, V.R., Barker, A.C., Carter, A.H.C., Hemming, D.L., Loader, N.J., and Robertson, I. 2004. Northern European trees show a progressively diminishing response to increasing atmospheric carbon dioxide concentrations. *Quaternary Science Reviews* **23**: 803–810.

Wayne, P.M., Reekie, E.G., and Bazzaz, F.A. 1998. Elevated CO₂ ameliorates birch response to high temperature and frost stress: implications for modeling climate-induced geographic range shifts. *Oecologia* **114**: 335–342.

Wilson, T.B., Webb, R.H., and Thompson, T.L. 2001. *Mechanisms of Range Expansion and Removal of Mesquite in Desert Grasslands of the Southwestern United States*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Wullschlegel, S.D. and Norby, R.J. 2001. Sap velocity and canopy transpiration in a sweetgum stand exposed to free-air CO₂ enrichment (FACE). *New Phytologist* **150**: 489–498.

Wyckoff, P.H. and Bowers, R. 2010. Response of the prairie-forest border to climate change: impacts of increasing drought may be mitigated by increasing CO₂. *Journal of Ecology* **98**: 197–208.

Zhou, Y. and Li, S. 1990. *Forestry in China*. Science Press, Beijing, China.

2.34 Wood Density

- Atmospheric CO₂ enrichment tends to increase wood density in both seedlings and mature trees, increasing a number of strength properties of their branches and trunks. Different species of trees may respond somewhat differently to atmospheric CO₂ enrichment, and they can respond with still greater variety under different environmental conditions.

Numerous experiments have demonstrated trees grown in air enriched with CO₂ nearly always sequester more biomass in their trunks and branches than do trees grown in ambient air. Several studies also have looked at the effects of elevated CO₂ on the density of that sequestered biomass, some of which are summarized here.

Rogers *et al.* (1983) observed no difference in the wood density of loblolly pine (*Pinus taeda*) trees grown at 340 and 718 ppm CO₂ for 10 weeks; but they found a 33% CO₂-induced increase in the wood density of sweetgum (*Liquidambar styraciflua*) trees grown at these concentrations for only eight weeks. Doyle (1987) and Telewski and Strain (1987) studied the same two tree species over three growing seasons in air of 350 and 650 ppm CO₂, finding no effect of atmospheric CO₂ enrichment on the stem density of sweetgum, but a mean increase of 9% in the stem density of loblolly pine.

Conroy *et al.* (1990) grew seedlings of two *Pinus radiata* families at 340 and 660 ppm CO₂ for 114 weeks, finding CO₂-induced trunk density increases for the two families of 5.4 and 5.6% when soil phosphorus was less than adequate and increases of 5.6 and 1.2% when it was nonlimiting. In a similar study, Hattenschwiler *et al.* (1996) grew six genotypes of clonally propagated four-year-old Norway spruce (*Picea abies*) for three years at CO₂ concentrations of 280, 420, and 560 ppm at three rates of wet nitrogen deposition. On average, they found wood density was 12% greater in the trees grown at

the two higher CO₂ concentrations than in the trees grown at 280 ppm.

Norby *et al.* (1996) grew yellow poplar or “tulip” trees (*Liriodendron tulipifera*) at ambient and ambient plus 300 ppm CO₂ for three years, during which time the wood density of the trees increased by approximately 7%. Tognetti *et al.* (1998) studied two species of oak tree—one deciduous (*Quercus pubescens*) and one evergreen (*Quercus ilex*)—growing in the vicinity of CO₂ springs in central Italy that raised the CO₂ concentration of the surrounding air by approximately 385 ppm. This increase in the air’s CO₂ content increased the wood density of the deciduous oaks by 4.2% and that of the evergreen oaks by 6.4%.

Telewski *et al.* (1999) grew loblolly pine trees for four years at ambient and ambient plus 300 ppm CO₂. Wood density determined directly from mass and volume measurements was increased by 15% by the extra CO₂, and average ring density determined by X-ray densitometry was increased by 4.5%.

Beismann *et al.* (2002) grew different genotypes of spruce and beech (*Fagus sylvatica*) seedlings for four years in open-top chambers maintained at atmospheric CO₂ concentrations of 370 and 590 ppm in combination with low and high levels of wet nitrogen application on both rich calcareous and poor acidic soils, to study the effects of these factors on seedling toughness (fracture characteristics) and rigidity (bending characteristics such as modulus of elasticity). They found some genotypes of each species were sensitive to elevated CO₂ while others were not. Similarly, some were responsive to elevated nitrogen deposition, but others were not. Moreover, such responses often were dependent upon soil type. Averaged across all tested genotypes, atmospheric CO₂ enrichment increased wood toughness in spruce seedlings grown on acidic soils by 12 and 18% at low and high levels of nitrogen deposition, respectively. In addition, atmospheric CO₂ enrichment increased this same wood property in spruce seedlings grown on calcareous soils by about 17 and 14% with low and high levels of nitrogen deposition, respectively. In contrast, elevated CO₂ had no significant effects on the mechanical wood properties of beech seedlings, regardless of soil type.

Kilpelainen *et al.* (2003) erected 16 open-top chambers within a 15-year-old stand of Scots pines growing on a nutrient-poor sandy soil of low nitrogen content near the Mekrijärvi Research Station of the University of Joensuu, Finland. Over the next three years they maintained the trees within these chambers in a well-watered condition, while they enriched the

air in half of the chambers to a mean daytime CO₂ concentration of approximately 580 ppm and maintained the air in half of each of the two CO₂ treatments at 2°C above ambient. In the ambient temperature treatment the 60% increase in the air's CO₂ concentration significantly increased latewood density by 27% and maximum wood density by 11%. In the elevated-temperature treatment the 60% increase in the air's CO₂ concentration significantly increased latewood density by 25% and maximum wood density by 15%. These changes led to mean overall CO₂-induced wood density increases of 2.8% in the ambient-temperature treatment and 5.6% in the elevated-temperature treatment.

Kostiainen *et al.* (2004) investigated the effects of elevated CO₂ (doubled concentration: 720 ppm vs. 360 ppm) and elevated nutrient input to soil (described as “heavy fertilization,” i.e., “higher than used in forestry in practice”) on a number of wood properties of 40-year-old Norway spruce (*Picea abies* L. Karst.) trees enclosed by open-top chambers for three years. They report previous data from this long-term study “showed fertilization decreased wood density (Mäkinen *et al.*, 2002),” and in the presence of elevated CO₂, such was still found to be the case in the new study, but only for earlywood density (a mean decrease of 3.8% over the three years of the study). In the case of latewood density, the extra CO₂ supplied to the trees overrode the negative effect of heavy fertilization and increased mean wood density by 4.6%. Moreover, in the treatment where no extra nutrients were supplied to the trees, both earlywood and latewood density were increased by the doubling of the air's CO₂ concentration: by 4.8% in the case of earlywood density and by 2.0% in the case of latewood density. Thus, under normal growing conditions, a doubling of the air's CO₂ concentration likely would increase the wood density of Norway spruce trees by about 2–5%.

Buitenwerf *et al.* (2012) analyzed changes in woody-plant density at three sites in South African savannas where the normal disturbance regime (fire and herbivores) was kept constant for either 30 or 50 years, noting “if global drivers had significant effects on woody plants, we would expect significant increases in tree densities and biomass over time under the constant disturbance regime.”

The four South African scientists report for the more arid savannas they analyzed there was no indication of global drivers promoting an increase in wood density over the period of their study. However, they found wood density tripled in a mesic savanna between the 1970s and 1990s; in another mesic

savanna it doubled from the mid-1990s to 2010; and “aerial photograph analysis on adjacent non-cleared areas showed an accompanying 48% increase in woody cover.” Buitenwerf *et al.* say their analysis “has shown significant increase in tree densities and stature that are consistent with global drivers promoting woody thickening.” They conclude “the only plausible candidate in the experimental areas is increasing CO₂ since there were no significant temperature or rainfall trends over the last 50 years.”

These observations make it clear different species of trees sometimes respond differently to atmospheric CO₂ enrichment, and they respond with still greater variety under different sets of environmental conditions. In general, however, atmospheric CO₂ enrichment tends to increase wood density in both seedlings and mature trees, thereby also increasing strength properties of their branches and trunks.

References

- Beismann, H., Schweingruber, F., Speck, T., and Korner, C. 2002. Mechanical properties of spruce and beech wood grown in elevated CO₂. *Trees* **16**: 511–518.
- Buitenwerf, R., Bond, W.J., Stevens, N., and Trollope, W.S.W. 2012. Increased tree densities in South African savannas: >50 years of data suggests CO₂ as a driver. *Global Change Biology* **18**: 675–684.
- Conroy, J.P., Milham, P.J., Mazur, M., and Barlow, E.W.R. 1990. Growth, dry weight partitioning and wood properties of *Pinus radiata* D. Don after 2 years of CO₂ enrichment. *Plant, Cell and Environment* **13**: 329–337.
- Doyle, T.W. 1987. Seedling response to CO₂ enrichment under stressed and non-stressed conditions. In: Jacoby Jr., G.C. and Hornbeck, J.W. (Eds.) *Proceedings of the International Symposium on Ecological Aspects of Tree-Ring Analysis*. National Technical Information Service, Springfield, VA, pp. 501–510.
- Hattenschwiler, S., Schweingruber, F.H., and Korner, C. 1996. Tree ring responses to elevated CO₂ and increased N deposition in *Picea abies*. *Plant, Cell and Environment* **19**: 1369–1378.
- Kilpeläinen A., Peltola, H., Ryyppo, A., Sauvala, K., Laitinen, K., and Kellomäki, S. 2003. Wood properties of Scots pines (*Pinus sylvestris*) grown at elevated temperature and carbon dioxide concentration. *Tree Physiology* **23**: 889–897.
- Kostiainen, K., Kaakinen, S., Saranpää, P., Sigurdsson, B.D., Linder, S., and Vapaavuori, E. 2004. Effect of elevated [CO₂] on stem wood properties of mature Norway spruce grown at different soil nutrient availability. *Global Change Biology* **10**: 1526–1538.

Plant Characteristics

- Makinen, H., Saranpaa, P., and Linder, S. 2002. Wood-density variation of Norway spruce in relation to nutrient optimization and fiber dimensions. *Canadian Journal of Forest Research* **32**: 185–194.
- Norby, R.J., Wullschleger, S.D., and Gunderson, C.A. 1996. Tree responses to elevated CO₂ and implications for forests. In: Koch, G.W. and Mooney, H.A. (Eds.) *Carbon Dioxide and Terrestrial Ecosystems*. Academic Press, New York, NY, pp. 1–21.
- Rogers, H.H., Bingham, G.E., Cure, J.D., Smith, J.M., and Surano, K.A. 1983. Responses of selected plant species to elevated carbon dioxide in the field. *Journal of Environmental Quality* **12**: 569–574.
- Telewski, F.W. and Strain, B.R. 1987. Densitometric and ring width analysis of 3-year-old *Pinus taeda* L. and *Liquidambar styraciflua* L. grown under three levels of CO₂ and two water regimes. In: Jacoby Jr., G.C. and Hornbeck, J.W. (Eds.) *Proceedings of the International Symposium on Ecological Aspects of Tree-Ring Analysis*. National Technical Information Service, Springfield, VA, pp. 494–500.
- Telewski, F.W., Swanson, R.T., Strain, B.R., and Burns, J.M. 1999. Wood properties and ring width responses to long-term atmospheric CO₂ enrichment in field-grown loblolly pine (*Pinus taeda* L.). *Plant, Cell and Environment* **22**: 213–219.
- Tognetti, R., Johnson, J.D., Michelozzi, M., and Raschi, A. 1998. Response of foliar metabolism in mature trees of *Quercus pubescens* and *Quercus ilex* to long-term elevated CO₂. *Environmental and Experimental Botany* **39**: 233–245.

3

Plants Under Stress

Key Findings

Introduction

3.1 Competition

- 3.1.1 C₃ vs. C₄ Plants
- 3.1.2 N-Fixers vs. Non-N-Fixers
- 3.1.3 Weeds vs. Non-Weeds

3.2 Disease

- 3.2.1 Legumes
- 3.2.2 Other Agricultural Plants
- 3.2.3 Trees

3.3 Heavy Metal Toxicity

3.4 Herbivory

- 3.4.1 Herbaceous Plants
- 3.4.2 Transgenic Plants
- 3.4.3 Woody Plants

3.5 Iron Stress

3.6 Light Stress

3.7 Nitrogen Insufficiency

- 3.7.1 Crops
- 3.7.2 Fungi
- 3.7.3 Grasses
- 3.7.4 Trees

3.8 Ozone Pollution

- 3.8.1 Agricultural Species
- 3.8.2 Tree Species

3.9 Non-Ozone Air Pollutants

3.10 Phosphorus Insufficiency

3.11 The Progressive Nitrogen Limitation Hypothesis

- 3.11.1 Grasslands
- 3.11.2 Loblolly Pine
- 3.11.3 Other Plants

3.12 Salinity Stress

3.13 Temperature Stress

- 3.13.1 Agricultural Crops
- 3.13.2 Grasslands
- 3.13.3 Woody Plants

3.14 UV-B Radiation Stress

3.15 Water Stress

- 3.15.1 Agricultural Crops
- 3.15.2 Grasslands
- 3.15.3 Woody Plants

3.16 Weeds

- 3.16.1 Non-Parasitic
- 3.16.2 Parasitic

Key Findings

The key findings of this chapter are presented in the bullet points below.

- There is little experimental or real-world evidence to support the suggestion C₃ plants may out-compete C₄ plants and thereby replace them in a high-CO₂ environment. (A C₃ plant is one in which CO₂ is fixed into a compound containing three carbon atoms before entering the Calvin cycle of photosynthesis. A C₄ plant fixes CO₂ into a compound containing four carbon atoms.)
- N-fixing legumes are not likely to out-compete non-N-fixing plants in various ecosystems.
- Future increases in the air's CO₂ content may

Climate Change Reconsidered II: Biological Impacts

increase the competitiveness of *non-weeds* over weeds.

- Atmospheric CO₂ enrichment asserts its greatest positive influence on diseased as opposed to healthy plants; it has the ability to significantly ameliorate the deleterious effects of stresses imposed on plants by numerous pathogenic invaders.
- Increases in the air's CO₂ content improve plants' ability to withstand the deleterious effects of heavy metals that may be present in soils at ordinarily toxic levels.
- Rising atmospheric CO₂ concentrations may reduce the frequency and severity of pest outbreaks detrimental to agriculture, while not seriously impacting herbivorous organisms found in natural ecosystems.
- Specific genetic alterations to crops may enable them to better withstand the assaults of insect pests, better bear the consequences of possible future increases in seasonal maximum air temperatures, and take advantage of the positive effects of atmospheric CO₂ enrichment on various plant properties and processes, while elevated CO₂ simultaneously reduces the severity of possible negative effects that could arise from the escape of transplanted genes into the natural environment.
- Data obtained from open experimental systems suggest herbivore damage to trees may decrease in a CO₂-enriched environment. If herbivore damage were to increase, other evidence suggests air of higher CO₂ concentration makes Earth's trees more capable of surviving severe defoliation.
- Higher CO₂ concentrations tend to reduce fluctuating asymmetry in plant leaves, leading to more symmetrical leaves that are less susceptible to attacks by herbivores, because they are under less stress of both genetic and environmental origin than leaves growing in less-CO₂-enriched air.
- Atmospheric CO₂ enrichment can stimulate biomass production in both iron-sufficient and iron-deficient plants, while it increases internal iron (Fe) use efficiency, stimulates root growth, and increases root exudation of Fe-mobilizing

phytosiderophores in sub-apical root zones, thereby increasing the competitiveness of plants with rhizosphere microorganisms such as barley in their quest for this trace element.

- Whether light intensity is high or low, or leaves are sunlit or shaded, when the CO₂ content of the air is increased, so are the various biological processes that lead to plant robustness. Less than optimal light intensities, therefore, do not negate the beneficial effects of atmospheric CO₂ enrichment. In fact, under low light conditions, the benefits of atmospheric CO₂ enrichment on plant growth are often relatively greater than when light conditions are ideal.
- The maximum benefits of elevated levels of atmospheric CO₂ for the growth and grain production of rice and wheat cannot be realized in soils that are highly deficient in nitrogen, but increasing nitrogen concentrations above what is considered adequate may not result in proportional gains in CO₂-induced growth and yield enhancement. Although there are significant exceptions to the rule, many agricultural crops experience increases in net photosynthesis and biomass production even when soil nitrogen concentrations are a limiting factor to growth.
- CO₂-induced stimulations of percent root infection by various fungi are generally greater under lower, rather than higher, soil nitrogen concentrations. This tendency implies elevated CO₂ will enhance fungal-plant interactions to a greater extent when soil nutrition is less-than-optimal for plant growth, which is the common state of most ecosystems not subjected to the fertilization practices typical of intensive agriculture.
- Atmospheric CO₂ enrichment stimulates photosynthesis and biomass production in grasses and grassland species when soil nitrogen availability is high and/or moderate. Where nitrogen availability is low, grasslands given enough time still have the ability to overcome soil nitrogen limitations and produce positive CO₂-induced growth responses.
- Generally speaking, the degree of soil nitrogen availability positively impacts the aerial fertilization effect of atmospheric CO₂ enrichment on the growth of young aspen, pine, spruce, and other

Plants Under Stress

young tree species by promoting a greater CO₂-induced growth enhancement in soils of adequate, as opposed to insufficient, nitrogen content.

- Atmospheric CO₂ enrichment typically reduces—and more often than not completely overrides—the negative effects of ozone pollution on the photosynthesis, growth, and yield of essentially all agricultural crops that have been experimentally evaluated.
- Earth's trees, like much of the rest of the biosphere, are better equipped to live long and productive lives in CO₂-enriched air, even when experiencing the generally negative influence of atmospheric ozone pollution.
- Although labeled by the United Nations and the U.S. Environmental Protection Agency as a dangerous air pollutant, not only is CO₂ not a “pollutant,” it is actually an anti-pollutant that helps plants overcome the negative effects of real air and soil pollutants and better enables their removal from polluted areas.
- Plants growing in CO₂-enriched air typically respond by increasing their biomass production, even under conditions of low soil phosphorus content, and this effect is especially strong among plants that possess the ability to increase root phosphatase activity.
- Contrary to the claim that low concentrations of soil nitrogen will curtail the ability of the productivity-enhancing effect of rising atmospheric CO₂ concentration to maintain increased plant growth and ecosystem carbon sequestration rates over the long term, real-world data from several multiyear experiments indicate additional CO₂-induced carbon input to the soil stimulates microbial decomposition and thus leads to more available soil nitrogen.
- Extensive experimentation on loblolly pine trees (plus several understory species) at the Duke Forest long-term free-air CO₂ enrichment (FACE) site has conclusively demonstrated the progressive nitrogen limitation hypothesis has been disproven, suggesting the growth-enhancing benefits of atmospheric CO₂ enrichment should continue as the air's CO₂ content rises.
- The buildup of soil salinity from repeated irrigations can produce growth stresses in agricultural plants, but these stresses can be overcome by the rise in the air's CO₂ concentration.
- As the atmosphere's CO₂ content rises, nearly all agricultural crops, grassland plants, and trees will exhibit enhanced rates of photosynthesis and biomass production that will not be diminished by any global warming that might accompany it. If ambient air temperatures rise concurrently, the growth-promoting effects of atmospheric CO₂ enrichment likely will rise even more as Earth gets “greener.”
- The rise in the air's CO₂ content is a powerful antidote for the deleterious biological impacts that might be caused by an increase in the flux of UV-B radiation at the surface of Earth due to depletion of the planet's stratospheric ozone layer.
- The rise in the atmosphere's CO₂ content likely will lead to substantial increases in the photosynthetic rates and biomass production of the world's plants, even under stressful conditions imposed by less-than-optimum soil moisture conditions.
- Non-parasitic weeds likely will be no more competitive in high-CO₂ conditions than they are today, and many of them could be a little less competitive. Atmospheric CO₂ enrichment may provide non-weeds with greater protection against weed-induced decreases in productivity, thereby increasing the competitiveness of non-weeds over weeds. And although atmospheric CO₂ enrichment increases the growth of many weeds, the fraction helped is likely not as large as among non-weeds.
- The rising CO₂ content of the air appears to reduce the negative effects of parasitic weed infection, so that infected host plants continue to exhibit positive (but somewhat reduced) growth responses to elevated CO₂.

Introduction

As was discussed in Chapters 1 and 2, the aerial fertilization effect of Earth's rising atmospheric CO₂

concentration is conferring multiple benefits on terrestrial plants and soils. Such benefits are almost universally acknowledged to occur when growing conditions are ideal, but some have countered that under predicted future CO₂-induced global warming, growing conditions for many plants will be less than ideal. Such counteracting forces to growth, they claim, might negate the benefits of atmospheric CO₂ enrichment. The focus of the current chapter, therefore, is to investigate such claims by examining the responses of plants under various stresses to atmospheric CO₂ enrichment.

As demonstrated in the many sections and subsections below, atmospheric CO₂ enrichment has been shown to ameliorate the negative effects of a number of environmental stresses. The growth enhancement produced by an increase in the air's CO₂ concentration is generally greater under stressful and resource-limited conditions than when growing conditions are ideal.

The physical and environmental stresses addressed below include competition from weeds, diseases, herbivory, nitrogen insufficiency, ozone pollution, phosphorus and nitrogen insufficiency, salinity, higher temperatures, drought, and weeds. IPCC predicts many of these stresses can be expected to increase in a warmer world, but (a) this is not what is revealed by the record of the twentieth century, which IPCC claims experienced “unprecedented” global warming, and (b) in nearly every case, CO₂ enrichment is shown experimentally to immunize plants from these stresses or mitigate their consequences. For example, atmospheric CO₂ enrichment typically reduces—and more often than not completely overrides—the negative effects of ozone pollution on the photosynthesis, growth, and yield of essentially all agricultural crops that have been experimentally evaluated. And the buildup of soil salinity from repeated irrigations can produce growth stresses in agricultural plants, but these stresses can be overcome by the rise in the air's CO₂ concentration.

This chapter contains good news for those concerned about mankind's ability to feed a growing population in coming years, an issue addressed in depth in the following chapter. Importantly, none of the models used to forecast the impact of global warming on crops makes any provision for these positive effects of CO₂ enrichment. One can only conclude that this invalidates their overly pessimistic predictions.

3.1 Competition

One of the concerns about rising concentrations of atmospheric CO₂ is that some plants might benefit more than others, resulting in competitive advantages and ecological changes that could be judged as “bad” because of their effects on wildlife or plants that are beneficial to mankind. This section addresses this issue by surveying research on the different effects of atmospheric CO₂ enrichment on C₃ and C₄ plants, nitrogen-fixers and non-nitrogen-fixers, and weeds and crops.

3.1.1 C₃ vs. C₄ Plants

- There is little experimental or real-world evidence from natural systems to support the suggestion C₃ plants may out-compete C₄ plants and thereby replace them in a high-CO₂ environment. (A C₃ plant is one in which CO₂ is fixed into a compound containing three carbon atoms before entering the Calvin cycle of photosynthesis. A C₄ plant fixes CO₂ into a compound containing four carbon atoms.)

C₃ plants typically respond better to atmospheric CO₂ enrichment than do C₄ plants in increasing their rates of photosynthesis and biomass production. Thus it has been suggested rising atmospheric CO₂ concentrations may lead to C₃ plants out-competing C₄ plants and displacing them, thereby decreasing the biodiversity of certain ecosystems. The story is much more complex than suggested by this simple scenario.

Wilson *et al.* (1998) grew 36 species of perennial grass common to tallgrass prairie ecosystems with and without arbuscular mycorrhizal fungi, finding the dry matter production of the C₃ species colonized by the fungi was the same as the non-inoculated C₃ species, but the fungal-colonized C₄ species produced, on average, 85% more dry matter than the non-inoculated C₄ species. This finding is important with respect to the relative responsiveness of C₃ and C₄ plants to atmospheric CO₂ enrichment; elevated levels of atmospheric CO₂ tend to enhance the mycorrhizal colonization of plant roots, which is known to make soil minerals and water more available for plant growth. This CO₂-induced fungal-mediated growth advantage, which Wilson *et al.*'s work suggests is more readily available to C₄ plants than C₃ plants, could counter the inherently greater CO₂-induced biomass response of C₃ plants relative to C₄ plants, leveling the playing field relative to their competition

for space in any given ecosystem.

BassiriRad *et al.* (1998) report elevated CO₂ enhanced the ability of the perennial C₄ grass *Bouteloua eriopoda* to increase its uptake of NO₃⁻ and PO₄³⁻ considerably more than the perennial C₃ shrubs *Larrea tridentata* and *Prosopis glandulosa*. And in an eight-year study of the effects of twice-ambient atmospheric CO₂ concentrations on a pristine tallgrass prairie in Kansas, Owensby *et al.* (1999) found the elevated CO₂ concentration did not affect the basal coverage of its C₄ species or their relative contribution to the composition of the ecosystem.

The anti-transpirant effect of atmospheric CO₂ enrichment discussed by Pospisilova and Catsky (1999) is also often more strongly expressed in C₄ plants than in C₃ plants, and it typically allows C₄ plants to better cope with water stress. In a study of the C₃ dicot *Abutilon theophrasti* and the C₄ dicot *Amaranthus retroflexus*, for example, Ward *et al.* (1999) found *Amaranthus retroflexus* exhibited a greater relative recovery from drought than did the C₃ species. This suggests, they write, “the C₄ species would continue to be more competitive than the C₃ species in regions receiving more frequent and severe droughts.”

Morgan *et al.* (2001) published the results of an open-top chamber study of a native shortgrass steppe ecosystem in Colorado (USA), where they exposed the enclosed ecosystems to atmospheric CO₂ concentrations of 360 and 720 ppm for two six-month growing seasons. In spite of an average air temperature increase of 2.6°C caused by the presence of the open-top chambers, the elevated CO₂ increased above-ground biomass production by an average of 38% in both years of the study, and when 50% of the standing green plant biomass was defoliated to simulate grazing halfway through the growing season, atmospheric CO₂ enrichment still increased above-ground biomass by 36%. The communities enriched with CO₂ also tended to have greater amounts of moisture in their soils than communities exposed to ambient air. This phenomenon likely contributed to the less negative and, therefore, less stressful plant water potentials measured in the CO₂-enriched plants. The elevated CO₂ did not preferentially stimulate the growth of C₃ species over C₄ species in these communities, nor did it significantly alter the percentage composition of C₃ and C₄ species in the shortgrass steppe ecosystem.

This result was very similar to what Wand *et al.* (1999) found in an extensive review of the scientific literature published between 1980 and 1997.

Analyzing nearly 120 individual responses of C₃ and C₄ grasses to elevated CO₂, they found average photosynthetic enhancements of 33 and 25%, respectively, for C₃ and C₄ plants, along with biomass enhancements of 44 and 33%, respectively, for a doubling of the air's CO₂ concentration. These larger growth responses in the C₄ species suggest “it may be premature to predict that C₄ grass species will lose their competitive advantage over C₃ grass species in elevated CO₂.”

Campbell *et al.* (2000) provided support for that conclusion. They reviewed research conducted between 1994 and 1999 by a worldwide network of 83 scientists associated with the Global Change and Terrestrial Ecosystems (GCTE) Pastures and Rangelands Core Research Project 1, published in more than 165 peer-reviewed scientific journal articles. After analyzing this body of research, the 17 scientists conclude the “growth of C₄ species is about as responsive to CO₂ concentration as [is that of] C₃ species when water supply restricts growth, as is usual in grasslands containing C₄ species.” Thus this group of scientists provided no evidence for the suggestion C₃ plants may out-compete C₄ plants and thereby replace them in high-CO₂ conditions.

Derner *et al.* (2003) studied the effects of atmospheric CO₂ enrichment to 200 ppm above ambient in a FACE experiment conducted in the field at Maricopa, Arizona (USA) in which they evaluated the growth of C₃ cotton (*Gossypium hirsutum* L.) and C₄ sorghum (*Sorghum bicolor* (L.) Moench) in monocultures and low- and high-density mixtures under both optimum and less than optimum soil water conditions. They found no significant CO₂-soil water interactions, and the 14 researchers thus report the plant growth responses to atmospheric CO₂ enrichment as averages of the wet and dry treatment results.

When grown in monoculture for two months, the aboveground biomass of cotton was 85% greater in the CO₂-enriched treatment than in the ambient-air treatment, and the aboveground biomass of sorghum was 2% lower in the CO₂-enriched air than in the ambient air. In the low-density plant mixture, these responses were exacerbated: the aboveground biomass of sorghum was reduced by 14% in the CO₂-enriched air, and cotton was increased by 154%. In the high-density mixture, this trend continued: sorghum biomass was reduced by 16% in the CO₂-enriched air, and cotton was increased by 276%.

When grown in monoculture, C₃ cotton was significantly stimulated by atmospheric CO₂ enrichment, and C₄ sorghum experienced a small growth

reduction. When grown in competition with each other, these positive and negative tendencies were both amplified, and more so when the crowding of the plants was greater.

This study merits careful attention. Importantly, soil water status did not impact the growth response of either species to atmospheric CO₂ enrichment, in contradiction of what had been observed in many earlier experiments (Idso and Idso, 1994). In addition, the negative response of sorghum to elevated CO₂ clashes with the results of several other studies of C₄ plants, where double-digit percentage increases in growth had been the rule (Poorter, 1993; Wand *et al.*, 1999). Thus it is necessary to consider still other experimental results.

Zeng *et al.* (2011) note, “among the 18 most harmful weeds in the world, 14 are C₄,” and “by contrast, of the 86 plant species that supply most of the world’s food, only 5 are C₄ (Patterson and Flint, 1995).” In addition, “studies comparing C₃ crops with C₄ weeds (Wary and Strain, 1987; Patterson *et al.*, 1984; Patterson, 1986; Patterson and Flint, 1990, 1995; Alberto *et al.*, 1996; Fround-Williams, 1996; Ziska, 2000) ... have demonstrated that elevated CO₂ favors the growth and development of C₃ over C₄ species.”

Zeng *et al.* grew rice (*Oryza sativa* L., a C₃ crop) in competition with barnyard grass (*Echinochloa crusgalli* L., a C₄ weed) in a standard paddy-field experiment conducted in ambient air and in air enriched with an extra 200 ppm of CO₂ via FACE technology at Xiaoji Village, Yangzhou City in Eastern China over a period of 120 days. The eight Chinese scientists and their Norwegian colleague found the elevated CO₂ significantly enhanced rice biomass (straw +27.3%, ears +37.6%), tillers (+20%), leaf area index (+11.7%), and net assimilation rate (+50.1%), but they note it reduced all but the last of these characteristics of barnyard grass: biomass (straw -43.6%, ears -47.9%), tillers (-46.1%), leaf area index (-27.3%), and net assimilation rate (+14.1%, the only positive result, but much less than the +50.1% of the rice). In addition, “the absolute uptake of C, N, P, K by rice was increased while those of barnyard grass decreased.” Zeng *et al.* write, “rising atmospheric CO₂ concentration could alter the competition between rice and barnyard grass in paddy fields in favor of rice.”

These studies show there is little experimental or real-world evidence to support the suggestion C₃ plants may out-compete C₄ plants and thereby replace them in a high-CO₂ environment.

References

- Alberto, M.P., Ziska, L.H., Cervancia, C.R., and Manalo, P.A. 1996. The influence of increasing carbon dioxide and temperature on competitive interactions between a C₃ crop and a C₄ weed. *Australian Journal of Plant Physiology* **23**: 795–802.
- BassiriRad, H., Reynolds, J.F., Virginia, R.A., and Brunelle, M.H. 1998. Growth and root NO₃⁻ and PO₄³⁻ uptake capacity of three desert species in response to atmospheric CO₂ enrichment. *Australian Journal of Plant Physiology* **24**: 353–358.
- Campbell, B.D., Stafford Smith, D.M., Ash, A.J., Fuhrer, J., Gifford, R.M., Hiernaux, P., Howden, S.M., Jones, M.B., Ludwig, J.A., Manderscheid, R., Morgan, J.A., Newton, P.C.D., Nosberger, J., Owensby, C.E., Soussana, J.F., Tuba, Z., and ZuoZhong, C. 2000. A synthesis of recent global change research on pasture and rangeland production: reduced uncertainties and their management implications. *Agriculture, Ecosystems and Environment* **82**: 39–55.
- Derner, J.D., Johnson, H.B., Kimball, B.A., Pinter Jr., P.J., Polley, H.W., Tischler, C.R., Bouttons, T.W., LaMorte, R.L., Wall, G.W., Adam, N.R., Leavitt, S.W., Ottman, M.J., Matthias, A.D., and Brooks, T.J. 2003. Above- and below-ground responses of C₃-C₄ species mixtures to elevated CO₂ and soil water availability. *Global Change Biology* **9**: 452–460.
- Fround-Williams, R.J. 1996. Weeds and climate change: Implications for their ecology and control. *Aspects of Applied Biology* **45**: 187–196.
- Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: a review of the past 10 years’ research. *Agricultural and Forest Meteorology* **69**: 153–203.
- Morgan, J.A., Lecain, D.R., Mosier, A.R., and Milchunas, D.G. 2001. Elevated CO₂ enhances water relations and productivity and affects gas exchange in C₃ and C₄ grasses of the Colorado shortgrass steppe. *Global Change Biology* **7**: 451–466.
- Owensby, C.E., Ham, J.M., Knapp, A.K., and Auen, L.M. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO₂. *Global Change Biology* **5**: 497–506.
- Patterson, D.T. 1986. Response of soybean (*Glycine max*) and three C₄ grass weeds to CO₂ enrichment during drought. *Weed Science* **34**: 203–210.
- Patterson, D.T. and Flint, E.P. 1990. Implications of increasing carbon dioxide and climate change for plant communities and competition in natural ecosystems. In:

Kimball, B.A. (Ed.) *Impact of Carbon Dioxide, Trace Gases and Climate Change on Global Agriculture*. American Society of Agronomy Special Publication 53. American Society of Agronomy, Madison, Wisconsin, USA, pp. 83–110.

Patterson, D.T. and Flint, E.P. 1995. Effect of environmental stress on weed/crop interactions. *Weed Science* **43**: 483–490.

Patterson, D.T., Flint, E.P., and Beyers, J.L. 1984. Effects of CO₂ enrichment on competition between a C₄ weed and a C₃ crop. *Weed Science* **32**: 101–105.

Poorter, H. 1993. Interspecific variation in the growth response of plants to an elevated ambient CO₂ concentration. *Vegetatio* **104/105**: 77–97.

Pospisilova, J. and Catsky, J. 1999. Development of water stress under increased atmospheric CO₂ concentration. *Biologia Plantarum* **42**: 1–24.

Wand, S.J.E., Midgley, G.F., Jones, M.H., and Curtis, P.S. 1999. Responses of wild C₄ and C₃ grass (Poaceae) species to elevated atmospheric CO₂ concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology* **5**: 723–741.

Ward, J.K., Tissue, D.T., Thomas, R.B., and Strain, B.R. 1999. Comparative responses of model C₃ and C₄ plants to drought in low and elevated CO₂. *Global Change Biology* **5**: 857–867.

Wary, S.M. and Strain, B.R. 1987. Competition in old-field perennials under CO₂ enrichment. *Functional Ecology* **1**: 145–149.

Wilson, G.W.T. and Hartnett, D.C. 1998. Interspecific variation in plant responses to mycorrhizal colonization in tallgrass prairie. *American Journal of Botany* **85**: 1732–1738.

Zeng, Q., Liu, B., Gilna, B., Zhang, Y., Zhu, C., Ma, H., Pang, J., Chen, G., and Zhu, J. 2011. Elevated CO₂ effects on nutrient competition between a C₃ crop (*Oryza sativa* L.) and a C₄ weed (*Echinochloa crusgalli* L.). *Nutrient Cycling in Agroecosystems* **89**: 93–104.

Ziska, L.H. 2000. The impact of elevated CO₂ on yield loss from a C₃ and C₄ weed in field-grown soybean. *Global Change Biology* **6**: 899–905.

3.1.2 N-Fixers vs. Non-N-Fixers

- N-fixing legumes are not likely to out-compete non-N-fixing plants in various ecosystems.

This section investigates the concern nitrogen-fixing

(N-fixing) plants might benefit more from atmospheric CO₂ enrichment than non-N-fixers and thus obtain a competitive advantage that could lead to some non-N-fixers being excluded from certain plant communities, thereby decreasing the biodiversity of those ecosystems.

In a two-year glasshouse study of simulated low-fertility ecosystems composed of grassland species common to Switzerland, Stocklin and Korner (1999) found atmospheric CO₂ enrichment gave nitrogen-fixing legumes an initial competitive advantage over non-N-fixers. However, it would be expected that over time a portion of the extra nitrogen fixed by these legumes would become available to neighboring non-N-fixing species, which would be able to use it to their own advantage, thereby preserving the species richness of the ecosystem over time. Thus, in a four-year study of an established (non-simulated) high grassland ecosystem located in the Swiss Alps, Arnone (1999) found no difference between the growth responses of N-fixing and non-N-fixing species to elevated levels of atmospheric CO₂.

In a study of mixed plantings of the grass *Lolium perenne* and the legume *Medicago sativa*, Matthies and Egli (1999) found elevated CO₂ did not influence competition between the two plants, either directly or indirectly via its effects on the root hemi-parasite *Rhinanthus alectorolophus*. And in a study of mixed plantings of two grasses and two legumes, Navas *et al.* (1999) observed plant responses to atmospheric CO₂ enrichment are more dependent on neighboring plant density than on neighboring plant identity.

The few studies of this question that have been conducted to date do not suggest N-fixing legumes will out-compete non-N-fixing plants in a world with higher CO₂ concentrations in the air.

References

Arnone III, J.A. 1999. Symbiotic N₂ fixation in a high Alpine grassland: effects of four growing seasons of elevated CO₂. *Functional Ecology* **13**: 383–387.

Matthies, D. and Egli, P. 1999. Response of a root hemiparasite to elevated CO₂ depends on host type and soil nutrients. *Oecologia* **120**: 156–161.

Navas, M.-L., Garnier, E., Austin, M.P., and Gifford, R.M. 1999. Effect of competition on the responses of grasses and legumes to elevated atmospheric CO₂ along a nitrogen gradient: differences between isolated plants, monocultures and multi-species mixtures. *New Phytologist* **143**: 323–331.

Stocklin, J. and Korner, C. 1999. Interactive effects of

elevated CO₂, P availability and legume presence on calcareous grassland: results of a glasshouse experiment. *Functional Ecology* 13: 200–209.

3.1.3 Weeds vs. Non-Weeds

- Future increases in the air's CO₂ content may increase the competitiveness of non-weeds over weeds.

Elevated CO₂ typically stimulates the growth of nearly all plant species in monoculture, including those deemed undesirable by humans, i.e., weeds. Consequently, it is important to determine how future increases in the air's CO₂ content may influence relationships between weeds and non-weeds when they grow competitively in mixed-species stands.

Dukes (2002) grew model serpentine grasslands common to California (USA) in competition with the invasive forb *Centaurea solstitialis* at atmospheric CO₂ concentrations of 350 and 700 ppm for one year. They found elevated CO₂ increased the biomass proportion of this weedy species in the community by a mere 1.2%, while total community biomass increased by 28%. Similarly, Gavazzi *et al.* (2000) grew loblolly pine seedlings for four months in competition with both C₃ and C₄ weeds at atmospheric CO₂ concentrations of 260 and 660 ppm, finding elevated CO₂ increased pine biomass by 22% while eliciting no response from either type of weed.

In a study of pasture ecosystems near Montreal, Canada, Taylor and Potvin (1997) found elevated CO₂ concentrations did not influence the number of native species returning after their removal (to simulate disturbance), even in the face of the introduced presence of the C₃ weed *Chenopodium album*, which normally competes quite effectively with several slower-growing crops in ambient air. Atmospheric CO₂ enrichment did not impact the growth of this weed in any measurable way.

Ziska *et al.* (1999) also studied the C₃ weed *C. album*, along with the C₄ weed *Amaranthus retroflexus*, in glasshouses maintained at atmospheric CO₂ concentrations of 360 and 720 ppm. They determined elevated CO₂ significantly increased the photosynthetic rate and total dry weight of the C₃ weed but had no effect on the C₄ weed. The growth response of the C₃ weed to a doubling of the air's CO₂ content was approximately 51%, about the same as the average 52% growth response tabulated by Idso (1992) and that obtained by Poorter (1993) for rapidly

growing wild C₃ species (54%). This finding suggests there is no enhanced dominance of the C₃ weed over other C₃ plants in a CO₂-enriched environment.

Wayne *et al.* (1999) studied another agricultural weed, field mustard (*Brassica kaber*), which was sown in pots at six densities, placed in atmospheric CO₂ concentrations of 350 and 700 ppm, and sequentially harvested during the growing season. Early in stand development, elevated CO₂ increased above-ground weed biomass in a density-dependent manner, with the greatest stimulation, 141%, occurring at the lowest density (corresponding to 20 plants per square meter) and the smallest stimulation, 59%, occurring at the highest density (corresponding to 652 plants per square meter). As stands matured, the density-dependence of the CO₂-induced growth response disappeared and CO₂-enriched plants exhibited an average above-ground biomass 34% greater than ambient-grown plants across a broad range of plant densities. This final growth stimulation was similar to most other herbaceous plants exposed to atmospheric CO₂ enrichment (30 to 50% biomass increases for a doubling of the air's CO₂ content), once again providing evidence atmospheric CO₂ enrichment confers no undue advantage on weeds at the expense of other plants.

In a study of a weed that affects both plants and animals, Caporn *et al.* (1999) grew bracken (*Pteridium aquilinum*)—which poses a serious weed problem and potential threat to human health in the United Kingdom and other regions—for 19 months in controlled-environment chambers maintained at atmospheric CO₂ concentrations of 370 and 570 ppm and normal or high levels of soil fertility. They found the high CO₂ treatment consistently increased rates of net photosynthesis by 30 to 70%, depending on soil fertility and time of year. However, the elevated CO₂ did not increase total plant dry mass or the dry mass of any plant organ, including rhizomes, roots, and fronds. The only significant effect of elevated CO₂ on bracken growth was observed in the normal nutrient regime, where elevated CO₂ reduced mean frond area.

In a study involving two parasitic species (*Striga hermonthica* and *Striga asiatica*), Watling and Press (1997) reported total parasitic biomass per host plant at an atmospheric CO₂ concentration of 700 ppm was 65% less than in ambient air. And in a related study, Dale and Press (1999) observed the presence of a parasitic plant (*Orobancha minor*) reduced its host's biomass by 47% in ambient air of 360 ppm CO₂ but by only 20% in air of 550 ppm CO₂.

These studies suggest, contrary to what IPCC has

claimed, the rise in the air's CO₂ content will not favor the growth of weedy species over crops and native plants. In fact, it may provide non-weeds greater protection against weed-induced decreases in their productivity and growth.

References

Caporn, S.J.M., Brooks, A.L., Press, M.C., and Lee, J.A. 1999. Effects of long-term exposure to elevated CO₂ and increased nutrient supply on bracken (*Pteridium aquilinum*). *Functional Ecology* **13**: 107–115.

Dale, H. and Press, M.C. 1999. Elevated atmospheric CO₂ influences the interaction between the parasitic angiosperm *Orobancha minor* and its host *Trifolium repens*. *New Phytologist* **140**: 65–73.

Dukes, J.S. 2002. Comparison of the effect of elevated CO₂ on an invasive species (*Centaurea solstitialis*) in monoculture and community settings. *Plant Ecology* **160**: 225–234.

Gavazzi, M., Seiler, J., Aust, W., and Zedaker, S. 2000. The influence of elevated carbon dioxide and water availability on herbaceous weed development and growth of transplanted loblolly pine (*Pinus taeda*). *Environmental and Experimental Botany* **44**: 185–194.

Idso, K.E. 1992. Plant responses to rising levels of carbon dioxide: a compilation and analysis of the results of a decade of international research into the direct biological effects of atmospheric CO₂ enrichment. *Climatological Publications Scientific Paper #23*, Office of Climatology, Arizona State University, Tempe, AZ.

Poorter, H. 1993. Interspecific variation in the growth response of plants to an elevated and ambient CO₂ concentration. *Vegetatio* **104/105**: 77–97.

Taylor, K. and Potvin, C. 1997. Understanding the long-term effect of CO₂ enrichment on a pasture: the importance of disturbance. *Canadian Journal of Botany* **75**: 1621–1627.

Watling, J.R. and Press, M.C. 1997. How is the relationship between the C₄ cereal *Sorghum bicolor* and the C₃ root hemi-parasites *Striga hermonthica* and *Striga asiatica* affected by elevated CO₂? *Plant, Cell and Environment* **20**: 1292–1300.

Wayne, P.M., Carnelli, A.L., Connolly, J., and Bazzaz, F.A. 1999. The density dependence of plant responses to elevated CO₂. *Journal of Ecology* **87**: 183–192.

Ziska, L.H., Teasdale, J.R., and Bunce, J.A. 1999. Future atmospheric carbon dioxide may increase tolerance to glyphosate. *Weed Science* **47**: 608–615.

3.2 Disease

3.2.1 Legumes

- Atmospheric CO₂ enrichment can ameliorate the deleterious effects of various stresses imposed on legumes by numerous pathogenic invaders, providing reason to conclude plants will gain the advantage as the air's CO₂ content rises in the future, enabling them to deal successfully with pathogenic organisms and the damage they inflict.

As the atmosphere's CO₂ content rises, nearly all plants should continue to exhibit increasing rates of photosynthesis and, as a result, increased biomass production. This section investigates whether such benefits are exhibited in legumes suffering from pathogenic diseases.

Chakraborty and Datta (2003) note a number of CO₂-induced changes in plant physiology, anatomy, and morphology have been implicated in increased plant resistance to disease and “can potentially enhance host resistance at elevated CO₂.” Among these phenomena they list “increased net photosynthesis allowing mobilization of resources into host resistance (Hibberd *et al.*, 1996a.); reduced stomatal density and conductance (Hibberd *et al.*, 1996b); greater accumulation of carbohydrates in leaves; more waxes, extra layers of epidermal cells and increased fiber content (Owensby, 1994); production of papillae and accumulation of silicon at penetration sites (Hibberd *et al.*, 1996a); greater number of mesophyll cells (Bowes, 1993); and increased biosynthesis of phenolics (Hartley *et al.*, 2000), among others.”

Chakraborty and Datta (2003) studied the aggressiveness of the fungal anthracnose pathogen *Colletotrichum gloeosporioides* by inoculating two isolates of it onto two cultivars of the tropical pasture legume *Stylosanthes scabra* (Fitzroy, which is susceptible to the fungal pathogen, and Seca, which is more resistant) over 25 sequential infection cycles in controlled-environment chambers filled with air of either 350 or 700 ppm CO₂. They determined the aggressiveness of the pathogen was reduced at the twice-ambient level of atmospheric CO₂, with aggressiveness defined as “a property of the pathogen reflecting the relative amount of damage caused to the host without regard to resistance genes (Shaner *et al.*, 1992).” They report “at twice-ambient CO₂ the overall level of aggressiveness of the two [pathogen] isolates was significantly reduced on both cultivars.”

Simultaneously, however, pathogen fecundity

was found to increase at twice-ambient CO₂. Chakraborty and Datta say their results “concur with the handful of studies that have demonstrated increased pathogen fecundity at elevated CO₂ (Hibberd *et al.*, 1996a; Klironomos *et al.*, 1997; Chakraborty *et al.*, 2000).” The overall increase in fecundity at high CO₂ “is a reflection of the altered canopy environment,” they write, in which “the 30% larger *S. scabra* plants at high CO₂ (Chakraborty *et al.*, 2000) makes the canopy microclimate more conducive to anthracnose development.”

In light of the opposing changes in pathogen behavior induced by the elevated level of atmospheric CO₂ in this experiment—reduced aggressiveness but increased fecundity—it was difficult to determine the ultimate impact of atmospheric CO₂ enrichment on the pathogen-host relationship of this particular plant. One year later, however, the publication of new research provided more insight.

Pangga *et al.* (2004) grew well-watered and well-fertilized seedlings of the Fitzroy cultivar of *Stylosanthes scabra* in a controlled-environment facility maintained at atmospheric CO₂ concentrations of either 350 or 700 ppm, where they inoculated six-, nine- and 12-week-old plants with *C. gloeosporioides*. Ten days after inoculation, they counted the anthracnose lesions on the plants and classified them as either resistant or susceptible.

They found “the mean number of susceptible, resistant, and total lesions per leaf averaged over the three plant ages was significantly ($P < 0.05$) greater at 350 ppm than at 700 ppm CO₂, reflecting the development of a level of resistance in susceptible cv. Fitzroy at high CO₂.” With respect to the plants inoculated at 12 weeks of age, they write those grown “at 350 ppm had 60 and 75% more susceptible and resistant lesions per leaf, respectively, than those [grown] at 700 ppm CO₂.”

In terms of infection efficiency (IE), the Australian scientists state their work “clearly shows that at 350 ppm overall susceptibility of the canopy increases with increasing age because more young leaves are produced on secondary and tertiary branches of the more advanced plants.” They note, “at 700 ppm CO₂, IE did not increase with increasing plant age despite the presence of many more young leaves in the enlarged canopy”; this finding, they write, “points to reduced pathogen efficiency or an induced partial resistance to anthracnose in Fitzroy at 700 ppm CO₂.” Consequently, as the air’s CO₂ content rises, it would appear (at least for the Fitzroy cultivar of this pasture legume) *Stylosanthes scabra*

will acquire a greater intrinsic resistance to the devastating anthracnose disease.

Lau *et al.* (2008) measured the amounts of pathogen damage done to the common prairie plant *Lespedeza capitata* growing in ambient and elevated (560 ppm) CO₂ treatments in the seventh and eighth years (2004 and 2005) of the BioCON study (Reich *et al.*, 2001) conducted at the Cedar Creek Natural History Area in Minnesota (USA), where the CO₂ treatments were applied during the daylight hours of each growing season.

Lau *et al.* write, disease incidence “was lower in the elevated CO₂ environment, although this difference [10% less in 2004 and 53% less in 2005] was statistically significant only in 2005 ($P < 0.01$).” They point out, “because disease caused major reductions in reproductive output, the effects of CO₂ on disease incidence may be important for *L. capitata* evolution and population dynamics.” In addition, they note, Strengbom and Reich (2006), “working in the same experimental site ... also found that elevated CO₂ ... reduced disease incidence on *Solidago rigida*.”

Eastburn *et al.* (2010) note, “globally, soybean is the most widely planted dicot crop and has economic significance due to its wide variety of uses, ranging from food and health products to printing inks and biodiesel [fuels],” but “little to no work has evaluated the influence of future atmospheric conditions on soybean diseases,” even though “worldwide yield losses to all soybean diseases combined are about 11% (Wrather *et al.*, 1997), which is equivalent to more than 24 million metric tons based on current production.”

Eastburn *et al.* evaluated the individual and combined effects of elevated carbon dioxide (CO₂, 550 ppm) and ozone (O₃, 1.2 times ambient) on three economically important soybean diseases—downy mildew, *Septoria* brown spot, and sudden death syndrome (SDS)—over the three-year period 2005–2007 under natural field conditions at the soybean free-air CO₂-enrichment (SoyFACE) facility on the campus of the University of Illinois (USA). The five researchers found “elevated CO₂ alone or in combination with O₃ significantly reduced downy mildew disease severity by 39–66% across the three years of the study.” They also report “elevated CO₂ alone or in combination with O₃ significantly increased brown spot severity in all three years,” but “the increase was small in magnitude.” Finally, “the atmospheric treatments had no effect on the incidence of SDS.”

Braga *et al.* (2006) examined the effects of

atmospheric CO₂ enrichment on another soybean pathogen in three independent experiments. They grew well-watered soybean (*Glycine max* (L.) Merr) plants of two cultivars (IAC-14, susceptible to stem canker disease, and IAC-18, resistant to stem canker disease) from seed through the cotyledon stage in 5-liter pots placed in open-top chambers maintained at atmospheric CO₂ concentrations of either 360 or 720 ppm in a glasshouse. They measured various plant properties and processes, concentrating on the production of glyceollins (the major phytoalexins, or anti-microbial compounds, produced in soybeans) in response to the application of β -glucan elicitor (derived from mycelial walls of *Phytophthora sojae*) to carefully created and replicated wounds in the surfaces of several soybean cotyledons.

The IAC-14 cultivar did not exhibit a CO₂-induced change in glyceollin production in response to elicitation—as Braga *et al.* had hypothesized would be the case, since this cultivar is susceptible to stem canker disease. But the IAC-18 cultivar, which has the potential to resist the disease to varying degrees, experienced a 100% CO₂-induced increase in the amount of glyceollins produced after elicitation, a response the researchers describe as remarkable. Braga *et al.* say the CO₂-induced response they observed “may increase the potential of the soybean defense since infection at early stages of plant development, followed by a long incubation period before symptoms appear, [as] is characteristic of the stem canker disease cycle caused by Dpm [*Diaporthe phaseolorum* (Cooke & Ellis) Sacc. f. sp. *Meridionalis* Morgan-Jones].” The response they observed “indicates that raised CO₂ levels forecasted for next decades may have a real impact on the defensive chemistry of the cultivars.”

Kretzschmar *et al.* (2009) noted “isoflavonoids constitute a group of natural products derived from the phenylpropanoid pathway, which is abundant in soybeans,” and “the inducible accumulation of low molecular weight antimicrobial pterocarpan phytoalexins, the glyceollins, is one of the major defense mechanisms implicated in soybean resistance.” The authors evaluated “the effect of an elevated CO₂ atmosphere on the production of soybean defensive secondary chemicals induced by nitric oxide and a fungal elicitor.” They grew soybeans from seed for nine days in a glasshouse in large, well-watered pots placed in open-top chambers maintained at atmospheric CO₂ concentrations of either 380 or 760 ppm, examining changes in the production of phytoalexins and some of their precursors in the

activity of three enzymes related to their biosynthetic pathways.

Kretzschmar *et al.* report “elevated CO₂ combined with nitric oxide resulted in an increase of intermediates and diverted end products (daidzein—127%, coumestrol—93%, genistein—93%, luteolin—89% and apigenin—238%) with a concomitant increase of 1.5–3.0 times in the activity of enzymes related to their biosynthetic routes.” These findings, the four Brazilian researchers write, are evidence of “changes in the pool of defense-related flavonoids in soybeans due to increased carbon availability, which may differentially alter the responsiveness of soybean plants to pathogens in CO₂ atmospheric concentrations such as those predicted for future decades.”

The studies reviewed here show elevated CO₂ can significantly ameliorate the deleterious effects of various stresses imposed on legume plants by numerous pathogenic invaders, but there remains a need to clarify some issues through further research. Nevertheless, the large number of ways in which elevated CO₂ has been demonstrated to increase plant resistance to pathogen attack gives reason to conclude plants will gain the advantage as the air’s CO₂ content climbs, enabling them to deal successfully with pathogenic organisms and the damage they inflict.

References

- Bowes, G. 1993. Facing the inevitable: Plants and increasing atmospheric CO₂. *Annual Review of Plant Physiology and Plant Molecular Biology* **44**: 309–332.
- Braga, M.R., Aidar, M.P.M., Marabesi, M.A., and de Godoy, J.R.L. 2006. Effects of elevated CO₂ on the phytoalexin production of two soybean cultivars differing in the resistance to stem canker disease. *Environmental and Experimental Botany* **58**: 85–92.
- Chakraborty, S. and Datta, S. 2003. How will plant pathogens adapt to host plant resistance at elevated CO₂ under a changing climate? *New Phytologist* **159**: 733–742.
- Chakraborty, S., Pangga, I.B., Lupton, J., Hart, L., Room, P.M., and Yates, D. 2000. Production and dispersal of *Colletotrichum gloeosporioides* spores on *Stylosanthes scabra* under elevated CO₂. *Environmental Pollution* **108**: 381–387.
- Eastburn, D.M., Degennaro, M.M., DeLucia, E.H., Dermody, O., and McElrone, A.J. 2010. Elevated atmospheric carbon dioxide and ozone alter soybean diseases at SoyFACE. *Global Change Biology* **16**: 320–330.

Climate Change Reconsidered II: Biological Impacts

Hartley, S.E., Jones, C.G., and Couper, G.C. 2000. Biosynthesis of plant phenolic compounds in elevated atmospheric CO₂. *Global Change Biology* **6**: 497–506.

Hibberd, J.M., Whitbread, R., and Farrar, J.F. 1996a. Effect of elevated concentrations of CO₂ on infection of barley by *Erysiphe graminis*. *Physiological and Molecular Plant Pathology* **48**: 37–53.

Hibberd, J.M., Whitbread, R., and Farrar, J.F. 1996b. Effect of 700 µmol per mol CO₂ and infection of powdery mildew on the growth and partitioning of barley. *New Phytologist* **134**: 309–345.

Klironomos, J.N., Rillig, M.C., Allen, M.F., Zak, D.R., Kubiske, M., and Pregitzer, K.S. 1997. Soil fungal-arthropod responses to *Populus tremuloides* grown under enriched atmospheric CO₂ under field conditions. *Global Change Biology* **3**: 473–478.

Kretschmar, F.S., Aidar, M.P.M., Salgado, I., and Braga, M.R. 2009. Elevated CO₂ atmosphere enhances production of defense-related flavonoids in soybean elicited by NO and a fungal elicitor. *Environmental and Experimental Botany* **65**: 319–329.

Lau, J.A., Strengbom, J., Stone, L.R., Reich, P.B., and Tiffin, P. 2008. Direct and indirect effects of CO₂, nitrogen, and community diversity on plant-enemy interactions. *Ecology* **89**: 226–236.

Owensby, C.E. 1994. Climate change and grasslands: ecosystem-level responses to elevated carbon dioxide. *Proceedings of the XVII International Grassland Congress*. Palmerston North, New Zealand: New Zealand Grassland Association, pp. 1119–1124.

Pangga, I.B., Chakraborty, S., and Yates, D. 2004. Canopy size and induced resistance in *Stylosanthes scabra* determine anthracnose severity at high CO₂. *Phytopathology* **94**: 221–227.

Reich, P.B., Tilman, D., Craine, J., Ellsworth, D., Tjoelker, M.G., Knops, J., Wedin, D., Naeem, S., Bahaeddin, D., Goth, J., Bengston, W., and Lee, T.D. 2001. Do species and functional groups differ in acquisition and use of C, N, and water under varying atmospheric CO₂ and N availability regimes? A field test with 16 grassland species. *New Phytologist* **150**: 435–448.

Shaner, G., Stromberg, E.L., Lacy, G.H., Barker, K.R., and Pirone, T.P. 1992. Nomenclature and concepts of aggressiveness and virulence. *Annual Review of Phytopathology* **30**: 47–66.

Strengbom, J. and Reich, P.B. 2006. Elevated CO₂ and increased N supply reduce leaf disease and related photosynthetic impacts on *Solidago rigida*. *Oecologia* **149**: 519–525.

Wrather, J.A., Anderson, T.R., Arsyad, D.M., Gai, J., Ploper, L.D., Porta-Puglia, A., Ram, H.H., and Yourinori, J.T. 1997. Soybean disease loss estimates for the top 10 soybean producing countries in 1994. *Plant Disease* **81**: 107–110.

3.2.2 Other Agricultural Plants

- Atmospheric CO₂ enrichment asserts its greatest positive influence on infected as opposed to healthy plants because it can significantly ameliorate the deleterious effects of various stresses imposed on plants by pathogenic invaders.

As the air's CO₂ content rises, nearly all plants should continue to exhibit increasing rates of photosynthesis and increased biomass production. This section examines whether such benefits occur in plants that are suffering from various pathogen-induced diseases, specifically non-legume agricultural plants.

Plessl *et al.* (2007) write, “potato late blight caused by the oomycete *Phytophthora infestans* (Mont.) de Bary is the most devastating disease of potato worldwide,” and “infection occurs through leaves and tubers followed by a rapid spread of the pathogen finally causing destructive necrosis.” The five researchers grew individual well-watered and fertilized plants of the potato cultivar Indira in controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 400 or 700 ppm. Four weeks after the start of the experiment, researchers cut the first three fully developed pinnate leaves from the plants and inoculated them with zoospores of *P. infestans* in Petri dishes containing water-agar. They evaluated the leaves' symptoms daily via comparison with control leaves similarly treated but unexposed to the pathogen.

The German scientists report the 400- to 700-ppm increase in CO₂ “dramatically reduced symptom development,” including extent of necrosis (down by 44% four days after inoculation and 65% five days after inoculation), area of sporulation (down by 100% four days after inoculation and 61% five days after inoculation), and sporulation intensity (down by 73% four days after inoculation and 17% five days after inoculation). These findings, Plessl *et al.* write, “clearly demonstrated that the potato cultivar Indira, which under normal conditions shows a high susceptibility to *P. infestans*, develops resistance against this pathogen after exposure to 700 ppm CO₂,” and “this finding agrees with results from Jwa

et al. (1995), who reported an increased tolerance of tomato plants to *Phytophthora* root rot when grown at elevated CO₂.”

Jwa and Walling (2001) grew tomato plants hydroponically for eight weeks in controlled-environment chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm. At week five of their study, they infected half of all plants growing in each CO₂ concentration with the fungal pathogen *Phytophthora parasitica*, which attacks plant roots and induces a water stress that decreases growth and yield. At the end of the study, they found the pathogenic infection had reduced total plant biomass by nearly 30% at both atmospheric CO₂ concentrations. However, the elevated CO₂ treatment had increased the total biomass of the healthy and diseased plants by the same amount (+30%), with the result that the infected tomato plants grown at 700 ppm CO₂ had biomass values essentially identical to those of the healthy tomato plants grown at 350 ppm CO₂. Thus, the extra CO₂ counterbalanced the negative effect of the pathogenic infection on overall plant productivity.

Malmstrom and Field (1997) grew individual oat plants for two months in pots placed in phytocells maintained at atmospheric CO₂ concentrations of 350 and 700 ppm, and they infected one-third of the plants with the barley yellow dwarf virus (BYDV), which affects more than 150 plant species worldwide, including all major cereal crops. They found elevated CO₂ stimulated rates of net photosynthesis in all plants, regardless of pathogen infection. However, the greatest percentage increase occurred in diseased specimens (48% vs. 34%). Moreover, atmospheric CO₂ enrichment decreased stomatal conductance by 50% in infected plants but by only 34% in healthy ones, which led to a CO₂-induced doubling of the instantaneous water-use efficiency of the healthy plants but a 2.7-fold increase in the diseased plants.

After 60 days of growth under these conditions, the researchers determined the extra CO₂ increased total plant biomass by 36% in infected plants but 12% in healthy plants. In addition, whereas elevated CO₂ had little effect on root growth in the healthy plants, it increased root biomass in the infected plants by up to 60%. Malmstrom and Field conclude CO₂ enrichment “may reduce losses of infected plants to drought” and “may enable diseased plants to compete better with healthy neighbors.”

Tiedemann and Firsching (2000) grew spring wheat plants from germination to maturity in controlled-environment chambers maintained at

ambient (377 ppm) and elevated (612 ppm) concentrations of atmospheric CO₂ and at ambient (20 ppb) and elevated (61 ppb) concentrations of ozone (and combinations thereof); the latter gas is typically toxic to most plants. In addition, they inoculated half the plants in each treatment with a leaf rust-causing fungus. The elevated CO₂ increased the photosynthetic rates of the diseased plants by 20 and 42% at the ambient and elevated ozone concentrations, respectively, and it also enhanced the yield of the infected plants, increasing it by 57%, even in the presence of high ozone concentrations.

Matros *et al.* (2006) grew tobacco plants (*Nicotiana tabacum* L.) in 16-cm-diameter pots filled with quartz sand in controlled-climate chambers maintained at either 350 or 1,000 ppm CO₂ for eight weeks, where they were irrigated daily with a complete nutrient solution containing either 5 or 8 mM NH₄NO₃. Some of the plants in each treatment were mechanically infected with the potato virus Y (PVY) when they were six weeks old. At the end of the study, the researchers harvested the plants and identified and quantified a number of their chemical constituents.

The researchers report “plants grown at elevated CO₂ and 5 mM NH₄NO₃ showed a marked and significant decrease in content of nicotine in leaves as well as in roots,” and at 8 mM NH₄NO₃ the same was found to be true of upper leaves but not of lower leaves and roots. With respect to the PVY part of the study, they further note the “plants grown at high CO₂ showed a markedly decreased spread of virus.” Both these findings would likely be considered beneficial by most people because potato virus Y infects many crops and ornamental plants worldwide, and nicotine is widely acknowledged to have significant negative impacts on human health (Topliss *et al.*, 2002).

In a study conducted in the BioCON (Biodiversity, Carbon dioxide, and Nitrogen effects on ecosystem functioning) FACE facility located at the Cedar Creek Natural History Area in east-central Minnesota (USA), Strengbom and Reich (2006) evaluated the effects of an approximately 190 ppm increase in the air’s daytime CO₂ concentration on leaf photosynthetic rates of stiff goldenrod (*Solidago rigida*) growing in monoculture for two full seasons, together with its concomitant effects on the incidence and severity of leaf spot disease. Although they found elevated CO₂ had no significant effect on plant photosynthetic rate in their study, they write, “both disease incidence and severity were lower on plants grown under elevated CO₂.” Specifically, “disease

incidence was on average more than twice as high under ambient as under elevated CO₂,” and “disease severity (proportion of leaf area with lesions) was on average 67% lower under elevated CO₂ compared to ambient conditions.”

Strengbom and Reich note the “indirect effects from elevated CO₂, i.e., lower disease incidence, had a stronger effect on realized photosynthetic rate than the direct effect of higher CO₂.” They conclude, “it may be necessary to consider potential changes in susceptibility to foliar diseases to correctly estimate the effects on plant photosynthetic rates of elevated CO₂.” In addition, they found the plants grown in CO₂-enriched air had lower leaf nitrogen concentrations than those grown in ambient air, as is often observed in studies of this type. They say their results “are, thus, also in accordance with other studies that have found reduced pathogen performance following reduced nitrogen concentration in plants grown under elevated CO₂ (Thompson and Drake, 1994).” In addition, they write, their results are “also in accordance with studies that have found increased [disease] susceptibility following increased nitrogen concentration of host plants (Huber and Watson, 1974; Nordin *et al.*, 1998; Strengbom *et al.*, 2002).”

Gamper *et al.* (2004) note arbuscular mycorrhizal fungi (AMF) are expected to modulate plant responses to elevated CO₂ by “increasing resistance/tolerance of plants against an array of environmental stressors (Smith and Read, 1997).” Investigating this subject in a set of experiments conducted over a seven-year period of free-air CO₂-enrichment on two of the world’s most extensively grown cool-season forage crops (*Lolium perenne* and *Trifolium repens*) at the Swiss FACE facility near Zurich, they determined “at elevated CO₂ and under [two] N treatments, AMF root colonization of both host plant species was increased,” and “colonization levels of all three measured intraradical AMF structures (hyphae, arbuscules and vesicles) tended to be higher.” They conclude these CO₂-induced benefits may lead to “increased protection against pathogens and/or herbivores.”

Al-Kayssi (2009) notes soil solarization “is a method of heating the soil by using polyethylene sheets as mulching over moistened soil, to retain solar radiation during the hot season,” so “soil-borne pathogens may be killed by lethal heat (>40°C) and weakened by sub-lethal heat (<38–40°C) to the extent that they are unable to cause damage to plants or they are more susceptible to chemical toxicants.” This

technique “has been successfully used to control soil-borne pathogens and weeds (Katan *et al.*, 1976; Mahrer, 1979; Grinstein *et al.*, 1979; Katan, 1981; Mahrer *et al.*, 1984; Avissar *et al.*, 1986; Al-Karaghoulis *et al.*, 1990; Al-Kayssi and Al-Karaghoulis, 1991).”

Al-Kayssi conducted a laboratory experiment where “clay soil samples infested with *Verticillium dahliae* were exposed to different CO₂ concentrations (350, 700, 1050, 1400, 1750 ppm air) and incubated in hot water baths at 35, 40, 45, 50 and 55°C,” while “field plots were exposed to the same CO₂ levels during soil solarization in three periods (1st of July to 30th of September, 1st of August to 30th of September, and 1st to 30th of September).”

The Iraqi researcher found higher than normal CO₂ contents in the soil increased maximum soil temperatures while reducing the length of time required to kill 90% of the propagules of *V. dahliae* in natural field soil with moisture content at field capacity. He notes this killing time parameter in soil heated to 35°C was reduced from 24 days at the normal ambient CO₂ concentration to 15 days at 1,750 ppm CO₂, and sub-lethal soil temperatures were raised to lethal levels as the soil’s CO₂ content was raised. This finding suggests a high-CO₂ environment could make soil solarization a more important method of controlling soil-borne pathogens and weeds than it is today.

These studies indicate atmospheric CO₂ enrichment asserts a relatively greater positive influence on infected as opposed to healthy plants. Moreover, they suggest elevated CO₂ can significantly ameliorate the deleterious effects of various stresses imposed on plants by pathogenic invaders. Consequently, as the atmosphere’s CO₂ concentration continues its upward climb, Earth’s vegetation should be increasingly better equipped to deal with pathogenic organisms and the damage they do.

References

- Al-Karaghoulis, A.A., Al-Kayssi, A.W., and Hasson, A.M. 1990. The photometric properties of different colored plastic mulches used for soil solarization. *Solar and Wind Technology* 7: 119–123.
- Al-Kayssi, A.W. 2009. Impact of elevated CO₂ concentrations in the soil on soil solarization efficiency. *Applied Soil Ecology* 43: 150–158.
- Al-Kayssi, A.W. and Al-Karaghoulis, A.A. 1991. Influence

of different colored plastic mulches used for soil solarization on the effectiveness of soil heating. *Soil Solarization* **109**: 297–308.

Avissar, R., Mahrer, Y., Margulies, L., and Katan, J. 1986. Field aging of transparent polyethylene mulch: I. Photometric properties. *Soil Science Society of America Journal* **50**: 202–205.

Gamper, H., Peter, M., Jansa, J., Luscher, A., Hartwig, U.A., and Leuchtmann, A. 2004. Arbuscular mycorrhizal fungi benefit from 7 years of free air CO₂ enrichment in well-fertilized grass and legume monocultures. *Global Change Biology* **10**: 189–199.

Grinstein, A., Orion, D., Greenberger, A., and Katan, J. 1979. Solar heating of the soil for the control of *Verticillium dahliae* and *Pratylenchus thornei* in potatoes. In: Shippers, B. and Gams, W. (Eds.) *Soilborne Plant Pathogens*. Academic Press, London, UK, pp. 431–438.

Huber, D.M. and Watson, R.D. 1974. Nitrogen form and plant disease. *Annual Reviews of Phytopathology* **12**: 139–155.

Jwa, N.-S. and Walling, L.L. 2001. Influence of elevated CO₂ concentration on disease development in tomato. *New Phytologist* **149**: 509–518.

Jwa, N.S., Walling, L., and McCool, P.M. 1995. Influence of elevated CO₂ on disease development and induction of PR proteins in tomato roots by *Phytophthora parasitica*. *Plant Physiology* **85** (Supplement): 1139.

Katan, J. 1981. Solar heating (solarization) of soil for control of soilborne pests. *Annual Review of Phytopathology* **19**: 211–236.

Katan, J., Greenberger, A., Alon, H., and Grinstein, A. 1976. Solar heating by polyethylene mulching for the control of diseases caused by soilborne pathogens. *Phytopathology* **66**: 683–688.

Mahrer, Y. 1979. Prediction of soil temperatures of a soil mulched with transparent polyethylene. *Journal of Applied Meteorology* **18**: 1263–1267.

Mahrer, Y., Naot, O., Rawitz, E., and Katan, J. 1984. Temperature and moisture regimes in soils mulched with transparent polyethylene. *Soil Science Society of America Journal* **48**: 362–367.

Malmstrom, C.M. and Field, C.B. 1997. Virus-induced differences in the response of oat plants to elevated carbon dioxide. *Plant, Cell and Environment* **20**: 178–188.

Matros, A., Amme, S., Kettig, B., Buck-Sorlin, G.H., Sonnewald, U., and Mock, H.-P. 2006. Growth at elevated CO₂ concentrations leads to modified profiles of secondary metabolites in tobacco cv. SamsunNN and to increased

resistance against infection with potato virus Y. *Plant, Cell and Environment* **29**: 126–137.

Nordin, A., Nasholm, T., and Ericson, L. 1998. Effects of simulated N deposition on understory vegetation of a boreal coniferous forest. *Functional Ecology* **12**: 691–699.

Plessl, M., Elstner, E.F., Rennenberg, H., Habermeyer, J., and Heiser, I. 2007. Influence of elevated CO₂ and ozone concentrations on late blight resistance and growth of potato plants. *Environmental and Experimental Botany* **60**: 447–457.

Smith, S.E. and Read, D.J. 1997. *Mycorrhizal Symbioses*. Academic Press, London, UK.

Strengbom, J., Nordin, A., Nasholm, T., and Ericson, L. 2002. Parasitic fungus mediates change in nitrogen-exposed boreal forest vegetation. *Journal of Ecology* **90**: 61–67.

Strengbom, J. and Reich, P.B. 2006. Elevated [CO₂] and increased N supply reduce leaf disease and related photosynthetic impacts on *Solidago rigida*. *Oecologia* **149**: 519–525.

Thompson, G.B. and Drake, B.G. 1994. Insect and fungi on a C₃ sedge and a C₄ grass exposed to elevated atmospheric CO₂ concentrations in open-top chambers in the field. *Plant, Cell and Environment* **17**: 1161–1167.

Tiedemann, A.V. and Firsching, K.H. 2000. Interactive effects of elevated ozone and carbon dioxide on growth and yield of leaf rust-infected versus non-infected wheat. *Environmental Pollution* **108**: 357–363.

Topliss, J.G., Clark, A.M., and Ernst, E., *et al.* 2002. Natural and synthetic substances related to human health. *Pure and Applied Chemistry* **74**: 1957–1985.

3.2.3 Trees

- The balance of evidence obtained to date demonstrates trees are better able to withstand pathogen attacks in CO₂-enriched air as opposed to ambient-CO₂ air.

Plant pathogens reduce growth in agricultural and natural ecosystems worldwide; estimates of financial loss due to such reductions amount to more than \$33 billion annually in the United States alone (Pimentel *et al.*, 2000). It is thus natural to wonder—and important to determine—how rising atmospheric CO₂ will affect plant-pathogen interactions. This section examines what researchers have learned about these phenomena from experiments conducted on

various types of trees.

Leaf spot disease, which is characterized by chlorotic to necrotic localized leaf lesions, is caused by the *Cercospora* (a large genus of ascomycete fungi) that affect, in the words of McElrone *et al.* (2010), “numerous economically important plant species around the world, including grapes, cereals, soybeans, peanuts, orchids, coffee, alfalfa and potatoes (Sinclair *et al.*, 1987),” as well as redbud (*Cercis canadensis*) and sweetgum (*Liquidambar styraciflua*) trees, such as those growing at the Duke Forest FACE facility in Orange County, North Carolina (USA), where McElrone *et al.* studied the disease throughout the growing seasons of five years (2000–2003 and 2005).

The six scientists assessed how elevated CO₂ (to 200 ppm above the ambient air’s CO₂ concentration) and natural interannual climatic variability affected the incidence and severity of leaf spot disease among the sweetgum and redbud trees growing in the several FACE rings at the Duke Forest site. In order “to determine how photosynthetic capacity surrounding pathogen damage was affected by CO₂ exposure, the spatial pattern of photosystem II operating efficiency was quantified on *C. canadensis* leaves still attached to plants with an imaging chlorophyll fluorometer,” they write.

McElrone *et al.* determined “disease incidence and severity for both species were greater in years with above average rainfall,” and “in years with above average temperatures, disease incidence for *Liquidambar styraciflua* was decreased significantly.” They also note elevated CO₂ increased disease incidence and severity “in some years.” However, they write, the “chlorophyll fluorescence imaging of leaves revealed that any visible increase in disease severity induced by elevated CO₂ was mitigated by higher photosynthetic efficiency in the remaining undamaged leaf tissue and in a halo surrounding lesions.” Although atmospheric CO₂ enrichment was sometimes observed to increase the incidence and severity of leaf spot disease, the photosynthesis-enhancing effect of the extra CO₂ compensated for the photosynthetic productivity lost to the disease by enhancing productivity in healthy portions of diseased leaves and in leaves without lesions, with no net ill effect.

Fleischmann *et al.* (2010) grew well-watered European Beech (*Fagus sylvatica* L.) trees from seed for four years in growth chambers maintained at either 400 or 700 ppm CO₂ in a greenhouse. During this period, they gave the trees an adequate supply of

all essential nutrients, but in the case of nitrogen (N), there were low N and high N treatments, where they gave the high-N treatment twice as much nitrogen as the low-N treatment. In addition, half of the seedlings were infected with *Phytophthora citricola*—a root pathogen known to infest the roots and trunks of European Beech trees—in the early summer of the third year of the study, and half of the trees in each treatment were harvested and examined at the ends of the third and fourth years of the experiment.

The three German researchers write, “chronic elevation of atmospheric CO₂ increased the susceptibility of beech seedlings towards the root pathogen *P. citricola*, while additional nitrogen supply reduced susceptibility.” They found 27% of the infected plants in the low-N high-CO₂ treatment had been killed by the pathogen by the end of their study, and only 9% of the infected plants in the high-N high-CO₂ treatment had died. Surviving beech seedlings of the low-N high-CO₂ treatment “managed to tolerate the root infection by (a) increasing their carbon gain, (b) improving their fine root functionality and (c) changing their allometric relation between below-ground and above-ground biomass.”

Fleischmann *et al.* conclude infected beech seedlings in the low-N high-CO₂ treatment responded to the pernicious pathogen and “enhanced [their] primary production rates in the second year of the experiment and increased above-ground biomass significantly as compared to control trees.”

Percy *et al.* (2002) grew the most widely distributed North American tree species—trembling aspen—in 12 30-m-diameter FACE rings near Rhinelander, Wisconsin (USA) in air maintained at ambient CO₂ and O₃ concentrations, ambient O₃ and elevated CO₂ (560 ppm during daylight hours), ambient CO₂ and elevated O₃ (46.4–55.5 ppb during daylight hours), and elevated CO₂ and O₃ over the period of each growing season from 1998 through 2001. Throughout the experiment they assessed several of the young trees’ growth characteristics, as well as their responses to poplar leaf rust (*Melampsora medusae*), which they note “is common on aspen and belongs to the most widely occurring group of foliage diseases.” They found elevated CO₂ alone did not alter rust occurrence, but elevated O₃ alone increased it by nearly fourfold. When applied together, the elevated CO₂ reduced the enhancement of rust development caused by elevated O₃ from nearly fourfold to just over twofold.

Parsons *et al.* (2003) grew two-year-old saplings of paper birch and three-year-old saplings of sugar

maple in well-watered and -fertilized pots from early May until late August in glasshouse rooms maintained at either 400 or 700 ppm CO₂. They found the whole-plant biomass of paper birch was increased by 55% in the CO₂-enriched portions of the glasshouse, and sugar maple was increased by 30%. In addition, concentrations of condensed tannins were increased by 27% in the paper birch (but not the sugar maple) saplings grown in the CO₂-enriched air. Parsons *et al.* conclude “the higher condensed tannin concentrations present in the birch fine roots may offer these tissues greater protection against soil-borne pathogens and herbivores.” Parsons *et al.* report CO₂-induced increases in fine root concentrations of total phenolics and condensed tannins also have been observed in warm temperate conifers by King *et al.* (1997), Entry *et al.* (1998), Gebauer *et al.* (1998), and Runion *et al.* (1999), and in cotton by Booker (2000).

McElrone *et al.* (2005) “assessed how elevated CO₂ affects a foliar fungal pathogen, *Phyllosticta minima*, of *Acer rubrum* [red maple] growing in the understory at the Duke Forest free-air CO₂ enrichment experiment in Durham, North Carolina, USA ... in the 6th, 7th, and 8th years of the CO₂ exposure.” Surveys conducted in those years “revealed that elevated CO₂ [to 200 ppm above ambient] significantly reduced disease incidence, with 22%, 27% and 8% fewer saplings and 14%, 4%, and 5% fewer leaves infected per plant in the three consecutive years, respectively.” They report the elevated CO₂ “also significantly reduced disease severity in infected plants in all years (e.g. mean lesion area reduced 35%, 50%, and 10% in 2002, 2003, and 2004, respectively).”

Hypothesizing these consequences could have resulted from a direct deleterious effect of elevated CO₂ on the fungal pathogen, McElrone *et al.* performed other experiments in controlled-environment chambers. These experiments revealed the elevated CO₂ benefited the fungal pathogen as well as the red maple saplings, as the authors report “exponential growth rates of *P. minima* were 17% greater under elevated CO₂.” They obtained similar results when they repeated the *in vitro* growth analysis two additional times in different growth chambers.

When “scanning electron micrographs verified that conidia germ tubes of *P. minima* infect *A. rubrum* leaves by entering through the stomata,” the researchers turned their attention to the pathogen’s mode of entry into the saplings’ foliage. In this investigation they report both stomatal size and

density were unaffected by atmospheric CO₂ enrichment, but “stomatal conductance was reduced by 21–36% under elevated CO₂, providing smaller openings for infecting germ tubes.” They conclude the reduced disease severity under elevated CO₂ was also likely due to altered leaf chemistry, as elevated CO₂ increased total leaf phenolic concentrations by 15% and tannin concentrations by 14%.

Because the phenomena they found to be important in reducing the amount and severity of fungal pathogen infection (leaf spot disease) of red maple have been demonstrated to be operative in most other plants as well, McElrone *et al.* state these CO₂-enhanced leaf defensive mechanisms “may be prevalent in many plant pathosystems where the pathogen targets the stomata.” They conclude their results “provide concrete evidence for a potentially generalizable mechanism to predict disease outcomes in other pathosystems under future climatic conditions.”

Runion *et al.* (2010) write, obligate pathogens “have a more intimate relationship with their host and must have the host to survive,” whereas facultative pathogens “live saprophytically and generally result in disease (or tend to be more severe) under conditions of plant stress such as low nutrition or water.” They grew well-watered and well-fertilized seedlings of loblolly pine (*Pinus taeda*) and northern red oak (*Quercus rubra*) out-of-doors in open-top chambers constructed in large soil bins located at the USDA-ARS National Soil Dynamics Laboratory in Auburn, Alabama (USA), where they exposed the plants to atmospheric CO₂ concentrations of either 360 or 720 ppm with or without infecting them with the fusiform rust fungus (the obligate pathogen *Cronartium quercuum* f.sp. *fusiforme*), and with or without infecting them with the pitch canker fungus (the facultative pathogen *Fusarium circinatum*) for various lengths of time ranging from weeks to a year, with each of the three experiments being conducted twice.

With respect to the pine *Fusarium* rust study, Runion *et al.* state “percent infection was not significantly affected by CO₂ concentration,” yet “the percentage of loblolly pine seedlings which died as a result of rust infection was generally significantly lower under elevated CO₂ in both runs of the experiment.” With respect to the oak *Fusarium* rust study, they report “the percent of oak seedlings with uredia was consistently lower for seedlings exposed to elevated CO₂ in both runs,” and “the percent of oak seedlings with telia was significantly lower for

seedlings exposed to elevated CO₂ at the 16 and 19 days evaluations in both runs of the experiment.” With respect to the pine pitch canker study, the four researchers say “the percent of loblolly pine seedlings which developed cankers following inoculation with the pitch canker fungus was consistently lower for seedlings grown under elevated CO₂ in both runs of the experiment ... with infection in elevated CO₂-grown seedlings remaining about half that of ambient-grown seedlings.”

Runion *et al.* conclude “disease incidence—regardless of pathogen type—may be reduced as atmospheric CO₂ concentration continues to rise,” which should significantly benefit the two species of trees in the high-CO₂ environment.

The balance of evidence obtained to date demonstrates an enhanced ability of trees to withstand pathogen attacks in CO₂-enriched as opposed to ambient-CO₂ air. As the atmosphere’s CO₂ concentration rises, Earth’s vegetation should fare better against the ravages inflicted on it by myriad debilitating plant diseases.

References

Booker, F.L. 2000. Influence of carbon dioxide enrichment, ozone and nitrogen fertilization on cotton (*Gossypium hirsutum* L.) leaf and root composition. *Plant, Cell and Environment* **23**: 573–583.

Entry, J.A., Runion, G.B., Prior, S.A., Mitchell, R.J., and Rogers, H.H. 1998. Influence of CO₂ enrichment and nitrogen fertilization on tissue chemistry and carbon allocation in longleaf pine seedlings. *Plant and Soil* **200**: 3–11.

Fleischmann, F., Raidl, S., and Osswald, W.F. 2010. Changes in susceptibility of beech (*Fagus sylvatica*) seedlings towards *Phytophthora citricola* under the influence of elevated atmospheric CO₂ and nitrogen fertilization. *Environmental Pollution* **158**: 1051–1060.

Gebauer, R.L., Strain, B.R., and Reynolds, J.F. 1998. The effect of elevated CO₂ and N availability on tissue concentrations and whole plant pools of carbon-based secondary compounds in loblolly pine. *Oecologia* **113**: 29–36.

King, J.S., Thomas, R.B., and Strain, B.R. 1997. Morphology and tissue quality of seedling root systems of *Pinus taeda* and *Pinus ponderosa* as affected by varying CO₂, temperature, and nitrogen. *Plant and Soil* **195**: 107–119.

McElrone, A.J., Hamilton, J.G., Krafnick, A.J., Aldea, M., Knepp, R.G., and DeLucia, E.H. 2010. Combined effects of

elevated CO₂ and natural climatic variation on leaf spot diseases of redbud and sweetgum trees. *Environmental Pollution* **158**: 108–114.

McElrone, A.J., Reid, C.D., Hoyer, K.A., Hart, E., and Jackson, R.B. 2005. Elevated CO₂ reduces disease incidence and severity of a red maple fungal pathogen via changes in host physiology and leaf chemistry. *Global Change Biology* **11**: 1828–1836.

Parsons, W.F.J., Kopper, B.J., and Lindroth, R.L. 2003. Altered growth and fine root chemistry of *Betula papyrifera* and *Acer saccharum* under elevated CO₂. *Canadian Journal of Forest Research* **33**: 842–846.

Percy, K.E., Awmack, C.S., Lindroth, R.L., Kubiske, M.E., Kopper, B.J., Isebrands, J.G., Pregitzer, K.S., Hendrey, G.R., Dickson, R.E., Zak, D.R., Oksanen, E., Sober, J., Harrington, R., and Karnosky, D.F. 2002. Altered performance of forest pests under atmospheres enriched by CO₂ and O₃. *Nature* **420**: 403–407.

Pimentel, D., Lach, L., and Zuniga, R., *et al.* 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* **50**: 53–65.

Runion, G.B., Entry, J.A., Prior, S.A., Mitchell, R.J., and Rogers, H.H. 1999. Tissue chemistry and carbon allocation in seedlings of *Pinus palustris* subjected to elevated atmospheric CO₂ and water stress. *Tree Physiology* **19**: 329–335.

Runion, G.B., Prior, S.A., Rogers, H.H., and Mitchell, R.J. 2010. Effects of elevated atmospheric CO₂ on two southern forest diseases. *New Forests* **39**: 275–285.

Sinclair, W.A., Lyon, H.H., and Johnson, W.T. 1987. *Diseases of Trees and Shrubs*. Cornell University Press, Ithaca, New York, USA.

3.3 Heavy Metal Toxicity

- Increases in the air’s CO₂ content improve plants’ ability to withstand the deleterious effects of heavy metals that may be present in soils at ordinarily toxic levels.

Noting copper (Cu) is “an essential micronutrient [that] plays a vital role in maintaining normal metabolism in higher plants,” but “is toxic to plant cells at higher concentrations and causes the inhibition of plant growth or even death,” Jia *et al.* (2007) grew a Japonica rice cultivar in control and Cu-contaminated soil for one full growing season at ambient and elevated atmospheric CO₂ concentrations (370 and 570 ppm), measuring leaf Cu concentrations at the tillering, jointing, heading, and ripening stages.

At the tillering stage of the plants' progression, leaf Cu concentrations in the plants growing in the Cu-contaminated soil of both CO₂ treatments were about 90% greater than those in the plants growing in the uncontaminated soil of both CO₂ treatments. By the time the plants had reached the jointing stage, the mean leaf Cu concentration in the plants growing in the Cu-contaminated soil in the CO₂-enriched air had dropped to the same level as the plants growing in uncontaminated soil in ambient air, and this equivalence was maintained throughout the plants' subsequent heading and ripening stages.

For the plants growing in contaminated soil in ambient air, leaf Cu concentrations remained 50% greater than those of the plants growing in contaminated soil in CO₂-enriched air at the end of the experiment. Thus the negative effect of a more-than-five-fold increase in soil Cu concentration, which increased leaf Cu concentration by approximately 90% at the crop tillering stage, was completely ameliorated throughout the rest of the crop's development by a 54% increase in the atmosphere's CO₂ concentration.

Jia *et al.* (2011a) note "mining and smelting, disposal of sewage sludge and use of cadmium (Cd) rich phosphate fertilizers have contaminated large areas throughout the world, causing an increase in the Cd content of the soil (Liu *et al.*, 2007)." This is, they note, an unfortunate development, because "cadmium is a non-essential element that negatively affects plant growth and development processes, such as respiration and photosynthesis (Vega *et al.*, 2006), water and mineral uptake (Singh and Tewari, 2003), cell division (Fojtova *et al.*, 2002) and cellular redox homeostasis (Romero-Puertas *et al.*, 2004)."

Jia *et al.* studied the interactive effects of Cd contamination and atmospheric CO₂ enrichment on a perennial ryegrass (*Lolium perenne*), growing it from seed hydroponically in half-strength Hoagland solution for three days, followed by growth in full-strength Hoagland solution for five and 20 days and at a range of Cd concentrations ranging from 0 to 160 µmol/liter. Regardless of Cd treatment, the five researchers found "the Cd concentration was much lower under elevated CO₂ than under ambient CO₂," most likely due to the "fast growth triggered by elevated CO₂," such that in their experiment "the dry biomass increased by 81.2% for shoots and 55.2% for roots under non-Cd stress, and an average of 99.1% for shoots and 68.5% for roots under Cd stress, respectively." The five Chinese scientists conclude, "under elevated CO₂, *L. perenne* may be better

protected against Cd stress with higher biomass, lower Cd concentration and better detoxification by phytochelatins." In addition, "lower Cd concentration in plants under elevated CO₂ may relieve the Cd toxicity to plants and reduce the risk of Cd transport in the food chain."

Jia *et al.* (2011b) obtained similar results when they hydroponically grew two important forage crops (*Lolium perenne* and *Lolium multiflorum*) at three different Cd (0, 4, and 16 mg/L) and two different atmospheric CO₂ (360 or 1,000 ppm) concentrations in individual pots in controlled-environment chambers for three weeks. They found "root morphological parameters, including root length, surface area, volume, tip number, and fine roots, all decreased under Cd exposure," whereas "by contrast, elevated levels of CO₂ significantly increased all those parameters in the presence of Cd, compared to the CO₂ control, suggesting that elevated levels of CO₂ had an ameliorating effect on Cd-induced stress." The extra 640 ppm of CO₂ also increased the shoot dry weight of *L. multiflorum* by 68%, 92%, and 90% and *L. perenne* by 65%, 61%, and 67% at low, medium, and high (0, 4, and 16 mg/L) cadmium concentrations. It increased the root dry weight of *L. multiflorum* by 65%, 54%, and 50% and *L. perenne* by 47%, 67%, and 10%. The researchers note, "total Cd uptake per pot, calculated on the basis of biomass, was significantly greater under elevated levels of CO₂ than under ambient CO₂," increasing by 42–73% in plant shoots. Meanwhile, elevated CO₂ resulted in a reduction of Cd concentration in the plants' tissues.

The seven scientists note the high Cd uptake under CO₂-enriched conditions for the two *Lolium* species indicate great potential for use in the phytoremediation of Cd-contaminated soils in a CO₂-enriched environment. Also, because of much greater biomass production, the reduction of Cd concentrations in the forage crops' tissues suggests the rise in the air's CO₂ content could improve the safety of these crops, as was demonstrated by Guo *et al.* (2006), who according to Jia *et al.* (2011b), "reported decreased Cd accumulation in leaves, stems, roots and grains of rice at elevated CO₂"; by Zheng *et al.* (2008), who "showed that *Pteridium revolutum* and *Pteridium aquilinum* grown on Cu-contaminated soils accumulated less Cu in plant tissues at elevated levels of CO₂ than at ambient CO₂," and by Li *et al.* (2010), who also "found that elevated levels of CO₂ diluted [rice] grain Cd concentration."

Tukaj *et al.* (2007) note cadmium has been demonstrated to cause "inhibition or inactivation of

many enzymes, thereby disturbing the growth, respiration, or photosynthesis in plant cells and algae (Tukendorf and Baszynski, 1991; Sanita di Toppi and Gabbrielli, 1999; Prasad *et al.*, 2001; Faller *et al.*, 2005).” The four Polish scientists grew the unicellular green alga *Scenedesmus armatus* for periods of one, two, and three days in batch cultures that contained a 93µM concentration of cadmium and were continuously bubbled with air of either 0.1% or 2% (v/v) CO₂—equivalent to approximately 1,000 and 20,000 ppm CO₂, respectively—while making a number of measurements of algal properties and physiological processes.

The researchers found the density of the cultures grown for three days at 2% CO₂ “was markedly higher in comparison to cultures grown at 0.1% CO₂ concentration mainly due to the growth rate acceleration during the first day of culture.” After 24 hours of cadmium exposure, for example, “growth was inhibited to about 49% at 0.1% CO₂, whereas at 2% CO₂ only to about 74% of the controls.” In addition, “cadmium inhibited the rate of oxygen evolution (70% of control) of cells cultured at 0.1% CO₂ [but] had no effect on the rate of oxygen evolution of cells cultured at 2% CO₂.”

The researchers state their results suggest the protective mechanism(s) directed against cadmium was (were) “more efficient in algae cultured under elevated CO₂ than algae cultured under low level of CO₂.” They also note “the main detoxifying strategy of plants contaminated by heavy metals is the production of phytochelatins (PCs),” as described by Cobbett (2000), and they report “cells grown at 2% CO₂—after 24 hours of exposure—produced much more PCs than cells cultured at 0.1% CO₂.” Their data indicate the CO₂-induced phytochelatin enhancement of their study was more than tenfold. They conclude, “algae living in conditions of elevated CO₂ are better protected against cadmium than those at ordinary CO₂ level.”

Taken together, the studies reviewed here bode well for the ability of plants in a CO₂-enriched environment to better deal with the problem of heavy metal soil toxicity.

References

- Cobbett, C.S. 2000. Phytochelatins and their roles in heavy metal detoxification. *Plant Physiology* **123**: 825–832.
- Faller, P., Kienzler, K., and Krieger-Liszkay, A. 2005. Mechanism of Cd²⁺ toxicity: Cd²⁺ inhibits photoactivation of Photosystem II by competitive binding to the essential Ca²⁺ site. *Biochimica et Biophysica Acta* **1706**: 158–164.
- Fojtova, M., Fulneckova, J., Fajkus, J., and Kovarik, A. 2002. Recovery of tobacco cells from cadmium stress is accompanied by DNA repair and increased telomerase activity. *Journal of Experimental Botany* **53**: 2151–2158.
- Guo, H.Y., Jia, H.X., Zhu, J.G., and Wang, X.R. 2006. Influence of the environmental behavior and ecological effect of cropland heavy metal contaminants by CO₂ enrichment in atmosphere. *Chinese Journal of Geochemistry* **25**: 10.1007/BF02840155.
- Jia, H.X., Guo, H.Y., Yin, Y., Wang, Q., Sun, Q., Wang, X.R., and Zhu, J.G. 2007. Responses of rice growth to copper stress under free-air CO₂ enrichment (FACE). *Chinese Science Bulletin* **52**: 2636–2641.
- Jia, Y., Ju, X., Liao, S., Song, Z., and Li, Z. 2011a. Phytochelatin synthesis in response to elevated CO₂ under cadmium stress in *Lolium perenne* L. *Journal of Plant Physiology* **168**: 1723–1728.
- Jia, Y., Tang, S.-r., Ju, X.-h., Shu, L.-n., Tu, S.-x., Feng, R.-w., and Giusti, L. 2011b. Effects of elevated CO₂ levels on root morphological traits and Cd uptakes of two *Lolium* species under Cd stress. *Journal of Zhejiang University—SCIENCE B (Biomedicine & Biotechnology)* **12**: 313–325.
- Li, Z.Y., Tang, S.R., Deng, X.F., Wang, R.G., and Song, Z.G. 2010. Contrasting effects of elevated CO₂ on Cu and Cd uptake by different rice varieties grown on contaminated soils with two levels of metals: implication for phytoextraction and food safety. *Journal of Hazardous Materials* **177**: 352–361.
- Liu, Y.G., Wang, X., Zeng, G.M., Qu, D., Gu, J.J., Zhou, M., and Chai, L. 2007. Cadmium-induced oxidative stress and response of the ascorbate-glutathione cycle in *Beckmeria nivea* (L.), Gaud. *Chemosphere* **69**: 99–107.
- Prasad, M.N.V., Malec, P., Waloszek, A., Bojko, M., and Strzalka, K. 2001. Physiological responses of *Lemna trisulca* L. (duckweed) to cadmium and copper bioaccumulation. *Plant Science* **161**: 881–889.
- Romero-Puertas, M.C., Rodriguez-Serrano, M., Corpas, F.J., and delRio, L.A. 2004. Cadmium-induced subcellular accumulation of O₂^{•-} and H₂O₂ in pea leaves. *Plant, Cell and Environment* **27**: 1122–1134.
- Sanita di Toppi, L. and Gabbrielli, R. 1999. Response to cadmium in higher plants. *Environmental and Experimental Botany* **41**: 105–130.
- Singh, P.K. and Tewari, R.K. 2003. Cadmium toxicity induced changes in plant water relations and oxidative metabolism of *Brassica juncea* L. plants. *Journal of Environmental Biology* **24**: 107–112.

Tukaj, Z., Bascik-Remisiewicz, A., Skowronski, T., and Tukaj, C. 2007. Cadmium effect on the growth, photosynthesis, ultrastructure and phytochelatin content of green microalga *Scenedesmus armatus*: A study at low and elevated CO₂ concentration. *Environmental and Experimental Botany* **60**: 291–299.

Tukendorf, A. and Baszynski, T. 1991. The *in vivo* effect of cadmium on photochemical activities in chloroplast of runner bean plants. *Acta Physiologiae Plantarum* **13**: 51–57.

Vega, J.M., Garbayo, I., Dominguez, M.J., and Vigar, J. 2006. Effect of abiotic stress on photosynthesis and respiration in *Chlamydomonas reinhardtii*: induction of oxidative stress. *Enzyme and Microbial Technology* **40**: 163–167.

Zheng, J.M., Wang, H.Y., Li, Z.Q., Tang, S.R., and Chen, Z.Y. 2008. Using elevated carbon dioxide to enhance copper accumulation in *Pteridium revolutum*, a copper-tolerant plant, under experimental conditions. *International Journal of Phytoremediation* **10**: 161–172.

3.4 Herbivory

By itself, a rising atmospheric CO₂ concentration may reduce the frequency and severity of pest outbreaks detrimental to agriculture, without seriously affecting herbivorous organisms found in natural ecosystems.

In addition, specific genetic alterations to crop plants may increase their resistance to assaults of insect pests, allow them to better bear the consequences of possible future increases in seasonal maximum air temperatures, and help them take advantage of the positive effects of atmospheric CO₂ enrichment on various plant properties and processes. At the same time, the elevated CO₂ would reduce the severity of possible negative effects that could arise from the escape of transplanted genes into the natural environment.

3.4.1 Herbaceous Plants

- Rising atmospheric CO₂ concentrations may reduce the frequency and severity of pest outbreaks detrimental to agriculture, without seriously impacting herbivorous organisms found in natural ecosystems.

Kerslake *et al.* (1998) grew five-year-old heather (*Calluna vulgaris*) plants collected from a Scottish moor in open-top chambers maintained at

atmospheric CO₂ concentrations of 350 and 600 ppm. Twice during the study, they allowed larvae of the destructive winter moth *Operophtera brumata*—whose outbreaks periodically cause extensive damage to heather moorland—to feed on current-year shoots. Feeding on the high-CO₂-grown foliage did not affect larval growth rates, development, or final pupal weights; nor was moth survivorship significantly altered. The three researchers conclude their study provides “no evidence that increasing atmospheric CO₂ concentrations will affect the potential for outbreak of *Operophtera brumata* on this host.”

Newman *et al.* (1999) inoculated tall fescue (*Festuca arundinacea*) plants growing in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm with bird cherry-oat aphids (*Rhopalosiphum padi*). After nine weeks, the plants growing in the CO₂-enriched air had experienced a 37% increase in productivity and were covered with far fewer aphids than the plants growing in ambient air. The result was a “win” for the favored plants and a “loss” for the destructive insects.

Goverde *et al.* (1999) collected four genotypes of *Lotus corniculatus* near Paris and grew them in controlled-environment chambers kept at atmospheric CO₂ concentrations of 350 and 700 ppm. Larvae of the Common Blue Butterfly (*Polyommatus icarus*) the researchers allowed to feed on the foliage produced in the CO₂-enriched air ate more, grew larger, and experienced shorter development times than larvae feeding on the foliage in the ambient-air treatment, suggesting this butterfly species will become more robust and plentiful as the air’s CO₂ content rises.

Brooks and Whittaker (1999) removed grassland monoliths containing eggs of the xylem-feeding spittlebug *Neophilaenus lineatus* from the UK’s Great Dun Fell in Cumbria and placed them in glasshouses maintained at atmospheric CO₂ concentrations of 350 and 600 ppm for two years. Survival of the spittlebug’s nymphal states was reduced by 24% in both of the generations produced in their experiment in the high-CO₂ treatment, suggesting this particular insect likely will cause less tissue damage to the plants of this species-poor grassland in a CO₂-enriched environment.

Joutei *et al.* (2000) grew bean (*Phaseolus vulgaris*) plants in controlled environments kept at atmospheric CO₂ concentrations of 350 and 700 ppm, into which they introduced the destructive agricultural mite *Tetranychus urticae*. They found female mites

produced 34% and 49% fewer offspring in the CO₂-enriched chambers in their first and second generations, respectively. These reductions in the reproductive success of this mite, which attacks more than 150 crop species worldwide, has important agricultural implications in terms of crop production.

Peters *et al.* (2000) fed foliage derived from FACE plots of calcareous grasslands of Switzerland (maintained at 350 and 650 ppm CO₂) to terrestrial slugs, finding they exhibited no preference with respect to the CO₂ treatment from which the foliage was derived. Also, in a study that targeted no specific insect pest, Castells *et al.* (2002) found a doubling of the air's CO₂ content enhanced the total phenolic contents of two Mediterranean perennial grasses (*Dactylis glomerata* and *Bromus erectus*) by 15% and 87%, respectively; these compounds tend to enhance mechanisms that allow plants to defend against and resist attacks by herbivores and pathogens.

Coviella and Trumble (2000) determined toxins produced by *Bacillus thuringiensis* (Bt)—which are applied to crop plants by spraying as a means of combating various crop pests—were “more efficacious” in cotton grown in an elevated CO₂ environment than in ambient air, an important benefit for modern agriculture. In addition, Coviella *et al.* (2000) write, “elevated CO₂ appears to eliminate differences between transgenic [Bt-containing] and nontransgenic plants for some key insect developmental/fitness variables including length of the larval stage and pupal weight,” which could prove significant for nature in the event of inadvertent Bt gene transference to wild relatives of transgenic crop lines.

Barbehenn *et al.* (2004b) note increases in the air's CO₂ content typically lead to greater decreases in the concentrations of nitrogen and, therefore, protein in the foliage of C₃ as compared to C₄ grasses, citing Wand *et al.* (1999). Barbehenn *et al.* write, “it has been predicted that insect herbivores will increase their feeding damage on C₃ plants to a greater extent than on C₄ plants (Lincoln *et al.*, 1984, 1986; Lambers, 1993).” The three researchers grew *Lolium multiflorum* Lam. (Italian ryegrass, a common C₃ pasture grass) and *Bouteloua curtipendula* (Michx.) Torr. (sideoats gramma, a native C₄ rangeland grass) in chambers maintained at either the ambient atmospheric CO₂ concentration of 370 ppm or 740 ppm for two months. They allowed newly molted sixth instar larvae of *Pseudaletia unipuncta* (a grass-specialist noctuid) and *Spodoptera frugiperda* (a generalist noctuid) to feed on the grasses' foliage.

As expected, foliage protein concentration

decreased by 20% in the C₃ grass, but by only 1% in the C₄ grass, when they were grown in CO₂-enriched air, and “to the extent that protein is the most limiting of the macronutrients examined, these changes represent a decline in the nutritional quality of the C₃ grass,” Barbehenn *et al.* write. However, and contrary to their expectations, they report “neither caterpillar species significantly increased its consumption rate to compensate for the lower concentration of protein in [the] C₃ grass,” noting “this result does not support the hypothesis that C₃ plants will be subject to greater rates of herbivory relative to C₄ plants in future [high-CO₂] atmospheric conditions (Lincoln *et al.*, 1984).” In addition, and “despite significant changes in the nutritional quality of *L. multiflorum* under elevated CO₂,” they note “no effect on the relative growth rate of either caterpillar species on either grass species resulted,” and there were “no significant differences in insect performance between CO₂ levels.” Barbehenn *et al.* suggest “post-ingestive mechanisms could provide a sufficient means of compensation for the lower nutritional quality of C₃ plants grown under elevated CO₂.”

Barbehenn *et al.* conclude “there will not be a single pattern that characterizes all grass feeders” with respect to their feeding preferences and developmental responses under conditions where certain C₃ plants may experience foliar protein concentrations lower than those they exhibit today, nor will the changes that may occur necessarily impede herbivore development or damage the health and vigor of their host plants.

Barbehenn *et al.* (2004a) fed some of the identical foliage of the same experiment to grasshopper (*Melanoplus sanguinipes*) nymphs reared to the fourth instar stage. They note “*M. sanguinipes* did not significantly increase its consumption rate when feeding on the C₃ grass grown under elevated CO₂,” which they say implies “post-ingestive mechanisms enable these grasshoppers to compensate for variable nutritional quality in their host plants.” They further suggest some of these post-ingestive responses may include “changes in gut size, food residence time, digestive enzyme levels, and nutrient metabolism (Simpson and Simpson, 1990; Bernays and Simpson, 1990; Hinks *et al.*, 1991; Zanutto *et al.*, 1993; Yang and Joern, 1994a,b).” If anything, *M. sanguinipes* growth rates were increased, perhaps by as much as 12%, when they fed on the C₃ foliage produced in the CO₂-enriched, as compared to the ambient-air treatment.

Therefore, just as was found in Barbehenn *et al.*

(2004b), the CO₂-induced decrease in leaf protein concentration observed in this study did not induce an increase in consumption in the C₃ plant studied, nor did it reduce the growth rate of the herbivore studied. Therefore, the scientists state, “although compensatory feeding was commonly observed in early studies [of this subject], the absence of compensatory feeding on C₃ plants grown under elevated CO₂ has since been observed frequently among herbivorous insects (Bezemer and Jones, 1998).”

Bidart-Bouzat *et al.* (2005) grew three genotypes of mouse-ear cress (*Arabidopsis thaliana*) from seed in pots placed in controlled-environment chambers maintained at either ambient CO₂ (360 ppm) or elevated CO₂ (720 ppm). On each of half of the plants (the herbivory treatment) in each of the CO₂ treatments, they placed two second instar larvae of the diamondback moth (*Plutella xylostella*) at bolting time and removed them at pupation, which resulted in an average of 20% of each plant’s total leaf area in the herbivory treatment being removed. Next, each pupa was placed in a gelatin capsule until adult emergence and ultimate death, after which insect gender was determined and the pupa’s weight recorded. At the end of the herbivory trial, leaves of the control and larvae-infested plants were analyzed for concentrations of individual glucosinolates—a group of plant-derived chemicals that can act as herbivore deterrents, as reported by Mauricio and Rausher (1997)—after which the researchers determined total glucosinolate production by summation of the individual glucosinolate assays. Finally, they evaluated various influences of elevated CO₂ on moth performance and their association with plant defense-related traits.

Bidart-Bouzat *et al.* found herbivory by larvae of the diamondback moth did not induce any increase in the production of glucosinolates in the mouse-ear cress in the ambient CO₂ treatment. They report, “herbivory-induced increases in glucosinolate contents, ranging from 28% to 62% above basal levels, were found under elevated CO₂ in two out of the three genotypes studied.” In addition, “elevated CO₂ decreased the overall performance of diamondback moths.” And because “induced defenses can increase plant fitness by reducing subsequent herbivore attacks (Agrawal, 1999; Kessler and Baldwin, 2004),” the three researchers suggest “the pronounced increase in glucosinolate levels under CO₂ enrichment may pose a threat not only for insect generalists that are likely to be more influenced by rapid changes in the concentration of these chemicals,

but also for other insect specialists more susceptible than diamondback moths to high glucosinolate levels (Stowe, 1998; Kliebenstein *et al.*, 2002).”

Ayres *et al.* (2008) reported the responses of belowground nematode herbivores to atmospheric CO₂ enrichment to approximately 350 ppm above ambient in experiments conducted on three grassland ecosystems in Colorado and California (USA) and Montpellier, France. They note “soil moisture increased in response to elevated CO₂ in the California, Colorado, and French stud[ies] (Hungate *et al.*, 1997; Nijs *et al.*, 2000; Morgan *et al.*, 2004).” They also found “elevated CO₂ increased root biomass by approximately 3–32% in the first 5 years of the Coloradoan study (Pendall *et al.*, 2004), by 23% after 6 years in the Californian study (Rillig *et al.*, 1999), and by 31% after 6 months in the French study (Dhillion *et al.*, 1996).” Regarding nematodes, they add, “CO₂ enrichment did not significantly affect the family richness, diversity, or PPI [plant parasitic nematode index] of herbivorous nematodes in the Colorado, California, or French study,” noting “in each experiment, neutral effects were the most frequent response to CO₂ enrichment.” The seven scientists conclude, “one consequence of increased root production, without changes in belowground herbivore populations, might be greater plant inputs to soil,” which “may lead to greater soil organic matter pools in grassland ecosystems, potentially enhancing soil carbon sequestration.”

Lau *et al.* (2008) measured the amounts of herbivore and pathogen damage done to the common prairie legume *Lespedeza capitata* growing in ambient and elevated (560 ppm) CO₂ treatments in the seventh and eighth years (2004 and 2005) of the BioCON study (Reich *et al.*, 2001) conducted at the Cedar Creek Natural History Area in Minnesota (USA), where the CO₂ treatments were applied during the daylight hours of each growing season. In this setting, three types of pests inflicted herbivore damage—generalist chewers (primarily grasshoppers), *Pachyschelus laevigatus* (Coleoptera: Buprestidae), and *Tortriodon* sp. (Lepidoptera)—and pathogen damage was caused by *Pythium* or *Fusarium* spp.

Lau *et al.* say they detected “no evidence that the CO₂ treatments affected herbivore damage.” As to pathogen damage, they found disease incidence “was lower in the elevated CO₂ environment, although this difference [10% less in 2004 and 53% less in 2005] was statistically significant only in 2005 (*P* < 0.01).” Therefore, and because “disease caused major

reductions in reproductive output,” the five researchers write, “the effects of CO₂ on disease incidence may be important for *L. capitata* evolution and population dynamics,” and this phenomenon should significantly benefit this species in a high-CO₂ environment. In addition, they note Strengbom and Reich (2006), “working in the same experimental site ... also found that elevated CO₂ ... reduced disease incidence on *Solidago rigida*.”

Coll and Hughes (2008) describe their work as “the first study that measured the effect of global atmospheric change on an omnivorous consumer,” exploring the impacts of elevated atmospheric CO₂ on the behavior and performance of an omnivorous bug (*Oeochalia schellenbergii*, Heteroptera: Pentatomidae) and its prey, a polyphagous chewing herbivorous pest (*Helicoverpa armigera*; Lepidoptera: Noctuidae), feeding on pea (*Pisum sativum*) foliage grown in controlled-environment cabinets maintained at atmospheric CO₂ concentrations of either 360 or 700 ppm. They found the *H. armigera* pests that fed on the elevated CO₂-grown pea plants were significantly smaller than those that fed on the ambient CO₂-grown pea plants, and the bigger *O. schellenbergii* bugs that fed on them “performed best when fed larvae from the elevated-CO₂ treatment,” because the prey of that treatment “were smaller and thus easier to subdue.” Only 13.3% of the predation attempts made on the larvae fed ambient-CO₂-grown foliage were successful, as compared to 78.2% for the larvae fed elevated-CO₂-grown foliage.

The two researchers conclude “elevated CO₂ may benefit generalist predators through increased prey vulnerability, which would put pest species under higher risk of predation.” Consequently, and “since omnivory is widespread in agroecosystems,” they argue “yield loss to most pest species will be lower under elevated atmospheric CO₂ levels, compared to the current condition.”

The majority of evidence to date suggests rising atmospheric CO₂ concentrations may reduce the frequency and severity of pest outbreaks detrimental to agriculture, without seriously impacting herbivorous organisms found in natural ecosystems.

References

- Agrawal, A.A. 1999. Induced-responses to herbivory in wild radish: effects on several herbivores and plant fitness. *Ecology* **80**: 1713–1723.
- Ayres, E., Wall, D.H., Simmons, B.L., Field, C.B., Milchunas, D.G., Morgan, J.A., and Roy, J. 2008. Belowground nematode herbivores are resistant to elevated atmospheric CO₂ concentrations in grassland ecosystems. *Soil Biology & Biochemistry* **40**: 978–985.
- Barbehenn, R.V., Karowe, D.N. and Chen, Z. 2004a. Performance of a generalist grasshopper on a C₃ and a C₄ grass: compensation for the effects of elevated CO₂ on plant nutritional quality. *Oecologia* **140**: 96–103.
- Barbehenn, R.V., Karowe, D.N., and Spickard, A. 2004b. Effects of elevated atmospheric CO₂ on the nutritional ecology of C₃ and C₄ grass-feeding caterpillars. *Oecologia* **140**: 86–95.
- Bernays, E.A. and Simpson, S.J. 1990. Nutrition. In: Chapman, R.F. and Joern, A. (Eds.) *Biology of Grasshoppers*. Wiley, New York, NY, pp. 105–127.
- Bezemer, T.M. and Jones, T.H. 1998. Plant-insect herbivore interactions in elevated atmospheric CO₂: quantitative analyses and guild effects. *Oikos* **82**: 212–222.
- Bidart-Bouzat, M.G., Mithen, R., and Berenbaum, M.R. 2005. Elevated CO₂ influences herbivory-induced defense responses of *Arabidopsis thaliana*. *Oecologia* **145**: 415–424.
- Brooks, G.L. and Whittaker, J.B. 1999. Responses of three generations of a xylem-feeding insect, *Neophilaenus lineatus* (Homoptera), to elevated CO₂. *Global Change Biology* **5**: 395–401.
- Castells, E., Roumet, C., Peñuelas, J., and Roy, J. 2002. Intraspecific variability of phenolic concentrations and their responses to elevated CO₂ in two Mediterranean perennial grasses. *Environmental and Experimental Botany* **47**: 205–216.
- Coll, M. and Hughes, L. 2008. Effects of elevated CO₂ on an insect omnivore: A test for nutritional effects mediated by host plants and prey. *Agriculture, Ecosystems and Environment* **123**: 271–279.
- Coviella, C.E., Morgan, D.J.W., and Trumble, J.T. 2000. Interactions of elevated CO₂ and nitrogen fertilization: Effects on production of *Bacillus thuringiensis* toxins in transgenic plants. *Environmental Entomology* **29**: 781–787.
- Coviella, C.E. and Trumble, J.T. 2000. Effect of elevated atmospheric carbon dioxide on the use of foliar application of *Bacillus thuringiensis*. *BioControl* **45**: 325–336.
- Dhillion, S.D., Roy, J., and Abrams, M. 1996. Assessing the impact of elevated CO₂ on soil microbial activity in a Mediterranean model ecosystem. *Plant & Soil* **187**: 333–342.
- Goverde, M., Bazin, A., Shykoff, J.A., and Erhardt, A. 1999. Influence of leaf chemistry of *Lotus corniculatus*

- (Fabaceae) on larval development of *Polyommatus icarus* (Lepidoptera, Lycaenidae): effects of elevated CO₂ and plant genotype. *Functional Ecology* **13**: 801–810.
- Hinks, C.R., Cheeseman, M.T., Erlandson, M.A., Olfert, O., and Westcott, N.D. 1991. The effects of kochia, wheat and oats on digestive proteinases and the protein economy of adult grasshoppers, *Malanoplus sanguinipes*. *Journal of Insect Physiology* **37**: 417–430.
- Hungate, B.A., Holland, E.A., Jackson, R.B., Chapin, F.S., Mooney, H.A., and Field, C.B. 1997. The fate of carbon in grasslands under carbon dioxide enrichment. *Nature* **388**: 576–579.
- Joutei, A.B., Roy, J., Van Impe, G., and Lebrun, P. 2000. Effect of elevated CO₂ on the demography of a leaf-sucking mite feeding on bean. *Oecologia* **123**: 75–81.
- Kerslake, J.E., Woodin, S.J., and Hartley, S.E. 1998. Effects of carbon dioxide and nitrogen enrichment on a plant-insect interaction: the quality of *Calluna vulgaris* as a host for *Operophtera brumata*. *New Phytologist* **140**: 43–53.
- Kessler, A. and Baldwin, I.T. 2004. Herbivore-induced plant vaccination. Part I. The orchestration of plant defenses in nature and their fitness consequences in the wild tobacco, *Nicotiana attenuata*. *Plant Journal* **38**: 639–649.
- Kliebenstein, D., Pedersen, D., Barker, B., and Mitchell-Olds, T. 2002. Comparative analysis of quantitative trait loci controlling glucosinolates, myrosinase and insect resistance in *Arabidopsis thaliana*. *Genetics* **161**: 325–332.
- Lambers, H. 1993. Rising CO₂, secondary plant metabolism, plant-herbivore interactions and litter decomposition. Theoretical considerations. *Vegetatio* **104/105**: 263–271.
- Lau, J.A., Strengbom, J., Stone, L.R., Reich, P.B., and Tiffin, P. 2008. Direct and indirect effects of CO₂, nitrogen, and community diversity on plant-enemy interactions. *Ecology* **89**: 226–236.
- Lincoln, D.E., Couvet, D., and Sionit, N. 1986. Responses of an insect herbivore to host plants grown in carbon dioxide enriched atmospheres. *Oecologia* **69**: 556–560.
- Lincoln, D.E., Sionit, N., and Strain, B.R. 1984. Growth and feeding response of *Pseudoplusia includens* (Lepidoptera: Noctuidae) to host plants grown in controlled carbon dioxide atmospheres. *Environmental Entomology* **13**: 1527–1530.
- Mauricio, R. and Rausher, M.D. 1997. Experimental manipulation of putative selective agents provides evidence for the role of natural enemies in the evolution of plant defense. *Evolution* **51**: 1435–1444.
- Morgan, J.A., Mosier, A.R., Milchunas, D.G., LeCain, D.R., Nelson, J.A., and Parton, W.J. 2004. CO₂ enhances productivity, alters species composition, and reduces digestibility of shortgrass steppe vegetation. *Ecological Applications* **14**: 208–219.
- Newman, J.A., Gibson, D.J., Hickam, E., Lorenz, M., Adams, E., Bybee, L., and Thompson, R. 1999. Elevated carbon dioxide results in smaller populations of the bird cherry-oat aphid *Rhopalosiphum padi*. *Ecological Entomology* **24**: 486–489.
- Nijs, I., Roy, J., Salager, J.-L., and Fabreguettes, J. 2000. Elevated CO₂ alters carbon fluxes in early successional Mediterranean ecosystems. *Global Change Biology* **6**: 981–994.
- Pendall, E., Mosier, A.R., and Morgan, J.A. 2004. Rhizodeposition stimulated by elevated CO₂ in a semiarid grassland. *New Phytologist* **162**: 447–458.
- Peters, H.A., Baur, B., Bazzaz, F., and Korner, C. 2000. Consumption rates and food preferences of slugs in a calcareous grassland under current and future CO₂ conditions. *Oecologia* **125**: 72–81.
- Reich, P.B., Tilman, D., Craine, J., Ellsworth, D., Tjoelker, M.G., Knops, J., Wedin, D., Naeem, S., Bahauddin, D., Goth, J., Bengston, W., and Lee, T.D. 2001. Do species and functional groups differ in acquisition and use of C, N, and water under varying atmospheric CO₂ and N availability regimes? A field test with 16 grassland species. *New Phytologist* **150**: 435–448.
- Rillig, M.C., Field, C.B., and Allen, M.F. 1999. Soil biota responses to long-term atmospheric CO₂ enrichment in two California annual grasslands. *Oecologia* **119**: 572–577.
- Simpson, S.J. and Simpson, C.L. 1990. The mechanisms of nutritional compensation by phytophagous insects. In: Bernays, E.A. (Ed.) *Insect-Plant Interactions*, Vol. 2. CRC Press, Boca Raton, FL, pp. 111–160.
- Stowe, K.A. 1998. Realized defense of artificially selected lines of *Brassica rapa*: effects of quantitative genetic variation in foliar glucosinolate concentration. *Environmental Entomology* **27**: 1166–1174.
- Strengbom, J. and Reich, P.B. 2006. Elevated CO₂ and increased N supply reduce leaf disease and related photosynthetic impacts on *Solidago rigida*. *Oecologia* **149**: 519–525.
- Wand, S.J.E., Midgley, G.F., Jones, M.H., and Curtis, P.S. 1999. Responses of wild C₄ and C₃ grass (Poaceae) species to elevated atmospheric CO₂ concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology* **5**: 723–741.
- Yang, Y. and Joern, A. 1994a. Gut size changes in relation to variable food quality and body size in grasshoppers. *Functional Ecology* **8**: 36–45.

Yang, Y. and Joern, A. 1994b. Influence of diet quality, developmental stage, and temperature on food residence time in the grasshopper *Melanoplus differentialis*. *Physiological Zoology* **67**: 598–616.

Zanotto, F.P., Simpson, S.J., and Raubenheimer, D. 1993. The regulation of growth by locusts through post-ingestive compensation for variation in the levels of dietary protein and carbohydrate. *Physiological Entomology* **18**: 425–434.

3.4.2 Transgenic Plants

- Specific genetic alterations to crop plants may improve their ability to withstand the assaults of insects pests, bear the consequences of possible future increases in seasonal maximum air temperatures, and take advantage of the positive effects of atmospheric CO₂ enrichment on various plant properties and processes. Meanwhile, elevated CO₂ reduces the severity of possible negative effects that could arise from the escape of transplanted genes into the natural environment.

Toxins produced by *Bacillus thuringiensis* (Bt) supplied to crops via foliar application have been used as a means of combating crop pests for well over half a century. The effectiveness of this management technique depends primarily on the amount of Bt-produced toxins ingested by targeted insects. This section examines how atmospheric CO₂ enrichment might impact this phenomenon.

If atmospheric CO₂ concentrations are high but soil nitrogen levels are low, foliar concentrations of nitrogen are generally reduced from what they are at ambient CO₂ concentrations, suggesting insects would have to eat more foliage to get their normal requirement of nitrogen for proper growth and development in CO₂-enriched air. By consuming more foliage, the insects also would ingest more Bt-produced toxins, and would thus be more severely impacted by those substances.

To test this hypothesis, Coviella and Trumble (2000) grew cotton plants in each of six Teflon-film chambers in a temperature-controlled greenhouse, where three of the chambers were maintained at an atmospheric CO₂ concentration of 370 ppm and three were maintained at 900 ppm CO₂. In addition, half of the plants in each chamber were given high levels of nitrogen (N) fertilization, and half received low levels (30 vs. 130 mg N/kg soil/week). After 45 days of growth under these conditions, the researchers

removed leaves from the plants and dipped them in a Bt solution, after which known amounts of treated leaf material were fed to *Spodoptera exigua* larvae and the responses measured and analyzed.

The two researchers determined the plants grown in the elevated CO₂ chambers did indeed have significantly lower foliar nitrogen concentrations than those grown in the ambient CO₂ chambers under the low N fertilization regime, but this was not the case under the high N regime. They also discovered older larvae fed with foliage grown in elevated CO₂ with low N fertilization consumed significantly more plant material than insects fed with foliage grown in ambient CO₂; but again, they found no differences with high N fertilization. Finally, and “consistent with the effect of higher Bt toxin intake due to enhanced consumption,” they found “insects fed on low N plants had significantly higher mortality in elevated CO₂.” They identified no such effect in the high N treatment. Consequently, with respect to pest management using Bt-produced toxins supplied to crops via foliar application, Coviella and Trumble conclude “increasing atmospheric CO₂ is making the foliar applications more efficacious.”

Coviella *et al.* (2000) addressed what happens to transgenic plants into which the Bt gene for producing the toxin has been artificially inserted. They grew cotton plants in 12 Teflon-film chambers in a temperature-controlled greenhouse, where six chambers were maintained at an atmospheric CO₂ concentration of 370 ppm and six were maintained at 900 ppm CO₂. Half of the cotton plants in each of these chambers were of a transgenic line containing the Bt gene for the production of the Cry1Ac toxin, which is mildly toxic for *Spodoptera exigua*, and the other half were of a near isogenic line without the Bt gene. Half of the plants in each chamber received low and high levels of N fertilization. Between 40 and 45 days after leaves emerged, researchers removed leaves from the plants and fed them to the *S. exigua* larvae, measuring and analyzing a number of larval responses and various leaf properties.

They found the low-N plants in the elevated CO₂ treatment had lower foliar N concentrations than the low-N plants in the ambient CO₂ treatment, and the transgenic plants from the low-N, high CO₂ treatment produced lower levels of Bt toxin than the transgenic plants from the low-N, ambient CO₂ treatment. The high level of N fertilization only partially compensated for the latter high-CO₂ effect, and in the ambient CO₂ treatment there was also a significant increase in days to pupation for insects fed transgenic plants.

This difference was not evident in elevated CO₂. Pupal weight in ambient CO₂ was significantly higher in non-transgenic plants, and again, this difference was not observed in elevated CO₂.

The three researchers write, “these results support the hypothesis that the lower N content per unit of plant tissue caused by the elevated CO₂ will result in lower toxin production by transgenic plants when nitrogen supply to the plants is a limiting factor.” They also note “elevated CO₂ appears to eliminate differences between transgenic and non-transgenic plants for some key insect developmental/fitness variables including length of the larval stage and pupal weight.”

These findings suggest, in the case of inadvertent Bt gene transference to wild relatives of transgenic crop lines, elevated levels of atmospheric CO₂ will tend to negate certain of the negative effects the wayward genes might otherwise inflict. The rise in the air’s CO₂ content could therefore constitute a buffer against this potential outcome.

Coviella *et al.*’s results also suggest transgenic crops designed to produce Bt-type toxins may become less effective in carrying out the objectives of their design as the air’s CO₂ content rises. Coupling this possibility with the fact the foliar application of *Bacillus thuringiensis* to crops should become even more effective in a higher-CO₂ world, as Coviella and Trumble found, it can be argued the implantation of toxin-producing genes in crops is not viable in the face of the rise in the air’s CO₂ content, which reduces that technique’s effectiveness at the same time it increases the effectiveness of direct foliar applications.

Although it is difficult to predict the future of genetic modification of crops for pesticidal purposes, it is useful to know the rise in the atmosphere’s CO₂ concentration will help both nature and agriculture, whatever the outcome of the current debate.

In a study of three different types of rice—a wild type (WT) and two transgenic varieties, one with 65% wild-type rubisco (AS-77) and one with 40% wild-type rubisco (AS-71)—Makino *et al.* (2000) grew plants from seed for 70 days in growth chambers maintained at 360 and 1,000 ppm CO₂. They harvested the plants and determined their biomass, finding the mean dry weights of the WT, AS-77, and AS-71 varieties grown in air of 360 ppm were, respectively, 5.75, 3.02, and 0.83 g. In air of 1,000 ppm CO₂, corresponding mean dry weights were 7.90, 7.40, and 5.65 g. Consequently, although the growth rates of the genetically engineered rice plants were far inferior to

the wild type when grown in normal air of 360 ppm CO₂ (with AS-71 producing less than 15% as much biomass as the wild type), when grown in air of 1,000 ppm CO₂ they experienced far greater CO₂-induced increases in growth: a 145% increase in the case of AS-77 and a 581% increase for AS-71. Thus, whereas the transgenic plants were highly disadvantaged in normal air of 360 ppm CO₂, they were found to be pretty much on an equal footing in highly CO₂-enriched air..

Chen *et al.* (2005) grew well-watered and well-fertilized plants of two varieties of cotton—one expressing Cry1A (c) genes from *Bacillus thuringiensis* and a non-transgenic cultivar from the same recurrent parent—in pots placed in open-top chambers maintained at either 375 or 750 ppm CO₂ in Sanhe County, Hebei Province, China, from planting in mid-May to harvest in October. During this period, they collected several immature bolls and analyzed them for various chemical characteristics, and they refrigerated others for later feeding to cotton bollworm larvae, whose growth characteristics they closely monitored. The five researchers found the elevated CO₂ treatment increased immature boll concentrations of condensed tannins by approximately 22% and 26% in transgenic and non-transgenic cotton, respectively. In addition, elevated CO₂ slightly decreased the body biomass of the cotton bollworms and reduced moth fecundity. The Bt treatment was even more effective in this regard, and the negative cotton bollworm responses were expressed most strongly in the combined Bt-high-CO₂ treatment. Chen *et al.* conclude the expected higher atmospheric CO₂ concentrations of the future will “either not change or only slightly enhance the efficacy of Bt technology against cotton bollworms.”

Chen *et al.* (2007) report growing the same two cotton cultivars under the same conditions from the time of planting on 10 May 2004 until the plants were harvested in October, after which egg masses of the cotton bollworms were reared in a growth chamber under ambient-CO₂ conditions. They fed three successive generations of bollworms either transgenic or non-transgenic cotton bolls from plants grown in either ambient or twice-ambient atmospheric CO₂ concentrations, assessing a number of physiological characteristics of the bollworms. Chen *et al.* report “both elevated CO₂ and transgenic Bt cotton increased larval lifespan,” but they decreased “pupal weight, survival rate, fecundity, frass output, relative and mean relative growth rates, and the efficiency of conversion of ingested and digested food.” They

write, “transgenic Bt cotton significantly decreased the population-trend index compared to non-transgenic cotton for the three successive bollworm generations, especially at elevated CO₂.”

The four researchers conclude the negative effects of elevated CO₂ on cotton bollworm physiology and population dynamics “may intensify through successive generations,” in agreement with the findings of Brooks and Whittaker (1998, 1999) and Wu *et al.* (2006). They conclude “both elevated CO₂ and transgenic Bt cotton are adverse environmental factors for cotton bollworm long-term population growth.”

Fu *et al.* (2008) note “heat stress is a major constraint to wheat production and negatively impacts grain quality, causing tremendous economic losses, and may become a more troublesome factor due to global warming.” They “introduced into wheat the maize gene coding for plastidal EF-Tu [protein synthesis elongation factor]” to assess “the expression of the transgene, and its effect on thermal aggregation of leaf proteins in transgenic plants,” and “the heat stability of photosynthetic membranes (thylakoids) and the rate of CO₂ fixation in young transgenic plants following exposure to heat stress.” They found “improved protection of leaf proteins against thermal aggregation, reduced damage to thylakoid membranes and enhanced photosynthetic capability following exposure to heat stress,” and these results “support the concept that EF-Tu ameliorates negative effects of heat stress by acting as a molecular chaperone.”

Fu *et al.* describe their work as “the first demonstration that a gene other than HSP [heat shock protein] gene can be used for improvement of heat tolerance,” noting it also indicates “the improvement is possible in a species that has a complex genome,” such as hexaploid wheat. They conclude their results “strongly suggest that heat tolerance of wheat, and possibly other crop plants, can be improved by modulating expression of plastidal EF-Tu and/or by selection of genotypes with increased endogenous levels of this protein.”

It appears specific genetic alterations to crop plants may improve their ability to withstand the assaults of insects pests, bear the consequences of possible future increases in seasonal maximum air temperatures, and take advantage of the positive effects of atmospheric CO₂ enrichment on various plant properties and processes. Elevated CO₂ reduces the severity of any negative effects that could arise from the escape of transplanted genes into the natural environment.

References

- Brooks, G.L. and Whittaker, J.B. 1998. Responses of multiple generations of *Gastrophysa viridula*, feeding on *Rumex obtusifolius*, to elevated CO₂. *Global Change Biology* 4: 63–75.
- Brooks, G.L. and Whittaker, J.B. 1999. Responses of three generations of a xylem-feeding insect, *Neophilaenus lineatus* (Homoptera), to elevated CO₂. *Global Change Biology* 5: 395–401.
- Chen, F., Wu, G., Ge, F., Parajulee, M.N., and Shrestha, R.B. 2005. Effects of elevated CO₂ and transgenic Bt cotton on plant chemistry, performance, and feeding of an insect herbivore, the cotton bollworm. *Entomologia Experimentalis et Applicata* 115: 341–350.
- Chen, F., Wu, G., Parajulee, M.N., and Ge, F. 2007. Long-term impacts of elevated carbon dioxide and transgenic Bt cotton on performance and feeding of three generations of cotton bollworm. *Entomologia Experimentalis et Applicata* 124: 27–35.
- Coviella, C.E., Morgan, D.J.W., and Trumble, J.T. 2000. Interactions of elevated CO₂ and nitrogen fertilization: Effects on production of *Bacillus thuringiensis* toxins in transgenic plants. *Environmental Entomology* 29: 781–787.
- Coviella, C.E. and Trumble, J.T. 2000. Effect of elevated atmospheric carbon dioxide on the use of foliar application of *Bacillus thuringiensis*. *BioControl* 45: 325–336.
- Fu, J., Momcilovic, I., Clemente, T.E., Nersesian, N., Trick, H.N., and Ristic, Z. 2008. Heterologous expression of a plastid EF-Tu reduces protein thermal aggregation and enhances CO₂ fixation in wheat (*Triticum aestivum*) following heat stress. *Plant Molecular Biology* 68: 277–288.
- Makino, A., Harada, M., Kaneko, K., Mae, T., Shimada, T., and Yamamoto, N. 2000. Whole-plant growth and N allocation in transgenic rice plants with decreased content of ribulose-1,5-bisphosphate carboxylase under different CO₂ partial pressures. *Australian Journal of Plant Physiology* 27: 1–12.
- Wu, G., Chen, J.F., and Ge, F. 2006. Response of multiple generations of cotton bollworm *Helicoverpa armigera* Hubner, feeding on spring wheat, to elevated CO₂. *Journal of Applied Entomology* 130: 2–9.

3.4.3 Woody Plants

Data obtained from open experimental systems in the field suggest herbivore damage to trees may decrease in a CO₂-enriched environment. However, if the opposite circumstances were to occur, other evidence

suggests air of higher CO₂ concentration would make trees more capable of surviving severe defoliation events. In addition, higher CO₂ concentrations tend to reduce fluctuating asymmetry in plant leaves, leading to more symmetrical leaves that are less susceptible to attacks by herbivores, because they are under less stress of both genetic and environmental origin than leaves growing in less-CO₂-enriched air.

3.4.3.1 Maple

- In contrast to the view herbivores will do more damage to trees, including maples, in CO₂-enriched air as a result of enhanced feeding on lower-quality foliage, data from open experimental systems suggest such damage may decrease in a CO₂-enriched environment. Evidence also suggests sugar maple may be more capable of surviving severe defoliation events that in the past have been implicated in the widespread decline of maples.

Insect pests have greatly affected trees in the past and likely will continue to do so in the future. The rise in the atmosphere's CO₂ concentration may affect this phenomenon. Here we review studies that have addressed this subject as it applies to three maple tree species.

Williams *et al.* (2003) studied *Acer rubrum* saplings beginning their fourth year of growth in open-top chambers maintained at four atmospheric CO₂/temperature combinations: ambient temperature, ambient CO₂; ambient temperature, elevated CO₂ (ambient + 300 ppm); elevated temperature (ambient + 3.5°C), ambient CO₂; and elevated temperature, elevated CO₂. They collected first instar gypsy moth larvae on various branches of the trees and observed their behavior. They report, "larvae feeding on CO₂-enriched foliage ate a comparably poorer food source than those feeding on ambient CO₂-grown plants, irrespective of temperature." Nevertheless, the "CO₂-induced reductions in foliage quality (e.g. nitrogen and water) were unrelated to insect mortality, development rate and pupal weight," and these and any other phytochemical changes that may have occurred "resulted in no negative effects on gypsy moth performance." They also write, "irrespective of CO₂ concentration, on average, male larvae pupated 7.5 days earlier and female larvae 8 days earlier at elevated temperature." They conclude the observed temperature-induced hastening of the insects'

development would likely expose the trees to less predation and parasitism risk.

Hamilton *et al.* (2004) note many single-species investigations suggest increases in atmospheric CO₂ will increase herbivory (Bezemer and Jones, 1998; Cannon, 1998; Coviella and Trumble, 1999; Hunter, 2001; Lincoln *et al.*, 1993; Whittaker, 1999). However, because there are so many feedbacks and complex interactions among the numerous components of real-world ecosystems, they warn one ought not put too much faith in these predictions until relevant real-world ecosystem-level experiments have been completed.

Hamilton *et al.* "measured the amount of leaf tissue damaged by insects and other herbivorous arthropods during two growing seasons in a deciduous forest understory continuously exposed to ambient (360 ppm) and elevated (560 ppm) CO₂ conditions." This forest, at the Duke Forest FACE facility near Chapel Hill, North Carolina (USA), was dominated by loblolly pine trees that accounted for fully 92% of the ecosystem's total woody biomass. It contained 48 species of other woody plants (trees, shrubs, and vines) that had naturally established themselves in the forest's understory. Hamilton *et al.* quantified the loss of foliage due to herbivory experienced by three deciduous tree species, one of which was *Acer rubrum*. They report, "we found that elevated CO₂ led to a trend toward reduced herbivory in [the] deciduous understory in a situation that included the full complement of naturally occurring plant and insect species." In 1999, for example, they determined "elevated CO₂ reduced overall herbivory by more than 40%," and in 2000 they say they observed "the same pattern and magnitude of reduction."

Hamilton *et al.* say they "found no evidence for significant changes in leaf nitrogen, C/N ratio, sugar, starch or total leaf phenolics in either year of [the] study." They note these findings agree with those of "another study performed at the Duke Forest FACE site that also found no effect of elevated CO₂ on the chemical composition of leaves of understory trees (Finzi and Schlesinger, 2002)."

Hamilton *et al.* conclude their landmark paper by emphasizing, "despite the large number of studies that predict increased herbivory, particularly from leaf chewers, under elevated CO₂, our study found a trend toward reduced herbivory two years in a row." In addition, they note their real-world results "agree with the only other large-scale field experiment that quantified herbivory for a community exposed to

elevated CO₂ (Stiling *et al.*, 2003)."

Consequently, and contrary to the predictions of increased destruction of natural ecosystems by insects and other herbivorous arthropods in a CO₂-enriched environment, just the opposite would appear to be the more likely outcome: greater plant productivity plus less foliage consumption by herbivores, "whether expressed on an absolute or a percent basis," as Hamilton *et al.* found in their study.

Knepp *et al.* (2005) quantified leaf damage caused by insects chewing on saplings of seven species (including *Acer rubrum*) in 2001, 2002, and 2003, and five additional species (including *Acer barbatum*) in 2001 and 2003, also at the Duke Forest FACE site. They found, "across the seven species measured in each of the three years, elevated CO₂ caused a reduction in the percentage of leaf area removed by chewing insects," such that "the percentage of leaf tissue damaged by insect herbivores was 3.8% per leaf under ambient CO₂ and 3.3% per leaf under elevated CO₂." The greatest effects occurred in 2001, when "across 12 species the average damage per leaf under ambient CO₂ was 3.1% compared with 1.7% for plants under elevated CO₂," which is "indicative of a 46% decrease in the total area and total mass of leaf tissue damaged by chewing insects in the elevated CO₂ plots."

Knepp *et al.* write, "given the consistent reduction in herbivory under high CO₂ across species in 2001, it appears that some universal feature of chemistry or structure that affected leaf suitability was altered by the treatment." They also note "forest herbivory may decrease under elevated CO₂ because of a decline in the abundance of chewing insects," citing Stiling *et al.* (2003) and noting "slower rates of development under elevated CO₂ prolongs the time that insect herbivores are susceptible to natural enemies, which may be abundant in open-top chambers and FACE experiments but absent from greenhouse experiments." In addition, they suggest "decreased foliar quality and increased per capita consumption under elevated CO₂ may increase exposure to toxins and insect mortality," also noting "CO₂-induced changes in host plant quality directly decrease insect fecundity," citing Coviella and Trumble (1999) and Awmack and Leather (2002).

Knepp *et al.* conclude, "in contrast to the view that herbivore damage will increase under elevated CO₂ as a result of compensatory feeding on lower quality foliage, our results and those of Stiling *et al.* (2003) and Hamilton *et al.* (2004) in open experimental systems suggest that damage to trees

may decrease."

Kruger *et al.* (1998) explored the consequences of an *increase* in herbivore-induced damage in a future CO₂-enriched world, although that is unlikely to occur. They grew well-watered and well-fertilized one-year-old *Acer saccharum* saplings in glasshouses maintained at atmospheric CO₂ concentrations of either 356 or 645 ppm for 70 days, to determine the effects of elevated CO₂ on photosynthesis and growth. On the 49th day of differential CO₂ exposure, they removed 50% of the saplings' leaf area from half of the trees in order to study the impact of concomitant simulated herbivory. They found the 70-day CO₂ enrichment treatment increased the total dry weight of the non-defoliated seedlings by about 10%. When the trees were stressed by simulated herbivory, the CO₂-enriched maples produced 28% more dry weight over the final phase of the study than the maples in the ambient-air treatment did. Kruger *et al.* conclude that in a high-CO₂ environment "sugar maple might be more capable of tolerating severe defoliation events which in the past have been implicated in widespread maple declines."

These studies indicate maple trees—and probably many, if not most, other trees—may fare much better against the periodic assaults of leaf-damaging herbivores as the air's CO₂ content continues to rise.

References

- Awmack, C.S. and Leather, S.R. 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* **47**: 817–844.
- Bezemer, T.M. and Jones, T.H. 1998. Plant-insect herbivore interactions in elevated atmospheric CO₂: quantitative analyses and guild effects. *Oikos* **82**: 212–222.
- Cannon, R.J. 1998. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology* **4**: 785–796.
- Coviella, C.E. and Trumble, J.T. 1999. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Conservation Biology* **13**: 700–712.
- Finzi, A.C. and Schlesinger, W.H. 2002. Species control variation in litter decomposition in a pine forest exposed to elevated CO₂. *Global Change Biology* **8**: 1217–1229.
- Hamilton, J.G., Zangerl, A.R., Berenbaum, M.R., Pippen, J., Aldea, M., and DeLucia, E.H. 2004. Insect herbivory in an intact forest understory under experimental CO₂ enrichment. *Oecologia* **138**: 10.1007/s00442-003-1463-5.

Hunter, M.D. 2001. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Agricultural and Forest Entomology* 3: 153–159.

Knepp, R.G., Hamilton, J.G., Mohan, J.E., Zangerl, A.R., Berenbaum, M.R., and DeLucia, E.H. 2005. Elevated CO₂ reduces leaf damage by insect herbivores in a forest community. *New Phytologist* 167: 207–218.

Kruger, E.L., Volin, J.C., and Lindroth, R.L. 1998. Influences of atmospheric CO₂ enrichment on the responses of sugar maple and trembling aspen to defoliation. *New Phytologist* 140: 85–94.

Lincoln, D.E., Fajer, E.D., and Johnson, R.H. 1993. Plant-insect herbivore interactions in elevated CO₂ environments. *Trends in Ecology and Evolution* 8: 64–68.

Stiling, P., Moon, D.C., Hunter, M.D., Colson, J., Rossi, A.M., Hymus, G.J., and Drake, B.G. 2003. Elevated CO₂ lowers relative and absolute herbivore density across all species of a scrub-oak forest. *Oecologia* 134: 82–87.

Whittaker, J.B. 1999. Impacts and responses at population level of herbivorous insects to elevated CO₂. *European Journal of Entomology* 96: 149–156.

Williams, R.S., Lincoln, D.E., and Norby, R.J. 2003. Development of gypsy moth larvae feeding on red maple saplings at elevated CO₂ and temperature. *Oecologia* 137: 114–122.

3.4.3.2 Oak

- Research suggests various insect pests will do decreasing amounts of damage to oak trees as the air's CO₂ concentration rises.

In order to determine whether the ongoing rise in the air's CO₂ content will exacerbate or ameliorate herbivore damage to oak trees, Dury *et al.* (1998) grew four-year-old *Quercus robur* seedlings in pots in greenhouses maintained at ambient and twice-ambient atmospheric CO₂ concentrations in combination with ambient and elevated (ambient plus 3°C) air temperatures for approximately one year, to study the interactive effects of elevated CO₂ and temperature on leaf nutritional quality. The researchers determined the elevated temperature treatment significantly reduced leaf palatability, and leaf toughness increased as a consequence of temperature-induced increases in condensed tannin concentrations. In addition, the imposition of higher temperatures significantly reduced leaf nitrogen content, as did elevated CO₂.

In one of the first attempts to move outside the

laboratory/greenhouse and study the effects of atmospheric CO₂ enrichment on trophic food webs in a natural ecosystem, Stiling *et al.* (1999) enclosed portions of a native scrub-oak community in Florida (USA) in 3.6-m-diameter open-top chambers and fumigated them with air having CO₂ concentrations of either 350 or 700 ppm for approximately one year, to see whether elevated CO₂ would impact leaf miner densities, feeding rates, and mortality in this nutrient-poor ecosystem.

They discovered total leaf miner densities were 38% less on the foliage of trees growing in CO₂-enriched air than on that of trees growing in ambient air. Atmospheric CO₂ enrichment consistently reduced the absolute numbers of the study's six leaf miner species. At the same time, the elevated CO₂ treatment increased the leaf area consumed by the less-abundant herbivore miners by approximately 40% relative to the areas mined by the more-abundant herbivores present on the foliage exposed to ambient air. Despite this increase in feeding, the leaf miners in the CO₂-enriched chambers experienced significantly greater mortality than those in the ambient-air chambers. And although CO₂-induced reductions in leaf nitrogen content played a minor role in this phenomenon, the greatest factor contributing to increased herbivore mortality was a four-fold increase in parasitization by various wasps, which could more readily detect the more-exposed leaf miners on the CO₂-enriched foliage.

In another study conducted on five scrub-oak forest species at the same experimental facility, Stiling *et al.* (2003) investigated the effects of an approximate doubling of the air's CO₂ concentration on a number of characteristics of several insect herbivores. As before, they report, the "relative levels of damage by the two most common herbivore guilds, leaf-mining moths and leaf-chewers (primarily larval lepidopterans and grasshoppers), were significantly lower in elevated CO₂ than in ambient CO₂, for all five plant species," and "the response to elevated CO₂ was the same across all plant species." In addition, "more host-plant induced mortality was found for all miners on all plants in elevated CO₂ than in ambient CO₂." In addition to the relative densities of insect herbivores being reduced in the CO₂-enriched chambers, and "even though there were more leaves of most plant species in the elevated CO₂ chambers," the total densities of leaf miners in the high-CO₂ chambers were also lower for all plant species. Consequently, it would appear a high-CO₂ environment may improve plants' ability to better

withstand various insect pests. Stiling *et al.* also note “reductions in herbivore loads in elevated CO₂ could boost plant growth beyond what might be expected based on pure plant responses to elevated CO₂.”

Rossi *et al.* (2004) studied the same ecosystem, which was dominated by two species of scrub oak (*Quercus geminata* and *Q. myrtifolia*) that accounted for more than 90% of the ecosystem’s biomass. They focused on the abundance of a guild of lepidopteran leafminers that attack the leaves of *Q. myrtifolia*, as well as on various leaf chewers, following 100 marked leaves in each of 16 open-top chambers (half exposed to ambient air and half exposed to air containing an extra 350 ppm of CO₂) for nine months, after which “differences in mean percent of leaves with leafminers and chewed leaves on trees from ambient and elevated chambers were assessed using paired *t*-tests.”

The researchers write, “both the abundance of the guild of leafmining lepidopterans and damage caused by leaf chewing insects attacking myrtle oak were depressed in elevated CO₂.” Leafminer abundance was 44% lower ($P = 0.096$) in the CO₂-enriched chambers compared to the ambient-air chambers, and the abundance of leaves suffering chewing damage was 37% lower ($P = 0.072$) in the CO₂-enriched air. Myrtle oak trees growing in their natural habitat likely will suffer far less damage from both leaf miners and leaf chewers as the air’s CO₂ concentration rises in the years ahead.

Working in the same ecosystem, where atmospheric enrichment with an extra 350 ppm of CO₂ was begun in May 1996, Hall *et al.* (2005b) studied the four species that dominate the community and are present in every experimental chamber: the three oaks (*Quercus myrtifolia*, *Q. chapmanii*, and *Q. geminata*) plus the nitrogen-fixing legume *Galactia elliottii*. At three-month intervals from May 2001 to May 2003, they removed undamaged leaves from each of these species in all chambers and analyzed them for various chemical constituents, and they scored 200 randomly selected leaves of each species in each chamber for the presence of six types of herbivore damage.

Throughout the study they found no significant differences between the CO₂-enriched and ambient-treatment leaves of any single species in terms of condensed tannins, hydrolyzable tannins, total phenolics, or lignin. However, in all four species together there were always greater concentrations of four important leaf constituents in the CO₂-enriched leaves, with across-species mean increases of 6.8% for condensed tannins, 6.1% for hydrolyzable tannins,

5.1% for total phenolics, and 4.3% for lignin. In addition, the researchers found large and often significant CO₂-induced decreases in all leaf damage categories among all species: chewing (-48%, $P < 0.001$), mines (-37%, $P = 0.001$), eye spot gall (-45%, $P < 0.001$), leaf tier (-52%, $P = 0.012$), leaf mite (-23%, $P = 0.477$), and leaf gall (-16%, $P = 0.480$). Hall *et al.* conclude the changes in leaf chemical constituents and herbivore damage “suggest that damage to plants may decline as atmospheric CO₂ levels continue to rise.”

In one final study of the Florida scrub-oak ecosystem, Hall *et al.* (2005a) examined the effects of an extra 350 ppm of CO₂ on litter quality, herbivore activity, and their interactions. Over the three years of this experiment (2000, 2001, 2002), they determined “changes in litter chemistry from year to year were far larger than the effects of CO₂ or insect damage, suggesting that these may have only minor effects on litter decomposition.” The one exception to this finding, they write, was “condensed tannin concentrations[, which] increased under elevated CO₂ regardless of species, herbivore damage, or growing season,” rising by 11% in 2000, 18% in 2001, and 41% in 2002 as a result of atmospheric CO₂ enrichment, as best as can be determined from their bar graphs.

The five researchers also report “lepidopteran larvae can exhibit slower growth rates when feeding on elevated CO₂ plants (Fajer *et al.*, 1991) and become more susceptible to pathogens, parasitoids, and predators (Lindroth, 1996; Stiling *et al.*, 1999),” noting further that at their field site, “which hosts the longest continuous study of the effects of elevated CO₂ on insects, herbivore populations decline[d] markedly under elevated CO₂ (Stiling *et al.*, 1999, 2002, 2003; Hall *et al.*, 2005b).”

The evidence accumulated to date with respect to herbivory in oak trees indicates various insect pests will do decreasing amounts of damage to such trees as the air’s CO₂ concentration climbs ever-higher.

References

- Dury, S.J., Good, J.E.G., Perrins, C.M., Buse, A., and Kaye, T. 1998. The effects of increasing CO₂ and temperature on oak leaf palatability and the implications for herbivorous insects. *Global Change Biology* 4: 55–61.
- Fajer, E.D., Bowers, M.D., and Bazzaz, F.A. 1991. The effects of enriched CO₂ atmospheres on the buckeye butterfly, *Junonia coenia*. *Ecology* 72: 751–754.

Hall, M.C., Stiling, P., Hungate, B.A., Drake, B.G., and Hunter, M.D. 2005a. Effects of elevated CO₂ and herbivore damage on litter quality in a scrub oak ecosystem. *Journal of Chemical Ecology* **31**: 2343–2356.

Hall, M.C., Stiling, P., Moon, D.C., Drake, B.G., and Hunter, M.D. 2005b. Effects of elevated CO₂ on foliar quality and herbivore damage in a scrub oak ecosystem. *Journal of Chemical Ecology* **31**: 267–285.

Lindroth, R.L. 1996. CO₂-mediated changes in tree chemistry and tree-Lepidoptera interactions. In: Koch, G.W. and Mooney, H.A. (Eds.) *Carbon Dioxide and Terrestrial Ecosystems*. Academic Press, San Diego, California, USA, pp. 105–120.

Rossi, A.M., Stiling, P., Moon, D.C., Cattell, M.V., and Drake, B.G. 2004. Induced defensive response of myrtle oak to foliar insect herbivory in ambient and elevated CO₂. *Journal of Chemical Ecology* **30**: 1143–1152.

Stiling, P., Cattell, M., Moon, D.C., Rossi, A., Hungate, B.A., Hymus, G., and Drake, B.G. 2002. Elevated atmospheric CO₂ lowers herbivore abundance, but increases leaf abscission rates. *Global Change Biology* **8**: 658–667.

Stiling, P., Moon, D.C., Hunter, M.D., Colson, J., Rossi, A.M., Hymus, G.J., and Drake, B.G. 2003. Elevated CO₂ lowers relative and absolute herbivore density across all species of a scrub-oak forest. *Oecologia* **134**: 82–87.

Stiling, P., Rossi, A.M., Hungate, B., Dijkstra, P., Hinkle, C.R., Knot III, W.M., and Drake, B. 1999. Decreased leaf-miner abundance in elevated CO₂: Reduced leaf quality and increased parasitoid attack. *Ecological Applications* **9**: 240–244.

3.4.3.3 Miscellaneous

- Numerous studies of numerous insect pests of numerous species of trees indicate atmospheric CO₂ enrichment may contribute to reduced herbivory in forest ecosystems.

Insect pests have had enormous impacts on Earth's trees and shrubs in the past. Will the anticipated increase in the atmosphere's CO₂ concentration exacerbate or ameliorate their effects? This section describes and discusses the results of several studies that address this question.

Docherty *et al.* (1997) grew beech and sycamore saplings in glasshouses maintained at atmospheric CO₂ concentrations of 350 and 600 ppm and allowed groups of three sap-feeding aphid species and two sap-feeding leafhopper species to feed on them.

Overall, they report elevated CO₂ had few significant effects on the performance of these insects, although there was a non-significant tendency for elevated CO₂ to reduce the individual weights and population sizes of the aphids.

Gleadow *et al.* (1998) grew eucalyptus seedlings in glasshouses maintained at 400 and 800 ppm CO₂ for six months, observing biomass increases of 98% and 134% in high and low nitrogen treatments, respectively. They also studied a sugar-based compound called prunasin, which produces cyanide in response to tissue damage caused by foraging herbivores. Although elevated CO₂ caused no significant change in leaf prunasin content, the proportion of nitrogen allocated to prunasin increased by approximately 20% in the CO₂-enriched saplings, suggesting a potential for increased prunasin had the eucalyptus saplings been under attack by herbivores.

In a study of simulated herbivory, Kruger *et al.* (1998) grew seedlings of one-year-old maple (*Acer saccharum*) and two-year-old aspen (*Populus tremuloides*) trees in glasshouses with atmospheric CO₂ concentrations of 356 and 645 ppm for 70 days. At the 49-day point of the experiment, half of the leaf area on half of the trees in each treatment was removed, and this defoliation caused the final dry weights of both species growing in ambient air to decline. In the CO₂-enriched glasshouse, on the other hand, the defoliated maple trees ended up weighing just as much as the non-defoliated maple trees. The defoliated aspen trees ended up weighing a little less, but not significantly less, than their non-defoliated counterparts. Thus, atmospheric CO₂ enrichment improved both species' ability to recover from the debilitating effect of leaf removal, suggesting a future world of higher atmospheric CO₂ concentration may make these trees better able to deal with physical damage inflicted on them by herbivores.

Lovelock *et al.* (1999) grew seedlings of the tropical tree *Copaifera aromatica* for 50 days in pots placed in open-top chambers maintained at atmospheric CO₂ concentrations of 390 and 860 ppm. At the 14-day point of the experiment, half of the seedlings in each treatment had about 40% of their total leaf area removed. None of the defoliated trees of either CO₂ treatment fully recovered from this manipulation, but at the end of the experiment the total plant biomass of the defoliated trees in the CO₂-enriched treatment was 15% greater than that of the defoliated trees in the ambient-CO₂ treatment.

Hattenschwiler and Schafellner (1999) grew seven-year-old spruce (*Picea abies*) trees at

atmospheric CO₂ concentrations of 280, 420, and 560 ppm and various nitrogen deposition treatments for three years, allowing nun moth larvae to feed on current-year needles for 12 days. Larvae placed on the CO₂-enriched foliage consumed less needle biomass than those placed on the ambient-grown foliage, regardless of nitrogen treatment. The larvae feeding on needles produced by the CO₂-enriched trees attained an average final biomass only two-thirds of that attained by the larvae that fed on needles produced at 280 ppm CO₂. The nun moth is a powerful defoliator that resides in most parts of Europe and East Asia between 40 and 60°N latitude; the results of this study suggest the rise in the air's CO₂ content likely will lead to significant reductions in damage to spruce and other coniferous trees by this insect pest.

Parsons *et al.* (2003) grew two-year-old saplings of paper birch (*Betula papyrifera* Marsh.) and three-year-old saplings of sugar maple (*Acer saccharum* Marsh.) in well-watered and -fertilized 16-L pots from early May until late August in glasshouse rooms maintained at either 400 or 700 ppm CO₂. The whole-plant biomass of paper birch was increased by 55% in the CO₂-enriched rooms, and the biomass of sugar maple was increased by 30%. Condensed tannins were unaltered in sugar maple but increased by 27% in paper birch in the CO₂-enriched treatment. The three researchers note, "the higher condensed tannin concentrations present in the birch fine roots may offer these tissues greater protection against soil-borne pathogens and herbivores." CO₂-induced increases in fine root concentrations of total phenolics and condensed tannins also have been observed in warm temperate conifers by King *et al.* (1997), Entry *et al.* (1998), Gebauer *et al.* (1998), and Runion *et al.* (1999), as well as in cotton by Booker (2000).

Holton *et al.* (2003) reared parasitized and non-parasitized forest tent caterpillars (*Malacosoma disstria*) on two quaking aspen (*Populus tremuloides*) genotypes (216, which is O₃-tolerant, and 259, which is O₃-sensitive) alone and in combination at the Aspen FACE site in northern Wisconsin (USA), in plots exposed to ambient air; ambient air + 200 ppm extra CO₂; ambient air + 50% extra ozone; and ambient air + 200 ppm extra CO₂ and 50% extra O₃. The researchers found "elevated CO₂ had little effect on both primary and secondary metabolites of aspen" and "had few biologically significant effects on forest tent caterpillar performance." Elevated O₃ altered foliar composition much more than did elevated CO₂, and it improved tent caterpillar

performance under ambient CO₂ conditions, but not in CO₂-enriched air. The extra CO₂ of this study totally thwarted the positive impact of the extra O₃ on caterpillar performance, thus possibly eliminating a major negative consequence for the trees.

Kuokkanen *et al.* (2003) grew two-year-old birch (*Betula pendula* Roth) seedlings in ambient air of 350 ppm CO₂ or air enriched to a CO₂ concentration of 700 ppm under conditions of either ambient temperature or ambient temperature plus 3°C for one full growing season in the field in closed-top chambers at the Mekrijärvi Research Station of the University of Joensuu in eastern Finland. During the middle of the summer, when carbon-based secondary compounds of birch leaves are fairly stable, they picked several leaves from each tree and determined their condensed tannin concentrations, along with the concentrations of other physiologically important substances.

The concentration of total phenolics, condensed tannins, and their derivatives significantly increased in the birch leaves produced in the CO₂-enriched air, as also was observed by Lavola and Julkunen-Titto (1994), Williams *et al.* (1994), Kinney *et al.* (1997), Bezemer and Jones (1998), and Kuokkanen *et al.* (2001). The extra 350 ppm of CO₂ nearly tripled condensed tannin concentrations in the ambient-temperature air, and it increased their concentrations in the elevated-temperature air by a factor greater than 3.5. The presence of condensed tannins in leaves tends to greatly reduce methane emissions from ruminants that feed on them, which in turn reduces the supposed global warming impact.

Mattson *et al.* (2004) write, "although there have been many studies on the effects of elevated CO₂ on the interaction between plants and their insect herbivores (see Bezemer and Jones, 1998; Hunter, 2001), comparable studies on mammalian herbivores are lacking altogether, even though mammals play important roles in dynamics of many ecosystems (McNaughton and Sabuni, 1988; Pastor and Naiman, 1992)." Mattson *et al.* grew one-year-old seedlings of silver birch (*Betula pendula*) in closed-top chambers for one summer and autumn in pots containing an unfertilized commercial peat maintained at three different soil nitrogen (N) levels (low = 0 kg N ha⁻¹, medium = 150 kg N ha⁻¹, high = 500 kg N ha⁻¹) and two temperature (T) levels (ambient and ambient + 3°C) in air of either 362 or 700 ppm CO₂ concentration. They carried out feeding trials with caged Eurasian hares (*Lepus timidus*) and performed chemical analyses of the tops of the seedlings and the

basal parts of their stems.

In a second experiment, they grew paper birch (*Betula papyrifera*) from seed for two 140-day growing seasons in well-watered and well-fertilized pots placed in FACE rings maintained at atmospheric CO₂ concentrations of either 362 or 562 ppm, after which (in an unplanned aspect of the study) North American eastern cottontail rabbits (*Sylvilagus floridanus*) fed *ad libitum*, consuming bark tissue down to the wood and scoring it, on the basal third of the seedlings. These tissues were tested for the presence of various herbivore-detering chemical constituents.

“As expected,” the six scientists write, “elevated CO₂ substantially increased the above-ground woody biomass growth of both paper birch (63%) and silver birch (21%).” In addition, noting “numerous studies have shown that elevated atmospheric CO₂ often, but not always, elicits increases in carbon partitioning to carbon-based secondary plant compounds,” which often act as deterrents to herbivory, they say their findings “confirm this general pattern in silver and paper birch.” Finally, they report high CO₂ reduced hare feeding on silver birch shoots by as much as 48%, and it reduced rabbit feeding on paper birch stems by about 51%. Neither temperature nor severe early season defoliation (another treatment) affected tree resistance against these mammalian herbivores.

Calling the anti-herbivory effect of elevated CO₂ “remarkably strong,” and noting rabbits “overwhelmingly preferred ambient CO₂ plants,” Mattson *et al.* say their data “clearly suggest that the defensive biochemistry of paper birch twigs as well as the main stem were [positively] altered as the result of elevated CO₂.”

Noting the “detrimental effects of ozone on plants are well known,” and “carbon dioxide generally affects trees in opposite ways to ozone,” Valcama *et al.* (2007) conducted a literature review they describe as “the first quantitative analysis of the interactive effects of elevated O₃ and elevated CO₂ on tree chemistry and herbivore performance,” based on the results of “63 studies conducted on 22 tree species and 10 insect herbivore species and published between 1990 and 2005.”

With respect to ways elevated O₃ may benefit insect herbivores that tend to damage trees, Valkama *et al.* say they determined “elevated O₃ significantly shortened development time of insect herbivores [when they are exposed and vulnerable to attack by various enemies] and increased their pupal mass in the overall dataset.” In addition, they report the

“relative growth rate of chewers was significantly increased by 3.5% under elevated O₃.” However, “these effects were counteracted by elevated CO₂,” such that “elevated O₃ in combination with CO₂ had no effect on herbivore performance”—except when elevated CO₂ was added to the O₃-enriched air, it not only counteracted the O₃-induced increase in pupal biomass, it actually reduced it by 7% below ambient air.

Valkama *et al.*’s analysis of much of the pertinent experimental data obtained prior to 2006 suggests in the interactions between insect herbivores and trees, the rise in the air’s CO₂ content likely plays an important role in negating, and in some cases even more than negating, the damage otherwise capable of being done to Earth’s forests by insect pests. Subsequent research has continued to demonstrate these effects.

Huttunen *et al.* (2007) grew silver birch (*Betula pendula* Roth) seedlings in pots filled with peat at three levels of nitrogen (N) fertility—no N, moderate N (130 kg N ha⁻¹) and high N (270 kg N ha⁻¹)—in climate-controlled closed-top chambers from mid-June to October 2002 at the Mekrijarvi Research Station of the University of Joensuu, Finland. The chambers were maintained at atmospheric CO₂ concentrations of either 360 or 720 ppm and at either ambient air temperatures or elevated air temperatures 2°C above ambient from June to August and 4°C above ambient for the remainder of the growing season. The researchers mimicked larval and adult leaf-feeding patterns exhibited during real-world defoliation by manually damaging the leaves of the seedlings by tearing off the apical halves of either 25% or 50% of all leaves greater than 1 cm in length on 1 July (mid-season) and again on 29 July (late-season). They determined total plant shoot and root biomass once the plants had gone dormant in October.

As best as can be determined from the six scientists’ bar graphs of their results, and averaged over all three defoliation treatments, the elevated CO₂ treatment increased the biomass of the seedlings in the moderate and high-N fertility treatments much more than it increased the biomass of the seedlings in the no-N fertility treatment (29 and 30%, respectively, vs. 13%). The same was also true of the combined elevated CO₂ and elevated temperature treatment, where the corresponding treatment-induced biomass increases were 34 and 36% vs. 20%, suggesting the heightened temperatures tended to augment the beneficial effects of the elevated CO₂ treatment, with the greatest amplification being manifest in the no-N

fertility treatment (54% vs. 17 and 20% in the moderate- and high-N treatments, respectively).

Averaged over all three N fertility treatments, the effect of the elevated CO₂ was to increase the plant biomass of the undefoliated seedlings by approximately 25%, the 25%-defoliated seedlings by 24%, and the 50%-defoliated seedlings by 22%. The effect of the combined elevated CO₂ and elevated temperature treatment was to increase the plant biomass of the same three categories of seedlings by approximately 31%, 30%, and 29%, respectively. Huttunen *et al.* conclude, “climatic change”—which they specifically defined to mean elevated atmospheric temperature and CO₂—“will have a positive impact on the compensatory ability of defoliated silver birch seedlings.”

In another study conducted with the same trees under the same conditions, Huttunen *et al.* (2008) studied leaf palatability to adult blue alder leaf beetles (*Agelastica alni*). They periodically measured a host of seedling parameters related to plant chemical and morphological defense properties. The researchers’ findings were varied and complex, but their most basic finding was that the blue alder leaf beetle’s “total leaf consumption was higher under the ambient climatic conditions than under elevated temperature, elevated CO₂, or the combination of elevated temperature and CO₂.”

Nabity *et al.* (2012) write, “arthropod herbivory can reduce plant productivity by removing photosynthetic leaf area,” noting Zangerl *et al.* (2002), Aldea *et al.* (2005, 2006), and Patankar *et al.* (2011) indicate, in some cases, “damage to leaf surfaces causes a reduction in the quantum efficiency of photosystem II fluorescence, which is highly correlated with the rate of carbon assimilation.” Working at the Aspen FACE site in north-central Wisconsin (USA), the four researchers studied how different types of herbivore damage (leaf-chewing, gall-forming, and leaf-folding) altered component processes of photosynthesis under both ambient and elevated (ambient + 200 ppm) atmospheric CO₂ concentrations in aspen (*Populus tremuloides*, genotype 216) trees, as well as how the damage caused by leaf-chewing insects impacted photosynthesis in birch (*Betula papyrifera*) trees.

The four researchers found “growth under elevated CO₂ reduced the distance that herbivore-induced reductions in photosynthesis propagated away from the point of damage in aspen and birch,” leading them to conclude, “at least for these species,” elevated CO₂ “may reduce the impact of herbivory on

photosynthesis,” a very positive development.

Hamilton *et al.* (2012) noted “the response of complex plant and animal communities to global change is highly variable (Tylianakis *et al.*, 2008),” but “recent studies have documented that loss of foliage to arthropod herbivores decreases under elevated CO₂ in woody communities (Hamilton *et al.*, 2004; Knepp *et al.*, 2005; Stiling and Cornelissen, 2007).” They also note the fitness and in some cases population size of herbivorous insects may decline in communities exposed to elevated CO₂ (Hillstrom and Lindroth, 2008; Hillstrom *et al.*, 2010),” although the “effects of elevated CO₂ on naturally-occurring arthropod assemblages have not yet been widely characterized.”

Working at the Duke Forest FACE facility in the Piedmont region of North Carolina (USA)—where three 30-meter-diameter plots of an expansive stand of loblolly pine had their atmospheric CO₂ concentrations boosted by about 200 ppm, and where three other such plots were maintained at the normal ambient CO₂ concentration—Hamilton *et al.* counted the numbers of arthropods found in each of the six plots every two weeks throughout June and July of 2005, assigning them to different feeding guilds. In addition, they analyzed stable isotope data for spiders collected in the ambient and elevated CO₂ plots in order to determine the extent herbivorous prey species moved into and out of the elevated CO₂ plots.

The seven U.S. scientists write their isotopic data “gave no indication that the treatment plots represented a ‘boundary’ to the movement of insects.” In addition, they determined there was no detectable effect of elevated CO₂ on the total number of individual arthropods in the two sets of treatment plots. However, they write, “there was an increase in the numbers of individuals collected in primarily predaceous orders (Araneae and Hymenoptera; from 60% to more than 150%) under elevated CO₂ and a decrease in the numbers in primarily herbivorous orders (Lepidoptera and Coleoptera; from -30 to -45%).” Hamilton *et al.* conclude “decreases in herbivorous arthropods and increases in predaceous arthropods may contribute to reduced herbivory under elevated CO₂ in forest systems.”

References

Aldea, M., Hamilton, J.G., Resti, J.P., Zangerl, A.R., Berenbaum, M.R., and DeLucia, E.H. 2005. Indirect effects of insect herbivory on leaf gas exchange in soybean. *Plant, Cell and Environment* **28**: 402–411.

- Aldea, M., Hamilton, J.G., Resti, J.P., Zangerl, A.R., Berenbaum, M.R., Frank, T.D., and DeLucia, E.H. 2006. Comparison of photosynthetic damage from arthropod herbivory and pathogen infection in understory hardwood samplings. *Oecologia* **149**: 221–232.
- Bezemer, T.M. and Jones, T.H. 1998. Plant-insect herbivore interactions in elevated atmospheric CO₂, quantitative analyses and guild effects. *Oikos* **82**: 212–222.
- Booker, F.L. 2000. Influence of carbon dioxide enrichment, ozone and nitrogen fertilization on cotton (*Gossypium hirsutum* L.) leaf and root composition. *Plant, Cell and Environment* **23**: 573–583.
- Docherty, M., Wade, F.A., Hurst, D.K., Whittaker, J.B., and Lea, P.J. 1997. Responses of tree sap-feeding herbivores to elevated CO₂. *Global Change Biology* **3**: 51–59.
- Entry, J.A., Runion, G.B., Prior, S.A., Mitchell, R.J., and Rogers, H.H. 1998. Influence of CO₂ enrichment and nitrogen fertilization on tissue chemistry and carbon allocation in longleaf pine seedlings. *Plant and Soil* **200**: 3–11.
- Gebauer, R.L., Strain, B.R., and Reynolds, J.F. 1998. The effect of elevated CO₂ and N availability on tissue concentrations and whole plant pools of carbon-based secondary compounds in loblolly pine. *Oecologia* **113**: 29–36.
- Gleadow, R.M., Foley, W.J., and Woodrow, I.E. 1998. Enhanced CO₂ alters the relationship between photosynthesis and defense in cyanogenic *Eucalyptus cladocalyx* F. Muell. *Plant, Cell and Environment* **21**: 12–22.
- Hamilton, J.G., Zangerl, A.R., Berenbaum, M.R., Pippen, J.S., Aldea, M., and DeLucia, E.H. 2004. Insect herbivory in an intact forest understory under experimental CO₂ enrichment. *Oecologia* **138**: 566–573.
- Hamilton, J., Zangerl, A.R., Berenbaum, M.R., Sparks, J.P., Elich, L., Eisenstein, A., and DeLucia, E.H. 2012. Elevated atmospheric CO₂ alters the arthropod community in a forest understory. *Acta Oecologica* **43**: 80–85.
- Hattenschwiler, S. and Schafellner, C. 1999. Opposing effects of elevated CO₂ and N deposition on *Lymantria monacha* larvae feeding on spruce trees. *Oecologia* **118**: 210–217.
- Hillstrom, M.L. and Lindroth, R.L. 2008. Elevated atmospheric carbon dioxide and ozone alter forest insect abundance and community composition. *Insect Conservation and Diversity* **1**: 233–241.
- Hillstrom, M.L., Vigue, L.M., Coyle, D.R., Raffa, K.F., and Lindroth, R.L. 2010. Performance of the invasive weevil *Polydrusus sericeus* is influenced by atmospheric CO₂ and host species. *Agricultural and Forest Entomology* **12**: 285–292.
- Holton, M.K., Lindroth, R.L., and Nordheim, E.V. 2003. Foliar quality influences tree-herbivore-parasitoid interactions: effects of elevated CO₂, O₃, and plant genotype. *Oecologia* **137**: 233–244.
- Hunter, M.D. 2001. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Agricultural and Forest Entomology* **3**: 153–159.
- Huttunen, L., Niemela, P., Julkunen-Titto, R., Heiska, S., Tegelberg, R., Rousi, M., and Kellomaki, S. 2008. Does defoliation induce chemical and morphological defenses in the leaves of silver birch seedlings under changing climate? *Chemoecology* **18**: 85–98.
- Huttunen, L., Niemela, P., Peltola, H., Heiska, S., Rousi, M., and Kellomaki, S. 2007. Is a defoliated silver birch seedling able to over-compensate the growth under changing climate? *Environmental and Experimental Botany* **60**: 227–238.
- King, J.S., Thomas, R.B., and Strain, B.R. 1997. Morphology and tissue quality of seedling root systems of *Pinus taeda* and *Pinus ponderosa* as affected by varying CO₂, temperature, and nitrogen. *Plant and Soil* **195**: 107–119.
- Kinney, K.K., Lindroth, R.L., Jung, S.M., and Nordheim, E.V. 1997. Effects of CO₂ and NO₃ availability on deciduous trees, phytochemistry and insect performance. *Ecology* **78**: 215–230.
- Knepp, R.G., Hamilton, J.G., Mohan, J.E., Zangerl, A.R., Berenbaum, M.R., and DeLucia, E.H. 2005. Elevated CO₂ reduces leaf damage by insect herbivores in a forest community. *New Phytologist* **167**: 207–218.
- Kruger, E.L., Volin, J.C., and Lindroth, R.L. 1998. Influences of atmospheric CO₂ enrichment on the responses of sugar maple and trembling aspen to defoliation. *New Phytologist* **140**: 85–94.
- Kuokkanen, K., Julkunen-Titto, R., Keinänen, M., Niemela, P., and Tahvanainen, J. 2001. The effect of elevated CO₂ and temperature on the secondary chemistry of *Betula pendula* seedlings. *Trees* **15**: 378–384.
- Kuokkanen, K., Yan, S., and Niemela, P. 2003. Effects of elevated CO₂ and temperature on the leaf chemistry of birch *Betula pendula* (Roth) and the feeding behavior of the weevil *Phyllobius maculicornis*. *Agricultural and Forest Entomology* **5**: 209–217.
- Lavola, A. and Julkunen-Titto, R. 1994. The effect of elevated carbon dioxide and fertilization on primary and secondary metabolites in birch, *Betula pendula* (Roth). *Oecologia* **99**: 315–321.

Lovelock, C.E., Posada, J., and Winter, K. 1999. Effects of elevated CO₂ and defoliation on compensatory growth and photosynthesis of seedlings in a tropical tree, *Copaifera aromatica*. *Biotropica* **31**: 279–287.

Mattson, W.J., Kuokkanen, K., Niemela, P., Julkunen-Tiitto, R., Kellomaki, S., and Tahvanainen, J. 2004. Elevated CO₂ alters birch resistance to Lagomorpha herbivores. *Global Change Biology* **10**: 1402–1413.

McNaughton, S.J. and Sabuni G.A. 1988. Large African mammals as regulators of vegetation structure. In: Werger, M.J.A., Van der Aart, P.J.M., During, H.J., and Verhoeven, J.T.A. (Eds.) *Plant Form and Vegetation Structure*. SPB Academic Publishing, The Hague, The Netherlands, pp. 339–354.

Nabity, P.D., Hillstrom, M.L., Lindroth, R.L., and DeLucia, E.H. 2012. Elevated CO₂ interacts with herbivory to alter chlorophyll fluorescence and leaf temperature in *Betula papyrifera* and *Populus tremuloides*. *Oecologia* **169**: 905–913.

Parsons, W.F.J., Kopper, B.J., and Lindroth, R.L. 2003. Altered growth and fine root chemistry of *Betula papyrifera* and *Acer saccharum* under elevated CO₂. *Canadian Journal of Forest Research* **33**: 842–846.

Pastor, J. and Naiman, R.J. 1992. Selective foraging and ecosystem processes in boreal forest. *American Naturalist* **139**: 690–705.

Patankar, R., Thomas, S.C., and Smith, S.M. 2011. A gall-inducing arthropod drives declines in canopy photosynthesis. *Oecologia* **167**: 701–709.

Runion, G.B., Entry, J.A., Prior, S.A., Mitchell, R.J., and Rogers, H.H. 1999. Tissue chemistry and carbon allocation in seedlings of *Pinus palustris* subjected to elevated atmospheric CO₂ and water stress. *Tree Physiology* **19**: 329–335.

Stiling, P. and Cornelissen, T. 2007. How does elevated carbon dioxide (CO₂) affect plant-herbivore interactions? A field experiment and meta-analysis of CO₂-mediated changes on plant chemistry and herbivore performance. *Global Change Biology* **13**: 1–20.

Tylianakis, J.M., Didham, R.K., Bascompte, J., and Wardle, D.A. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* **11**: 1351–1363.

Valkama, E., Koricheva, J., and Oksanen, E. 2007. Effects of elevated O₃, alone and in combination with elevated CO₂, on tree leaf chemistry and insect herbivore performance: a meta-analysis. *Global Change Biology* **13**: 184–201.

Williams, R.S., Lincoln, D.E., and Thomas, R.B. 1994. Loblolly pine grown under elevated CO₂ affects early instar pine sawfly performance. *Oecologia* **98**: 64–71.

Zangerl, A.R., Hamilton, J.G., Miller, T.J., Crofts, A.R., Oxborough, K., Berenbaum, M.R., and DeLucia, E.H. 2002. Impact of folivory on photosynthesis is greater than the sum of its holes. *Proceedings of the National Academy of Sciences USA* **99**: 1088–1091.

3.4.3.4 Fluctuating Asymmetry

- Higher concentrations of atmospheric CO₂ tend to reduce fluctuating asymmetry in plant leaves, leading to more symmetrical leaves that appear to be less susceptible to attacks by herbivores.

Fluctuating asymmetry (FA) is the term used to describe small variations from perfect symmetry in otherwise bilaterally symmetrical characters in an organism (Moller and Swaddle, 1997). It is thought to arise in consequence of developmental instability experienced during ontogeny that is caused by various stresses, including both genetic and environmental factors (Martel *et al.*, 1999; Cornelissen and Stiling, 2005). It has been studied extensively in animals but less so in plants (Moller and Shykoff, 1999).

In the first study to address the effects of atmospheric CO₂ enrichment on leaf asymmetry and herbivore response, Cornelissen *et al.* (2004) studied native scrub-oak community at the Kennedy Space Center, Titusville, Florida (USA), which is dominated by myrtle oak (*Quercus myrtifolia*) and sand live oak (*Quercus geminata*), under atmospheric CO₂ concentrations of either 370 or 700 ppm. Based on measurements of distances from the leaf midrib to the left and right edges of the leaf at its widest point and leaf areas on the left and right sides of the leaf midrib, Cornelissen *et al.* determined “asymmetric leaves were less frequent in elevated CO₂, and, when encountered, they were less asymmetric than leaves growing under ambient CO₂.” In addition, “*Q. myrtifolia* leaves under elevated CO₂ were 15.0% larger than in ambient CO₂ and *Q. geminata* leaves were 38.0% larger in elevated CO₂ conditions.” They also report “elevated CO₂ significantly increased tannin concentration for both *Q. myrtifolia* and *Q. geminata* leaves,” and “asymmetric leaves contained significantly lower concentrations of tannins than symmetric leaves for both *Q. geminata* and *Q. myrtifolia*.”

Cornelissen *et al.* write, “a possible explanation for [reduced asymmetry in leaves under elevated CO₂] is the fact that, in contrast to other environmental stresses, which can cause negative

effects on plant growth, the predominant effect of elevated CO₂ on plants is to promote growth with consequent reallocation of resources (Docherty *et al.*, 1996).” Another possibility, they say, “is the fact that CO₂ acts as a plant fertilizer,” and, as a result, “elevated CO₂ ameliorates plant stress compared with ambient levels of CO₂,” which is one of the well-documented biological benefits of atmospheric CO₂ enrichment documented by Idso and Idso (1994).

As to the ancillary finding of CO₂-induced increases in tannin concentrations in the leaves of both oaks (a mean increase of approximately 35% for *Q. myrtifolia* and 43% for *Q. geminata*), it should be noted this phenomenon may provide both species with greater protection against herbivores, and part of that protection may be associated with the observed CO₂-induced reductions in the amount and degree of asymmetry in the leaves of the CO₂-enriched trees. Consistent with this hypothesis, Stiling *et al.* (1999, 2003) found higher abundances of leaf miners in the leaves of the trees in the ambient CO₂ chambers, where asymmetric leaves were more abundant, and in the current study it was determined leaf miners attacked asymmetric leaves more frequently than would be expected by chance alone in both CO₂ treatments.

In further support of this CO₂-induced benefit, Cornelissen and Stiling (2005) evaluated patterns of asymmetry in 40 leaves from each of 30 trees of each of two species of oak—sand live oak (*Quercus geminata*) and turkey oak (*Q. laevis*)—at the University of South Florida Botanical Garden in Tampa, Florida (USA), well before any herbivores had begun to attack the trees that growing season. They examined patterns of leaf asymmetry, leaf quality, and herbivory for 30 individual trees of each of the two oak species from March to October of the same year.

The “before and after” measurements indicate differential herbivory patterns neither caused nor affected patterns of leaf FA. The authors write, “herbivores may use asymmetry as a cue to plant quality and suitable oviposition sites,” as plants with a higher percentage of asymmetric leaves were attacked more frequently by various leaf miners, as were leaves on the same plant more asymmetric. Cornelissen and Stiling report, “asymmetric leaves of both plant species exhibited better nutritional quality for herbivores than symmetric leaves,” with asymmetric leaves possessing “significantly lower concentrations of tannins [-22% for *Q. geminata* and -36% for *Q. laevis*] and higher nitrogen content [+8%

for both species].”

Kaligarić *et al.* (2008) measured the degree of FA in “undamaged (not grazed, not visibly attacked by herbivores or pathogens) fully developed leaves” of the Mediterranean shrub *Myrtus communis* L. growing along an atmospheric CO₂ gradient (570, 530, 490, 450, 410, and 370 ppm) moving away from a natural CO₂ spring, “I Borboi,” near Lajatico (Pisa, Tuscany, Italy) at distances of 2, 18, 34, 50, 66, and 82 m, respectively, from the CO₂ source.

The four researchers report they found “a significant and negative correlation between CO₂ concentration and leaf FA,” such that “with increased CO₂ concentration the leaf FA decreased.” This result, they write, “confirms what was obtained by Cornelissen *et al.* (2004) on *Quercus myrtifolia* and *Quercus geminata* (in a short-term experiment).” In addition, they note “*Myrtus communis*, grown under elevated CO₂ concentration at ‘I Borboi,’ showed a reduction in xylem embolism and an increase in hydraulic efficiency (Tognetti *et al.*, 2001),” stating “improved water relations could represent a good explanation for the observed reduction in leaf FA [as the air’s CO₂ content increased].”

Kaligarić *et al.* conclude “adaptation and selection could explain the tendency towards decreased leaf FA in plants from the CO₂ spring relative to ambient conditions,” since “the more symmetrical leaves under long-term elevated CO₂ concentration were more developmentally stable in these conditions.”

References

- Cornelissen, T. and Stiling, P. 2005. Perfect is best: low leaf fluctuating asymmetry reduces herbivory by leaf miners. *Oecologia* **142**: 46–56.
- Cornelissen, T., Stiling, P., and Drake, B. 2004. Elevated CO₂ decreases leaf fluctuating asymmetry and herbivory by leaf miners on two oak species. *Global Change Biology* **10**: 27–36.
- Docherty, M., Hurst, D.K., Holopainen, J.K., Whittaker, J.B., Lea, P.J., and Watt, A.D. 1996. Carbon dioxide-induced changes in beech foliage cause female beech weevil larvae to feed in a compensatory manner. *Global Change Biology* **2**: 335–341.
- Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: a review of the past 10 years’ research. *Agricultural and Forest Meteorology* **69**: 153–203.

Kaligarić, M., Tognetti, R., Janzeković, F., and Raschi, A. 2008. Leaf fluctuating asymmetry of *Myrtus communis* L., affected by increases in atmospheric CO₂ concentration: Evidence from a natural CO₂ spring. *Polish Journal of Environmental Studies* 17: 503–508.

Martel, J., Lempa, K., and Haukioja, E. 1999. Effects of stress and rapid growth on fluctuating asymmetry and insect damage in birch leaves. *Oikos* 86: 208–216.

Møller, A.P. and Swaddle, J.P. 1997. *Asymmetry, Developmental Stability and Evolution*. Oxford University Press, Oxford, UK.

Møller, A.P. and Shykoff, P. 1999. Morphological developmental stability in plants: patterns and causes. *International Journal of Plant Sciences* 160: S135–S146.

Stiling, P., Moon, D.C., Hunter, M.D., Colson, J., Rossi, A.M., Hymus, G.J., and Drake, B.G. 2003. Elevated CO₂ lowers relative and absolute herbivore density across all species of a scrub-oak forest. *Oecologia* 134: 82–87.

Stiling, P., Rossi, A.M., Hungate, B., Dijkstra, P., Hinkle, C.R., Knot III, W.M., and Drake, B. 1999. Decreased leaf-miner abundance in elevated CO₂: Reduced leaf quality and increased parasitoid attack. *Ecological Applications* 9: 240–244.

Tognetti, R., Longobucco, A., Raschi, A., and Jones, M.B. 2001. Stem hydraulic properties and xylem vulnerability to embolism in three co-occurring Mediterranean shrubs at a natural CO₂ spring. *Australian Journal of Plant Physiology* 28: 257–268.

3.5 Iron Stress

- Atmospheric CO₂ enrichment can stimulate biomass production in both iron-sufficient and iron-deficient plants, and it increases internal iron (Fe) use efficiency, stimulates root growth, and increases root exudation of Fe-mobilizing phytosiderophores in sub-apical root zones, thereby increasing the competitiveness of plants with rhizosphere microorganisms in their quest for this trace element.

Little is known about the interaction of CO₂ and iron stress on the growth of plants; few researchers have investigated this topic. In one study, Haase *et al.* (2008) grew barley (*Hordeum vulgare* L. cv. Europa) plants from seed for four weeks—both hydroponically in nutrient solution having adequate or less-than-adequate iron (Fe) concentrations (+Fe and -Fe, respectively), as well as in rhizobox microcosms filled with soil under the same two conditions of iron

availability—in controlled-environment chambers maintained at atmospheric CO₂ concentrations of either ambient CO₂ (400 ppm) or elevated CO₂ (800 ppm). They found the elevated atmospheric CO₂ treatment stimulated biomass production in both the Fe-sufficient and Fe-deficient barley plants, in both hydroponics and soil culture. They also discovered three CO₂-induced modifications in plant activity: “(i) increased internal Fe use efficiency, (ii) stimulation of root growth, and (iii) increased root exudation of Fe-mobilizing phytosiderophores in the sub-apical root zones.”

Since phytosiderophores act as metal chelators that mobilize sparingly soluble inorganic forms of iron and zinc and make them more readily available to plants, the eight researchers suggest atmospheric CO₂ enrichment increases the competitiveness of plants such as barley with rhizosphere microorganisms in their quest for these often difficult-to-obtain trace elements, which helps to explain the strong growth response of barley to atmospheric CO₂ enrichment they observed, even when iron availability was low.

Jin *et al.* (2009) grew 20-day-old plants for an additional seven days in controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 350 or 800 ppm in an iron (Fe)-sufficient medium with a soluble Fe source or under Fe-limited conditions in a medium containing the sparingly soluble hydrous Fe(III)-oxide. They found the elevated CO₂ increased plant growth in both the Fe-sufficient and Fe-limited media, with shoot fresh weight increasing by 22% and 44%, respectively, and root fresh weight increasing by 43% and 97%, respectively. Jin *et al.* report, “the elevated CO₂ under Fe-limited conditions enhance[d] root growth, root hair development, proton release, root FCR [ferric chelate reductase] activity, and expressions of LeFR1 and LeIRT1 genes [which respectively encode FCR and the Fe(II) transporter in tomato], all of which enable plants to access and accumulate more Fe.” Also, as would be expected, “the associated increase in Fe concentrations in the shoots and roots alleviated Fe-deficiency-induced chlorosis.”

Jin *et al.* state the bioavailability of iron to terrestrial plants “is often limited (Guerinot and Yi, 1994), particularly in calcareous soils, which represent 30% of the Earth’s [land] surface (Imsande, 1998).” They conclude “Fe nutrition in plants is likely to be affected by the continued elevation of atmospheric CO₂, which, in turn, will affect crop production.” As their work strongly suggests, those

important effects should be highly beneficial, and Sasaki *et al.* (1998) suggest even wider biospheric benefits, demonstrating elevated CO₂ concentrations significantly enhanced both the ferric reductase activity and Fe uptake capacity of the marine alga *Chlorococcum littorale* cultured in Fe-limited media.

References

Guerinot, M.L. and Yi, Y. 1994. Iron: nutritious, noxious, and not readily available. *Plant Physiology* **104**: 815–820.

Haase, S., Rothe, A., Kania, A., Wasaki, J., Romheld, V., Engels, C., Kandeler, E., and Neumann, G. 2008. Responses to iron limitation in *Hordeum vulgare* L. as affected by the atmospheric CO₂ concentration. *Journal of Environmental Quality* **37**: 1254–1262.

Imsande, J. 1998. Iron, sulfur, and chlorophyll deficiencies: a need for an integrative approach in plant physiology. *Physiologia Plantarum* **103**: 139–144.

Jin, C.W., Du, S.T., Chen, W.W., Li, G.X., Zhang, Y.S., and Zheng, S.J. 2009. Elevated carbon dioxide improves plant iron nutrition through enhancing the iron-deficiency-induced responses under iron-limited conditions in tomato. *Plant Physiology* **150**: 272–280.

Sasaki, T., Kurano, N., and Miyachi, S. 1998. Induction of ferric reductase activity and of iron uptake capacity in *Chlorococcum littorale* cells under extremely high-CO₂ and iron-deficient conditions. *Plant & Cell Physiology* **39**: 405–410.

3.6 Light Stress

- Whether light intensity is high or low, or leaves are sunlit or shaded, an increase in the CO₂ content of the air increases the biological processes that lead to plant robustness. Less than optimal light intensities do not negate the beneficial effects of atmospheric CO₂ enrichment. In fact, under low light conditions, the benefits of atmospheric CO₂ enrichment on plant growth are often relatively greater than when light conditions are ideal.

Granados and Korner (2002) grew three tropical understory vines (*Gonolobus cteniophorus*, *Ceratophytum tetragonolobum*, and *Thinouia tomocarpa*) for seven months in controlled-environment chambers maintained at atmospheric CO₂ concentrations of 280, 420, 560, and 700 ppm in combination with low and high light intensities, to study the interactive effects of the two parameters on the vines' growth. Plant biomass was found to be

61% greater at high light than at low light. However, the greatest relative CO₂-induced growth response in each species occurred in the low light environment. Increasing the atmospheric CO₂ concentration from 280 to 420 ppm, for example, increased *Gonolobus* biomass by 86 and 32% in low and high light environments, respectively, *Ceratophytum* biomass by 249 and 24% in low and high light environments, respectively, and *Thinouia* biomass by 65% in low light.

Harnos *et al.* (2002) grew winter wheat (*Triticum aestivum* L. cv. Emma) in open-top chambers maintained at atmospheric CO₂ concentrations of 365 and 700 ppm. Among other things, they too report elevated CO₂ stimulated photosynthetic rates to a greater extent under light-limiting than under non-light-limiting conditions. Twice-ambient CO₂ concentrations increased net photosynthesis rates by approximately 100% in upper-canopy leaves and by about 770% further down in the canopy, where light intensity was 60% less than in the upper canopy. This indicates increasing atmospheric CO₂ concentrations likely will lead to enhanced photosynthesis rates by winter wheat plants, even in leaves deep in their canopies, where irradiance is severely reduced due to shading by upper-canopy leaves.

Louche-Tessandier *et al.* (1999) grew potato plantlets inoculated with an arbuscular mycorrhizal fungus at various light intensities and super CO₂ enrichment of approximately 10,000 ppm, finding the unusually high CO₂ concentration produced an unusually high degree of root colonization by the beneficial mycorrhizal fungus, which typically helps supply water and nutrients to plants. It did so irrespective of the degree of light intensity to which the potato plantlets were exposed.

Leakey *et al.* (2002) grew seedlings of *Shorea leprosula* (an under-story rainforest tree) in controlled environments maintained at atmospheric CO₂ concentrations of 376 and 711 ppm in combination with low irradiance treatments delivered in either a uniform or intermittent (sunfleck) manner for about seven months, to study the effects of elevated CO₂ and low light intensity on photosynthesis and growth in this species. They found the initial steady-state rates of photosynthesis measured in the shade in CO₂-enriched leaves were approximately 109% greater than those observed in ambient-grown leaves. In addition, seedlings in the sunfleck treatment grown in elevated CO₂ displayed post-irradiance rates of photosynthesis 14% greater than those observed in control seedlings. Taken together, these increases in

photosynthesis led to CO₂-induced increases in carbon uptake 59 and 89% greater than those observed in control seedlings subjected to uniform and sunfleck light treatments, respectively. The seedlings subjected to uniform irradiance produced more biomass than those exposed to sunfleck irradiance, but the CO₂-induced percentage increase in biomass was greater under the sunfleck irradiance regime (60%) than under the uniform irradiance regime (25%).

Rasineni *et al.* (2011) write, “excess light limits photosynthesis by photoinhibition, resulting in reduced carbon gain and also causing photo-damage (Oquist and Huner, 1993; Pastenes *et al.*, 2003; Allakhverdiev and Murata, 2004; Nishiyama *et al.*, 2006),” and thus “plants grown in tropical climates usually experience significantly high irradiance leading to the strong midday depression of photosynthesis (Hymus *et al.*, 2001).” They utilized two open-top chambers in the Botanical Gardens of the University of Hyderabad, India—each of which contained four six-month-old specimens of the fast-growing tropical *Gmelina arborea* tree, which they maintained at optimum moisture and nutrient levels—to measure several plant physiological properties and processes related to leaf photosynthesis and photosystem II (PSII) photochemistry and photoinhibition at both ambient and elevated CO₂ concentrations (360 and 460 ppm, respectively), working with “well-expanded and light-exposed leaves randomly chosen from the upper half of the plant canopy.”

The three Indian scientists determined there were no significant differences in CO₂ assimilation rates between the ambient and elevated CO₂ grown plants during early morning hours, but thereafter “photosynthesis typically maximized between 0900 hours and 1000 hours in both ambient and elevated CO₂-grown plants,” which experienced net photosynthetic rates of 20 and 32.5 $\mu\text{mol}/\text{m}^2/\text{s}$, respectively, for a CO₂-induced enhancement of 62%, which for the more standard CO₂ enrichment of 300 ppm would be an enhancement of roughly 180%. Subsequently, during the midday period of 1100–1300 hours, the net photosynthesis rate was still significantly enhanced by about 37% (roughly equivalent to a 300-ppm induced increase of more than 100%) in the elevated CO₂ treatment. After that, the difference between the net photosynthetic rates of the two CO₂ treatments once again became insignificant.

Noting the “elevated CO₂ treatment mitigated PSII-photoinhibition through enhanced electron trans-

port rates and through efficient biochemical reactions in leaves of *G. arborea*,” Rasineni *et al.* conclude their data “demonstrate that future increases in atmospheric CO₂ may have positive effects on photochemical efficiency in fast growing tropical tree species,” allowing them to take great advantage of the high-light midday period of potential maximum growth in Earth’s tropical regions.

Kerstiens (1998) provided further evidence elevated atmospheric CO₂ helps to ameliorate the stress of low light intensities in trees, analyzing the results of 15 previously published studies of trees having differing degrees of shade tolerance. He found elevated CO₂ caused greater relative biomass increases in shade-tolerant species than in shade-intolerant or sun-loving species. In more than half the studies he analyzed, shade-tolerant species experienced CO₂-induced relative growth increases two to three times greater than those of less shade-tolerant species.

In an extended follow-up review analyzing 74 observations from 24 studies, Kerstiens (2001) reports twice-ambient CO₂ concentrations increased the relative growth response of shade-tolerant and shade-intolerant woody species by an average of 51 and 18%, respectively. Similar results were reported by Poorter and Perez-Soba (2001), who performed a detailed meta-analysis of research results pertaining to this topic, and subsequently by Kubiske *et al.* (2002), who measured photosynthetic acclimation in aspen and sugar maple trees. Low light intensity, therefore, is by no means a barrier to the benefits of an increase in the air’s CO₂ content.

Herrick and Thomas (1999) found a 200 ppm increase in the air’s CO₂ concentration enhanced the photosynthetic rates of sunlit and shaded leaves of sweetgum trees by 92 and 54%, respectively, at one time of year, and by 166 and 68% at another time. Naumburg and Ellsworth (2000) report a 200 ppm increase in the air’s CO₂ content boosted steady-state photosynthetic rates in leaves of four hardwood understory species by an average of 60 and 40% under high and low light intensities, respectively. Even though these photosynthetic responses were significantly less in shaded leaves, they were still substantial, with mean increases ranging from 40 to 68% for a 60% increase in atmospheric CO₂ concentration.

Under extremely low light intensities, the benefits arising from atmospheric CO₂ enrichment may be small, but oftentimes they are very important in terms of plant carbon budgeting. Hattenschwiler (2001), for

example, found seedlings of five temperate forest species favored with an additional 200 ppm of CO₂ under light intensities only 3.4 and 1.3% of full sunlight exhibited CO₂-induced biomass increases ranging from 17 to 74%. Similarly, Naumburg *et al.* (2001) found a 200 ppm increase in the air's CO₂ content enhanced photosynthetic carbon uptake in three of four hardwood understory species more than twofold in three of the four species under light irradiances as low as 3% of full sunlight.

Sefcik *et al.* (2006) grew seedlings of two shade-tolerant northern hardwood tree species—sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* J.F. Ehrh.)—as well as seedlings of two shade-intolerant northern hardwood tree species—black cherry (*Prunus serotina* J.F. Ehrh.) and paper birch (*Betula papyrifera* Marsh.)—for two full growing seasons inside open-top chambers maintained at either ambient (383 ppm) or elevated (658 ppm) atmospheric CO₂ concentrations in an overarching 90-year-old nitrogen-limited northern hardwood forest in Michigan (USA). They determined the seedlings' responses to atmospheric CO₂ enrichment in two contrasting degrees of shade: moderate shade (14.2 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ = 5.6% full sun) and deep shade (6.5 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ = 2.2% full sun). Sefcik *et al.* state “the magnitude of enhancement from exposure to elevated CO₂ was similar for both shade-tolerance groups,” with the elevated CO₂ treatment increasing the mean light-saturated net photosynthetic rate by 63% in the shade-tolerant species and by 67% in the shade-intolerant species. More important, they write, “seedlings grown in deep shade, regardless of shade-tolerance group, showed a greater long-term photosynthetic enhancement to elevated CO₂ than those grown in moderate shade,” with the mean long-term enhancement being 47% in moderate shade and a much larger 97% in deep shade.

Noting the same type of photosynthetic response “has also been found in a number of other studies, suggesting that the impact of a CO₂-enriched atmosphere increases as light becomes more limiting (Hattenschwiler, 2001; Granados and Korner, 2002; Leakey *et al.*, 2002),” Sefcik *et al.* conclude, “if long-term enhancement of photosynthesis in elevated CO₂ and deep shade translates into greater survival, especially for shade-intolerant species, this could have profound successional implications for nitrogen-limited northern hardwood forest composition in a future higher CO₂ atmosphere.”

Elevated CO₂ often reduces a plant's light

compensation point, which is the light intensity at which the amount of carbon fixed by photosynthesis is equal to that lost by respiration. Above that particular light intensity, net photosynthesis is positive. Below it, net photosynthesis is negative, and if prolonged, the plant will ultimately die. This phenomenon is especially beneficial to vegetation growing in deep shade beneath forest canopies that block out much of the incoming sunlight (Kubiske and Pregitzer, 1996; Osborne *et al.*, 1997), and it also helps aquatic plants extend their life zones to greater depths (Zimmerman *et al.*, 1997).

Whether light intensity is high or low, or leaves are shaded or sunlit, an increase in the CO₂ content of the air increases the various biological processes that lead to plant robustness. Less than optimal light intensities do not negate the beneficial effects of atmospheric CO₂ enrichment.

References

- Allakhverdiev, S.I. and Murata, N. 2004. Environmental stress inhibits the synthesis de novo of proteins involved in the photodamage-repair cycle of photosystem II in *Synechocystis* sp. PCC 6803. *Biochimica et Biophysica Acta* **1657**: 23–32.
- Granados, J. and Korner, C. 2002. In deep shade, elevated CO₂ increases the vigor of tropical climbing plants. *Global Change Biology* **8**: 1109–1117.
- Harnos, N., Tuba, Z., and Szente, K. 2002. Modelling net photosynthetic rate of winter wheat in elevated air CO₂ concentrations. *Photosynthetica* **40**: 293–300.
- Hattenschwiler, S. 2001. Tree seedling growth in natural deep shade: functional traits related to interspecific variation in response to elevated CO₂. *Oecologia* **129**: 31–42.
- Herrick, J.D. and Thomas, R.B. 1999. Effects of CO₂ enrichment on the photosynthetic light response of Sun and shade leaves of canopy sweetgum trees (*Liquidambar styraciflua*) in a forest ecosystem. *Tree Physiology* **19**: 779–786.
- Hymus, G.J., Baker, N.R., and Long, S.P. 2001. Growth in elevated CO₂ can both increase and decrease photochemistry and photoinhibition of photosynthesis in a predictable manner. *Dactylis glomerata* growth in two levels of nitrogen nutrition. *Plant Physiology* **127**: 1204–1211.
- Kerstiens, G. 1998. Shade-tolerance as a predictor of responses to elevated CO₂ in trees. *Physiologia Plantarum* **102**: 472–480.

Kerstiens, G. 2001. Meta-analysis of the interaction between shade-tolerance, light environment and growth response of woody species to elevated CO₂. *Acta Oecologica* **22**: 61–69.

Kubiske, M.E. and Pregitzer, K.S. 1996. Effects of elevated CO₂ and light availability on the photosynthetic response of trees of contrasting shade tolerance. *Tree Physiology* **16**: 351–358.

Kubiske, M.E., Zak, D.R., Pregitzer, K.S., and Takeuchi, Y. 2002. Photosynthetic acclimation of overstory *Populus tremuloides* and understory *Acer saccharum* to elevated atmospheric CO₂ concentration: interactions with shade and soil nitrogen. *Tree Physiology* **22**: 321–329.

Leakey, A.D.B., Press, M.C., Scholes, J.D., and Watling, J.R. 2002. Relative enhancement of photosynthesis and growth at elevated CO₂ is greater under sunflecks than uniform irradiance in a tropical rain forest tree seedling. *Plant, Cell and Environment* **25**: 1701–1714.

Louche-Tessandier, D., Samson, G., Hernandez-Sebastia, C., Chagvardieff, P., and Desjardins, Y. 1999. Importance of light and CO₂ on the effects of endomycorrhizal colonization on growth and photosynthesis of potato plantlets (*Solanum tuberosum*) in an in vitro tripartite system. *New Phytologist* **142**: 539–550.

Naumburg, E. and Ellsworth, D.S. 2000. Photosynthetic sunfleck utilization potential of understory saplings growing under elevated CO₂ in FACE. *Oecologia* **122**: 163–174.

Naumburg, E., Ellsworth, D.S., and Katul, G.G. 2001. Modeling dynamic understory photosynthesis of contrasting species in ambient and elevated carbon dioxide. *Oecologia* **126**: 487–499.

Nishiyama, Y., Allakhverdiev, S.I., and Murata, N. 2006. A new paradigm for the action of reactive oxygen species in the photoinhibition of photosystem II. *Biochimica et Biophysica Acta* **1757**: 742–749.

Oquist, G. and Huner, N.P.A. 1993. Cold-hardening-induced resistance to photoinhibition of photosynthesis in winter rye is dependent upon an increased capacity for photosynthesis. *Planta* **189**: 150–156.

Osborne, C.P., Drake, B.G., LaRoche, J., and Long, S.P. 1997. Does long-term elevation of CO₂ concentration increase photosynthesis in forest floor vegetation? *Plant Physiology* **114**: 337–344.

Pastenes, C., Santa-Maria, E., Infante, R., and Franck, N. 2003. Domestication of the Chilean guava (*Ugni molinae* Turcz.) a forest understory shrub, must consider light intensity. *Scientia Horticulturae* **98**: 71–84.

Poorter, H. and Perez-Soba, M. 2001. The growth response

of plants to elevated CO₂ under non-optimal environmental conditions. *Oecologia* **129**: 1–20.

Rasineni, G.K., Guha, A., and Reddy, A.R. 2011. Elevated atmospheric CO₂ mitigated photoinhibition in a tropical tree species, *Gmelina arborea*. *Journal of Photochemistry and Photobiology B: Biology* **103**: 159–165.

Sefcik, L.T., Zak, D.R., and Ellsworth, D.S. 2006. Photosynthetic responses to understory shade and elevated carbon dioxide concentration in four northern hardwood tree species. *Tree Physiology* **26**: 1589–1599.

Zimmerman, R.C., Kohrs, D.G., Steller, D.L., and Alberte, R.S. 1997. Impacts of CO₂-enrichment on productivity and light requirements of eelgrass. *Plant Physiology* **115**: 599–607.

3.7 Nitrogen Insufficiency

Numerous studies have investigated the effects of different soil nitrogen (N) concentrations on plant responses to increases in the air's CO₂ content, because some scientists have claimed a deficiency of soil nitrogen reduces the relative growth stimulation in plants that is typically provided by elevated concentrations of atmospheric CO₂. This section investigates that claim for various crops, fungi, grasses, and young trees.

The results of these experiments indicate some plants sometimes will not respond to atmospheric CO₂ enrichment at low levels of soil N, and others will. Some plants respond equally well to increases in the air's CO₂ content when growing in soils exhibiting a whole range of N concentrations. Most commonly, however, plants respond ever-better to rising atmospheric CO₂ concentrations as soil N concentrations rise. Interestingly, Earth's atmosphere and land surface are currently undergoing joint increases in CO₂ and N concentrations. Thus, the outlook is good for continually increasing terrestrial vegetative productivity as these trends continue.

3.7.1 Crops

The maximum benefits of elevated levels of atmospheric CO₂ for the growth and grain production of rice and wheat cannot be realized in soils that are highly deficient in nitrogen, but increasing nitrogen concentrations above what is considered adequate may not result in proportional gains in CO₂-induced growth and yield enhancement. Although there are significant exceptions to the rule, many agricultural

crops experience increases in net photosynthesis and biomass production even when soil nitrogen concentrations are a limiting factor to growth.

3.7.1.1 Rice

- The maximum benefits of elevated levels of atmospheric CO₂ for the growth and grain production of rice cannot be realized in soils that are highly deficient in nitrogen, but increasing nitrogen concentrations above what is considered adequate may not result in proportional gains in CO₂-induced growth and yield enhancement.

Does a deficiency of soil nitrogen lessen the relative growth and yield stimulation of rice that is typically provided by elevated levels of atmospheric CO₂? In exploring this question, Weerakoon *et al.* (1999) grew seedlings of two rice cultivars for 28 days in glasshouses maintained at atmospheric CO₂ concentrations of 373, 545, 723, and 895 ppm under conditions of low, medium, and high soil nitrogen content. After four weeks of treatment, they found photosynthesis significantly increased with increasing nitrogen availability and atmospheric CO₂ concentration. Averaged across all nitrogen regimes, plants grown at 895 ppm CO₂ exhibited photosynthetic rates 50 percent greater than those observed in plants grown at ambient CO₂. Total plant dry weight also increased with increasing atmospheric CO₂. In addition, the percentage growth enhancement resulting from CO₂ enrichment increased with increasing soil nitrogen—from 21 percent at the lowest soil nitrogen concentration to 60 percent at the highest concentration.

Using a different CO₂ enrichment technique, Weerakoon *et al.* (2000) grew rice in open-top chambers maintained at atmospheric CO₂ concentrations of approximately 350 and 650 ppm during a wet and dry growing season and under a range of soil nitrogen contents. Early in both growing seasons, plants exposed to elevated atmospheric CO₂ concentrations intercepted significantly more sunlight than plants fumigated with ambient air, due to CO₂-induced increases in leaf area index. This phenomenon occurred regardless of soil nitrogen content, but it disappeared shortly after canopy closure in all treatments. Later, mature canopies achieved similar leaf area indexes at identical levels of soil nitrogen supply, but mean season-long radiation use efficiency—the amount of biomass

produced per unit of solar radiation intercepted—was 35 percent greater in CO₂-enriched vs. ambient-grown plants and tended to increase with increasing soil nitrogen content.

Utilizing a third approach to CO₂ enrichment, Kim *et al.* (2003) grew rice crops from the seedling stage to maturity at atmospheric CO₂ concentrations of ambient and ambient plus 200 ppm using FACE technology and three levels of applied nitrogen—low (LN, 4 g N m⁻²), medium (MN, 8 and 9 g N m⁻²), and high (HN, 15 g N m⁻²)—for three cropping seasons (1998–2000). They report “the yield response to elevated CO₂ in crops supplied with MN (+14.6%) or HN (+15.2%) was about twice that of crops supplied with LN (+7.4%),” confirming the importance of nitrogen availability to the response of rice to atmospheric CO₂ enrichment previously determined by Kim *et al.* (2001) and Kobaysahi *et al.* (2001).

These observations indicate the maximum benefits of elevated levels of atmospheric CO₂ for the growth and grain production of rice cannot be realized in soils highly deficient in nitrogen, but increasing nitrogen concentrations above what is considered adequate may not result in proportional gains in CO₂-induced growth and yield enhancement.

References

- Kim, H.-Y., Liefferring, M., Kobayashi, K., Okada, M., Mitchell, M.W., and Gumpertz, M. 2003. Effects of free-air CO₂ enrichment and nitrogen supply on the yield of temperate paddy rice crops. *Field Crops Research* **83**: 261–270.
- Kim, H.-Y., Liefferring, M., Miura, S., Kobayashi, K., and Okada, M. 2001. Growth and nitrogen uptake of CO₂-enriched rice under field conditions. *New Phytologist* **150**: 223–229.
- Kobayashi, K., Liefferring, M., and Kim, H.-Y. 2001. Growth and yield of paddy rice under free-air CO₂ enrichment. In: Shiyomi, M. and Koizumi, H. (Eds.) *Structure and Function in Agroecosystem Design and Management*. CRC Press, Boca Raton, FL, USA, pp. 371–395.
- Weerakoon, W.M.W., Ingram, K.T., and Moss, D.D. 2000. Atmospheric carbon dioxide and fertilizer nitrogen effects on radiation interception by rice. *Plant and Soil* **220**: 99–106.
- Weerakoon, W.M., Olszyk, D.M., and Moss, D.N. 1999. Effects of nitrogen nutrition on responses of rice seedlings to carbon dioxide. *Agriculture, Ecosystems and Environment* **72**: 1–8.

3.7.1.2 Wheat

- The maximum benefits of elevated levels of atmospheric CO₂ for the growth and grain production of wheat cannot be realized in soils that are highly deficient in nitrogen, but increasing nitrogen concentrations above what is considered adequate may not result in proportional gains in CO₂-induced growth and yield enhancement.

Smart *et al.* (1998) grew wheat from seed for 23 days in controlled-environment chambers maintained at atmospheric CO₂ concentrations of 360 and 1,000 ppm and two concentrations of soil nitrate, finding the extra CO₂ increased average plant biomass by approximately 15 percent, irrespective of soil nitrogen content. In a more realistic FACE experiment, however, Brooks *et al.* (2000) grew spring wheat for two seasons at atmospheric CO₂ concentrations of 370 and 570 ppm at both high and low levels of nitrogen fertility, obtaining twice the yield enhancement (16 percent vs. 8 percent) in the high nitrogen treatment.

Vilhena-Cardoso and Barnes (2001) grew spring wheat for two months in environmental chambers fumigated with air containing atmospheric CO₂ concentrations of either 350 or 700 ppm at ambient and elevated (75 ppb) ozone levels, and supplied the plants with either low, medium, or high levels of soil nitrogen. With respect to biomass production, the elevated CO₂ treatment increased total plant dry weight by 44, 29, and 12 percent at the high, medium, and low soil nitrogen levels, respectively. Although elevated ozone by itself reduced plant biomass, the simultaneous application of elevated CO₂ completely ameliorated its detrimental effects on biomass production, irrespective of soil nitrogen supply.

Why do the plants of some studies experience a major reduction in the relative growth stimulation provided by atmospheric CO₂ enrichment under low soil nitrogen conditions, whereas other studies find the aerial fertilization effect of elevated CO₂ to be independent of root-zone nitrogen concentration? Based on studies of both potted and hydroponically grown plants, Farage *et al.* (1998) determined low root-zone nitrogen concentrations need not lead to photosynthetic acclimation (less than maximum potential rates of photosynthesis) in elevated CO₂, as long as root-zone nitrogen supply is adequate to meet plant nitrogen needs to maintain the enhanced relative growth rate that is made possible by atmospheric CO₂ enrichment. When supply cannot meet this need, as is

often the case in soils with limited nitrogen reserves, the aerial fertilization effect of atmospheric CO₂ enrichment begins to be reduced and causes less-than-potential CO₂-induced growth stimulation. Nevertheless, the acclimation process is the plant's "first line of defense" to keep its productivity from falling even further than it otherwise would, as it typically mobilizes nitrogen from "excess" rubisco and sends it to other plant sink tissues to maintain growth and development (Theobald *et al.*, 1998).

Although atmospheric CO₂ enrichment tends to increase the growth and yield of wheat under a wide range of soil nitrogen concentrations, including some that are very low, considerably greater CO₂-induced enhancements are possible when more soil nitrogen is available. The response can saturate at high soil nitrogen levels, with excess nitrogen providing little or no extra yield.

References

- Brooks, T.J., Wall, G.W., Pinter Jr., P.J., Kimball, B.A., LaMorte, R.L., Leavitt, S.W., Matthias, A.D., Adamsen, F.J., Hunsaker, D.J., and Webber, A.N. 2000. Acclimation response of spring wheat in a free-air CO₂ enrichment (FACE) atmosphere with variable soil nitrogen regimes. 3. Canopy architecture and gas exchange. *Photosynthesis Research* **66**: 97–108.
- Farage, P.K., McKee, I.F., and Long, S.P. 1998. Does a low nitrogen supply necessarily lead to acclimation of photosynthesis to elevated CO₂? *Plant Physiology* **118**: 573–580.
- Smart, D.R., Ritchie, K., Bloom, A.J., and Bugbee, B.B. 1998. Nitrogen balance for wheat canopies (*Triticum aestivum* cv. Veery 10) grown under elevated and ambient CO₂ concentrations. *Plant, Cell and Environment* **21**: 753–763.
- Theobald, J.C., Mitchell, R.A.C., Parry, M.A.J., and Lawlor, D.W. 1998. Estimating the excess investment in ribulose-1,5-bisphosphate carboxylase/oxygenase in leaves of spring wheat grown under elevated CO₂. *Plant Physiology* **118**: 945–955.
- Vilhena-Cardoso, J. and Barnes, J. 2001. Does nitrogen supply affect the response of wheat (*Triticum aestivum* cv. Hanno) to the combination of elevated CO₂ and O₃? *Journal of Experimental Botany* **52**: 1901–1911.

3.7.1.3 Other Crops

- Agricultural crops generally experience greater

CO₂-induced percentage increases in net photosynthesis and biomass production even when soil nitrogen concentrations are a limiting factor, although there are some significant exceptions to the rule.

Zerihun *et al.* (2000) grew sunflowers for one month in pots of three different soil nitrogen concentrations placed in open-top chambers maintained at atmospheric CO₂ concentrations of 360 and 700 ppm. The extra CO₂ of the CO₂-enriched chambers reduced average rates of root nitrogen uptake by about 25%, which by itself would tend to reduce tissue nitrogen contents and the relative growth rates of the seedlings. However, the elevated CO₂ also increased photosynthetic nitrogen-use efficiency by an average of 50%, which tends to increase the relative growth rates of seedlings. The latter of these two competing effects was more powerful, leading to an increase in whole plant biomass. At the conclusion of the one-month study, the CO₂-enriched plants exhibited whole plant biomass values 44, 13, and 115 percent greater than those of the plants growing in ambient air at low, medium, and high levels of soil nitrogen, respectively. These findings demonstrate low tissue nitrogen contents do not necessarily preclude a growth response to atmospheric CO₂ enrichment, particularly if photosynthetic nitrogen-use efficiency is enhanced, which is typically the case, as it was in this study. Nevertheless, the greatest CO₂-induced growth increase of Zerihun *et al.*'s study was exhibited by the plants growing in the high soil nitrogen treatment.

Deng and Woodward (1998) grew strawberries in environment-controlled glasshouses maintained at atmospheric CO₂ concentrations of 390 and 560 ppm for nearly three months. The strawberries were supplied with fertilizers containing three levels of nitrogen. The extra CO₂ increased rates of net photosynthesis and total plant dry weight at all three nitrogen levels, but the increases were not significant. Nevertheless, they provided the CO₂-enriched plants with enough additional sugar and physical mass to support significantly greater numbers of flowers and fruits than the plants grown at 390 ppm CO₂. This effect ultimately led to total fresh fruit weights 42 and 17 percent greater in the CO₂-enriched plants that received the highest and lowest levels of nitrogen fertilization, respectively, once again indicating a greater growth response at higher nitrogen levels.

Newman *et al.* (2003) investigated the effects of two levels of nitrogen fertilization and an approximate doubling of the air's CO₂ concentration on the

growth of tall fescue, an important forage crop. The plants were initially grown from seed in greenhouse flats, but after 16 weeks the researchers transplanted them into 19-liter pots filled with potting media given periodic applications of a slow-release fertilizer. Over the next two years of outdoor growth, the researchers periodically clipped, divided, and repotted the plants to ensure they did not become root-bound. At the end of that time, they placed the plants in 20 1.3-m-diameter open-top chambers, half of which were maintained at the ambient atmospheric CO₂ concentration and half of which received an approximately doubled CO₂ concentration of 700 ppm. In addition, half of the pots in each CO₂ treatment received 0.0673 kg N m⁻² applied over a period of three consecutive days, and half received only one-tenth that amount. Researchers repeated the entire procedure three times during the 12-week study.

The researchers found the plants grown in the high-CO₂ air photosynthesized 15 percent more and produced 53 percent more dry matter (DM) under low N conditions and 61 percent more DM under high N conditions. The percent of organic matter (OM) was little changed, except under elevated CO₂ and high N, when %OM (as %DM) increased by 3 percent. In this study too, then, the greatest relative increase in productivity occurred under high soil N availability.

Demmers-Derks *et al.* (1998) grew sugar beets as an annual crop in controlled-environment chambers at atmospheric CO₂ concentrations of 360 and 700 ppm and air temperatures of ambient and ambient plus 3°C for three consecutive years. In addition to exposing the plants to these CO₂ and temperature combinations, the researchers supplied the sugar beets with solutions of low and high nitrogen content. Averaged across all three years and both temperature regimes, the extra CO₂ of this study enhanced total plant biomass by 13 and 25% in the low and high nitrogen treatments, respectively. In addition, it increased root biomass by 12 and 26%. As with sunflowers, strawberries, and tall fescue, elevated CO₂ produced the largest growth responses in the sugar beets that received a high supply of nitrogen.

Romanova *et al.* (2002) grew sugar beets from seed for one month in controlled-environment chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm, fertilizing them with three levels of nitrate-nitrogen. The plants grown in CO₂-enriched air exhibited rates of net photosynthesis approximately 50% greater than those of the plants grown in ambient air, regardless of soil nitrate

availability. These CO₂-induced increases in photosynthetic carbon uptake contributed to 60, 40, and 30% above-ground organ dry weight increases in plants receiving one-half, standard, and three-fold levels of soil nitrate, respectively. Root weights were less responsive to atmospheric CO₂ enrichment, displaying 10 and 30% increases in dry weight at one-half and standard nitrate levels but no increase at the high soil nitrate concentration. In this study, the role of soil nitrogen fertility was opposite that observed in the four prior studies in the case of above-ground biomass production, but mixed in the case of belowground biomass production.

Fangmeier *et al.* (2000) grew barley plants in containers in open-top chambers maintained at atmospheric CO₂ concentrations of either 360 or 650 ppm and either a high or low nitrogen fertilization regime. The elevated CO₂ had the greatest relative impact on yield when the plants were grown under the less-than-optimum low-nitrogen regime—a 48 percent increase vs. 31 percent under high-nitrogen conditions.

Kimball *et al.* (2002) summarized the findings of most FACE studies conducted on agricultural crops since the introduction of that technology in the late 1980s. In response to a 300 ppm increase in the air's CO₂ concentration, rates of net photosynthesis in several C₃ grasses were enhanced by an average of 46% under conditions of ample soil nitrogen supply and by 44% when nitrogen was limiting to growth. The differential for above-ground biomass production was much larger, with the C₃ grasses wheat, rice, and ryegrass showing an average increase of 18% at ample nitrogen but only 4% at low nitrogen. As to belowground biomass production, they experienced an average increase of 70% at ample nitrogen and 58% at low nitrogen. Similarly, clover experienced a 38% increase in belowground biomass production at ample soil nitrogen and a 32% increase at low soil nitrogen. Finally, with respect to agricultural yield—the true indicator of food and fiber production—wheat and ryegrass showed an average increase of 18% at ample nitrogen, and wheat saw only a 10% increase at low nitrogen.

These results indicate most agricultural crops generally experience greater CO₂-induced relative (percentage) increases in net photosynthesis and biomass production even when soil nitrogen concentrations are a limiting factor, although there are some exceptions to the rule.

References

- Demmers-Derks, H., Mitchell, R.A.G., Mitchell, V.J., and Lawlor, D.W. 1998. Response of sugar beet (*Beta vulgaris* L.) yield and biochemical composition to elevated CO₂ and temperature at two nitrogen applications. *Plant, Cell and Environment* **21**: 829–836.
- Deng, X. and Woodward, F.I. 1998. The growth and yield responses of *Fragaria ananassa* to elevated CO₂ and N supply. *Annals of Botany* **81**: 67–71.
- Fangmeier, A., Chrost, B., Hogy, P., and Krupinska, K. 2000. CO₂ enrichment enhances flag leaf senescence in barley due to greater grain nitrogen sink capacity. *Environmental and Experimental Botany* **44**: 151–164.
- Kimball, B.A., Kobayashi, K., and Bindi, M. 2002. Responses of agricultural crops to free-air CO₂ enrichment. *Advances in Agronomy* **77**: 293–368.
- Newman, J.A., Abner, M.L., Dado, R.G., Gibson, D.J., Brookings, A., and Parsons, A.J. 2003. Effects of elevated CO₂, nitrogen and fungal endophyte-infection on tall fescue: growth, photosynthesis, chemical composition and digestibility. *Global Change Biology* **9**: 425–437.
- Romanova, A.K., Mudrik, V.A., Novichkova, N.S., Demidova, R.N., and Polyakova, V.A. 2002. Physiological and biochemical characteristics of sugar beet plants grown at an increased carbon dioxide concentration and at various nitrate doses. *Russian Journal of Plant Physiology* **49**: 204–210.
- Zerihun, A., Gutschick, V.P., and BassiriRad, H. 2000. Compensatory roles of nitrogen uptake and photosynthetic N-use efficiency in determining plant growth response to elevated CO₂: Evaluation using a functional balance model. *Annals of Botany* **86**: 723–730.

3.7.2 Fungi

- CO₂-induced stimulation of root infection by various fungi (which tends to benefit the plants) is generally greater under lower soil nitrogen concentrations. This implies elevated CO₂ will enhance fungal-plant interactions to a greater extent when soil nutrition is less than optimal for plant growth, which is the common state of most ecosystems not subjected to fertilization practices typical of intensive agriculture.

Nearly all plants establish intimate relationships with different fungal species at one point or another in their life cycles, and these fungi commonly aid plants in the acquisition of water and nutrients. In addition,

fungus-plant interactions are often affected by variations in atmospheric CO₂ and soil nitrogen concentrations.

In a one-year study conducted by Walker *et al.* (1998), ponderosa pine seedlings exposed to elevated atmospheric CO₂ concentrations of 525 and 700 ppm displayed total numbers of ectomycorrhizal fungi on their roots 170 and 85% greater, respectively, than those observed on roots of ambient-grown seedlings.

Rillig *et al.* (1998) found three grasses and two herbs fumigated with ambient air and air containing an extra 350 ppm CO₂ for four months displayed various root infection responses by arbuscular mycorrhizal fungi, which varied with soil nitrogen supply. At low soil nitrogen contents, elevated CO₂ increased the percent root infection by this type of fungi in all five annual grassland species. At high soil nitrogen, this trend was reversed in four of the five species.

Rillig and Allen (1998) made several important observations regarding the effects of elevated CO₂ and soil nitrogen status on fungus-plant interactions. First, after growing three-year-old shrubs at an atmospheric CO₂ concentration of 750 ppm for four months, they reported non-significant 19 and 9% increases in percent root infected by arbuscular mycorrhizal fungi at low and high soil nitrogen concentrations, respectively. In addition, elevated CO₂ significantly increased the percent root infection by arbuscules, which are the main structures involved in the symbiotic exchange of carbon and nutrients between a host plant and its associated fungi, by more than 14-fold at low soil nitrogen concentrations. In addition, the length of fungal hyphae more than doubled with atmospheric CO₂ enrichment in the low soil nitrogen regime, and in the high soil nitrogen treatment elevated CO₂ increased the percent root infection by vesicles, which are organs used by arbuscular mycorrhizal fungi for carbon storage, by approximately 2.5-fold.

These observations suggest elevated CO₂ affects fungus-plant interactions in positive ways that may depend on soil nitrogen status. Typically, it appears CO₂-induced stimulations of percent root infection by various fungal components is greater under lower soil nitrogen concentrations. This tendency implies elevated CO₂ will enhance fungus-plant interactions to a greater extent when soil nutrition is less than optimal for plant growth, which is commonly the case for most ecosystems not subjected to cultural fertilization practices typical of intensive agricultural production.

References

- Rillig, M.C. and Allen, M.F. 1998. Arbuscular mycorrhizae of *Gutierrezia sarothrae* and elevated carbon dioxide: evidence for shifts in C allocation to and within the mycobiont. *Soil Biology and Biochemistry* **30**: 2001–2008.
- Rillig, M.C., Allen, M.F., Klironomos, J.N., Chiariello, N.R., and Field, C.B. 1998. Plant species-specific changes in root-inhabiting fungi in a California annual grassland: responses to elevated CO₂ and nutrients. *Oecologia* **113**: 252–259.
- Walker, R.F., Johnson, D.W., Geisinger, D.R., and Ball, J.T. 1998. Growth and ectomycorrhizal colonization of ponderosa pine seedlings supplied different levels of atmospheric CO₂ and soil N and P. *Forest Ecology and Management* **109**: 9–20.

3.7.3 Grasses

- Atmospheric CO₂ enrichment stimulates photosynthesis and biomass production in grasses and grassland species when soil nitrogen availability is high or moderate. Where nitrogen availability is low, grasslands are able to overcome soil nitrogen limitations and produce positive CO₂-induced growth responses, given enough time.

Perennial ryegrass (*Lolium perenne* L.) has been used as a model species in many experiments to help elucidate grassland responses to atmospheric CO₂ enrichment and soil nitrogen availability. In the FACE study of Rogers *et al.* (1998), for example, ryegrass plants exposed to 600 ppm CO₂ exhibited a 35% increase in their photosynthetic rates without regard to soil nitrogen availability. However, when ryegrass was grown in plastic ventilated tunnels at twice-ambient concentrations of atmospheric CO₂, the CO₂-induced photosynthetic response was about 3-fold greater in a higher soil nitrogen regime (Casella and Soussana, 1997).

Similarly, in an open-top chamber study Davey *et al.* (1999) found an atmospheric CO₂ concentration of 700 ppm stimulated photosynthesis by 30% in this species when it was grown with moderate, but not low, soil nitrogen availability. Thus, CO₂-induced photosynthetic stimulations in perennial ryegrass can be influenced by soil nitrogen content, with greater positive responses typically occurring under higher, as opposed to lower, soil nitrogen availability.

With respect to biomass production, van Ginkel and Gorissen (1998) report a doubling of the

atmospheric CO₂ concentration increased shoot biomass of perennial ryegrass by 28%, regardless of soil nitrogen concentration. In the more revealing six-year FACE study of Daepf *et al.* (2000), however, plants grown at 600 ppm CO₂ and high soil nitrogen availability continually increased their dry matter production over that observed in ambient-treatment plots, from 8% more in the first year to 25% more at the close of year six. When grown at a low soil nitrogen availability, CO₂-enriched plants exhibited an initial 5% increase in dry matter production, which dropped to a negative 11% in year two. This negative trend was thereafter turned around, reaching a 9% stimulation at the end of the study. These data demonstrate elevated CO₂ increases perennial ryegrass biomass, even under conditions of low soil nitrogen availability, especially under conditions of long-term atmospheric CO₂ enrichment.

Lutze *et al.* (1998) report microcosms of the C₃ grass *Danthonia richardsonii* grown for four years in glasshouses fumigated with air containing 720 ppm CO₂ displayed total photosynthetic carbon gains 15–34% higher than those of ambient-grown microcosms, depending on the soil nitrogen concentration. And in a clearer depiction of photosynthetic responses to soil nitrogen, Davey *et al.* (1999) note the photosynthetic rates of *Agrostis capillaries* exposed to twice-ambient levels of atmospheric CO₂ for two years were 12 and 38% greater than rates measured in control plants grown at 350 ppm CO₂ under high and low soil nitrogen regimes, respectively. They also reported CO₂-induced photosynthetic stimulations of 25 and 74% for *Trifolium repens* subjected to high and low soil nitrogen regimes, respectively. Thus the greatest CO₂-induced percentage increase in photosynthesis occurred under the least favorable soil nitrogen conditions.

With respect to biomass production, Navas *et al.* (1999) state 60 days' exposure to 712 ppm CO₂ increased biomass production of *Danthonia richardsonii*, *Phalaris aquatica*, *Lotus pedunculatus*, and *Trifolium repens* across a large soil nitrogen gradient. With slightly more detail, Cotrufo and Gorissen (1997) reported average CO₂-induced increases in whole-plant dry weights of *Agrostis capillaries* and *Festuca ovina* 20% greater than those of their respective controls, regardless of soil nitrogen availability. And Ghannoum and Conroy (1998) report three *Panicum* grasses grown for two months at twice-ambient levels of atmospheric CO₂ and high soil nitrogen availability displayed similar increases in total plant dry mass about 28% greater than those

of their respective ambient-grown controls. At low nitrogen, however, elevated CO₂ had no significant effect on the dry mass of two of the species, and it decreased in the third species.

It is clear atmospheric CO₂ enrichment stimulates photosynthesis and biomass production in grasses and grassland species when soil nitrogen availability is high or moderate. Under lower soil nitrogen conditions, atmospheric CO₂ enrichment can have the same positive effect, but it also can have a reduced positive effect, no effect, or a negative effect. In light of the one long-term study that lasted six years, however, it is likely, given enough time, grasslands can overcome soil nitrogen limitations and produce positive CO₂-induced growth responses. Because the rising CO₂ content of the air is likely to continue for a long time to come, occasional nitrogen limitations on the aerial fertilization effect of atmospheric CO₂ enrichment of grasslands likely will become less restrictive as time goes on.

References

- Casella, E. and Soussana, J-F. 1997. Long-term effects of CO₂ enrichment and temperature increase on the carbon balance of a temperate grass sward. *Journal of Experimental Botany* **48**: 1309–1321.
- Cotrufo, M.F. and Gorissen, A. 1997. Elevated CO₂ enhances below-ground C allocation in three perennial grass species at different levels of N availability. *New Phytologist* **137**: 421–431.
- Daepf, M., Suter, D., Almeida, J.P.F., Isopp, H., Hartwig, U.A., Frehner, M., Blum, H., Nosberger, J., and Luscher, A. 2000. Yield response of *Lolium perenne* swards to free air CO₂ enrichment increased over six years in a high N input system on fertile soil. *Global Change Biology* **6**: 805–816.
- Davey, P.A., Parsons, A.J., Atkinson, L., Wadge, K., and Long, S.P. 1999. Does photosynthetic acclimation to elevated CO₂ increase photosynthetic nitrogen-use efficiency? A study of three native UK grassland species in open-top chambers. *Functional Ecology* **13**: 21–28.
- Ghannoum, O. and Conroy, J.P. 1998. Nitrogen deficiency precludes a growth response to CO₂ enrichment in C₃ and C₄ *Panicum* grasses. *Australian Journal of Plant Physiology* **25**: 627–636.
- Lutze, J.L. and Gifford, R.M. 1998. Carbon accumulation, distribution and water use of *Danthonia richardsonii* swards in response to CO₂ and nitrogen supply over four years of growth. *Global Change Biology* **4**: 851–861.

Navas, M.-L., Garnier, E., Austin, M.P., and Gifford, R.M. 1999. Effect of competition on the responses of grasses and legumes to elevated atmospheric CO₂ along a nitrogen gradient: differences between isolated plants, monocultures and multi-species mixtures. *New Phytologist* **143**: 323–331.

Rogers, A., Fischer, B.U., Bryant, J., Frehner, M., Blum, H., Raines, C.A., and Long, S.P. 1998. Acclimation of photosynthesis to elevated CO₂ under low-nitrogen nutrition is affected by the capacity for assimilate utilization. Perennial ryegrass under free-air CO₂ enrichment. *Plant Physiology* **118**: 683–689.

Van Ginkel, J.H. and Gorissen, A. 1998. In situ decomposition of grass roots as affected by elevated atmospheric carbon dioxide. *Soil Science Society of America Journal* **62**: 951–958.

3.7.4 Trees

3.7.4.1 Aspen

- Typically, the aerial fertilization effect of atmospheric CO₂ enrichment stimulates the growth of young aspen trees in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting.

Does a deficiency of soil nitrogen lessen the relative growth stimulation of young quaking aspen (*Populus tremuloides* Michx) trees that is typically provided by elevated concentrations of atmospheric CO₂? Kubiske *et al.* (1998) grew cuttings of four quaking aspen genotypes for five months at CO₂ concentrations of 380 or 720 ppm and low or high soil nitrogen in open-top chambers in the field in Michigan (USA). Elevated CO₂ significantly increased net photosynthesis, regardless of soil nitrogen content, although there were no discernible increases in above-ground growth in the five-month study period. Belowground, elevated CO₂ significantly increased fine root production, but only in the high soil nitrogen treatment.

Zak *et al.* (2000) and Curtis *et al.* (2000) grew six aspen genotypes from cuttings in open-top chambers for 2.5 growing seasons at atmospheric CO₂ concentrations of 350 and 700 ppm on soils containing either adequate or inadequate supplies of nitrogen. At the end of this period, Curtis *et al.* found the trees growing in the doubled-CO₂ treatment exhibited rates of net photosynthesis 128 and 31% greater than those of the trees growing in the ambient-air treatment on

the high- and low-nitrogen soils, respectively. Zak *et al.* also determined the CO₂-induced biomass increases of the trees in the high- and low-nitrogen soils to be 38 and 16%, respectively.

Mikan *et al.* (2000) grew aspen cuttings for two years in open-top chambers receiving atmospheric CO₂ concentrations of 367 and 715 ppm in soils of low and high soil nitrogen concentrations. They report elevated CO₂ increased the total biomass of the aspen cuttings by 50 and 26% in the high and low soil nitrogen treatments, respectively, and it increased coarse root biomass by 78 and 24% in the same respective treatments.

Wang and Curtis (2001) grew cuttings of two male and two female aspen trees for about five months in open-top chambers maintained at atmospheric CO₂ concentrations of 380 and 765 ppm on soils of high and low nitrogen content. The male cuttings exhibited a modest difference in the CO₂-induced increase in total biomass (58 and 66% in the high- and low-nitrogen soils, respectively), and the female cuttings showed a much greater difference (82 and 22% in the same respective treatments).

Taken together, these observations suggest the aerial fertilization effect of atmospheric CO₂ enrichment stimulates the growth of young aspen trees in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting.

References

- Curtis, P.S., Vogel, C.S., Wang, X.Z., Pregitzer, K.S., Zak, D.R., Lussenhop, J., Kubiske, M., and Teeri, J.A. 2000. Gas exchange, leaf nitrogen, and growth efficiency of *Populus tremuloides* in a CO₂-enriched atmosphere. *Ecological Applications* **10**: 3–17.
- Kubiske, M.E., Pregitzer, K.S., Zak, D.R., and Mikan, C.J. 1998. Growth and C allocation of *Populus tremuloides* genotypes in response to atmospheric CO₂ and soil N availability. *New Phytologist* **140**: 251–260.
- Mikan, C.J., Zak, D.R., Kubiske, M.E., and Pregitzer, K.S. 2000. Combined effects of atmospheric CO₂ and N availability on the belowground carbon and nitrogen dynamics of aspen mesocosms. *Oecologia* **124**: 432–445.
- Wang, X. and Curtis, P.S. 2001. Gender-specific responses of *Populus tremuloides* to atmospheric CO₂ enrichment. *New Phytologist* **150**: 675–684.
- Zak, D.R., Pregitzer, K.S., Curtis, P.S., Vogel, C.S., Holmes, W.E., and Lussenhop, J. 2000. Atmospheric CO₂,

soil-N availability, and allocation of biomass and nitrogen by *Populus tremuloides*. *Ecological Applications* **10**: 34–46.

3.7.4.2 Pine

- Typically, the aerial fertilization effect of atmospheric CO₂ enrichment stimulates the growth of young pine trees in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting.

In a review of 11 papers dealing with both loblolly pine (*Pinus taeda* L.) and ponderosa pine (*Pinus ponderosa* Dougl.), Johnson *et al.* (1998) report when soil nitrogen levels were extremely deficient or so high as to be toxic, growth responses to atmospheric CO₂ enrichment in both species were negligible. For moderate soil nitrogen deficiencies, however, a doubling of the air's CO₂ content sometimes boosted growth by as much as 1,000%. In addition, atmospheric CO₂ enrichment mitigated the negative growth response of ponderosa pine to extremely high soil nitrogen concentrations.

Walker *et al.* (1998) raised ponderosa pine tree seedlings for two growing seasons in open-top chambers having CO₂ concentrations of 350, 525 and 700 ppm on soils of low, medium, and high nitrogen content. They found elevated CO₂ had little effect on most growth parameters after the first growing season, the one exception being belowground biomass, which increased with both CO₂ and soil nitrogen. After two growing seasons, however, elevated CO₂ significantly increased all growth parameters, including tree height, stem diameter, shoot weight, stem volume, and root volume, with the greatest responses typically occurring at the highest CO₂ concentration in the highest soil nitrogen treatment. Root volume at 700 ppm CO₂ and high soil nitrogen, for example, exceeded all other treatments by at least 45%, as did shoot volume, by 42%. Similarly, at high CO₂ and soil nitrogen, coarse root and shoot weights exceeded those at ambient CO₂ and high nitrogen by 80 and 88%, respectively.

Walker *et al.* (2000) published another paper on the same trees and treatments after five years of growth. At this time, the trees exposed to the twice-ambient levels of atmospheric CO₂ had heights 43, 64, and 25% greater than those of trees exposed to ambient air and conditions of high, medium, and low

soil nitrogen, respectively. The trunk diameters of the 700 ppm trees were 24, 73, and 20% greater than the trunk diameters of the ambient-grown trees exposed to high, medium, and low levels of soil nitrogen.

Entry *et al.* (1998) grew one-year-old longleaf pine seedlings for 20 months in pots of high and low soil nitrogen content in open-top chambers maintained at atmospheric CO₂ concentrations of 365 or 720 ppm, finding the elevated CO₂ caused no overall change in whole-plant biomass at low soil nitrogen, but at high soil nitrogen, it increased it by 42%. After two years of these treatments, Runion *et al.* (1999) report rates of net photosynthesis were about 50% greater in the high CO₂ treatment, irrespective of soil nitrogen content and water content.

Finzi and Schlesinger (2003) measured and analyzed the pool sizes and fluxes of inorganic and organic nitrogen (N) in the floor and top 30 cm of the mineral soil of the Duke Forest at the five-year point of a long-term FACE study, where half of the experimental plots were enriched with an extra 200 ppm of CO₂. They had hypothesized “the increase in carbon fluxes to the microbial community under elevated CO₂ would increase the rate of N immobilization over mineralization,” leading to a decline in the significant CO₂-induced stimulation of forest net primary production that developed over the first two years of the experiment (DeLucia *et al.*, 1999; Hamilton *et al.*, 2002). Quite to the contrary, however, they discovered “there was no statistically significant change in the cycling rate of N derived from soil organic matter under elevated CO₂.” Neither was the rate of net N mineralization significantly altered by elevated CO₂, nor was there any statistically significant difference in the concentration or net flux of organic and inorganic N in the forest floor and top 30 cm of mineral soil after five years of CO₂ fumigation. Thus they found no support for their hypothesis of growth stimulation provided by elevated levels of atmospheric CO₂ gradually becoming insignificant before the stand reached its equilibrium biomass—although they continued to cling to this unsubstantiated belief.

Taken together, these observations indicate the aerial fertilization effect of atmospheric CO₂ enrichment stimulates the growth of young pine trees in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting. Evidence also suggests at some point the response to increasing soil nitrogen saturates, and beyond that point, higher N

concentrations may reduce the growth response of young pine trees to elevated CO₂.

References

DeLucia, E.H., Hamilton, J.G., Naidu, S.L., Thomas, R.B., Andrews, J.A., Finzi, A., Lavine, M., Matamala, R., Mohan, J.E., Hendrey, G.R., and Schlesinger, W.H. 1999. Net primary production of a forest ecosystem with experimental CO₂ enrichment. *Science* **284**: 1177–1179.

Entry, J.A., Runion, G.B., Prior, S.A., Mitchell, R.J., and Rogers, H.H. 1998. Influence of CO₂ enrichment and nitrogen fertilization on tissue chemistry and carbon allocation in longleaf pine seedlings. *Plant and Soil* **200**: 3–11.

Finzi, A.C. and Schlesinger, W.H. 2003. Soil-nitrogen cycling in a pine forest exposed to 5 years of elevated carbon dioxide. *Ecosystems* **6**: 444–456.

Hamilton, J.G., DeLucia, E.H., George, K., Naidu, S.L., Finzi, A.C., and Schlesinger, W.H. 2002. Forest carbon balance under elevated CO₂. *Oecologia* **131**: 250–260.

Johnson, D.W., Thomas, R.B., Griffin, K.L., Tissue, D.T., Ball, J.T., Strain, B.R., and Walker, R.F. 1998. Effects of carbon dioxide and nitrogen on growth and nitrogen uptake in ponderosa and loblolly pine. *Journal of Environmental Quality* **27**: 414–425.

Runion, G.B., Mitchell, R.J., Green, T.H., Prior, S.A., Rogers, H.H., and Gjerstad, D.H. 1999. Longleaf pine photosynthetic response to soil resource availability and elevated atmospheric carbon dioxide. *Journal of Environmental Quality* **28**: 880–887.

Walker, R.F., Geisinger, D.R., Johnson, D.W., and Ball, J.T. 1998. Atmospheric CO₂ enrichment and soil N fertility effects on juvenile ponderosa pine: Growth, ectomycorrhizal development, and xylem water potential. *Forest Ecology and Management* **102**: 33–44.

Walker, R.F., Johnson, D.W., Geisinger, D.R., and Ball, J.T. 2000. Growth, nutrition, and water relations of ponderosa pine in a field soil as influenced by long-term exposure to elevated atmospheric CO₂. *Forest Ecology and Management* **137**: 1–11.

3.7.4.3 Spruce

- Typically, the aerial fertilization effect of CO₂ enrichment stimulates the growth of young spruce trees in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting.

Egli *et al.* (1998) rooted saplings of different genotypes of Norway spruce (*Picea abies* L. Karst.) directly into calcareous or acidic soils in open-top chambers and exposed them to atmospheric CO₂ concentrations of 370 or 570 ppm and low or high soil nitrogen contents. The authors report elevated CO₂ generally stimulated light-saturated rates of photosynthesis under all conditions by as much as 35%, regardless of genotype, which consistently led to increases in above-ground biomass production, also regardless of genotype without respect to soil type or nitrogen content.

Murray *et al.* (2000) grew Sitka spruce (*Picea sitchensis* (Bong.) Carr.) seedlings for two years in pots in open-top chambers maintained at atmospheric CO₂ concentrations of 355 and 700 ppm, where in the last year of the study, half of the seedlings received one-tenth of the optimal soil nitrogen supply recommended for this species and the other half received twice the optimal amount. The extra CO₂ increased the seedlings' light-saturated rates of net photosynthesis by 19 and 33% in the low- and high-nitrogen treatments, respectively, and it increased their total biomass by 0 and 37% in these same treatments. Murray *et al.* note there was a reallocation of biomass from above-ground organs (leaves and stems) into roots in the low-nitrogen treatment, and they remark this phenomenon "may provide a long-term mechanism by which Sitka spruce could utilize limited resources both more efficiently and effectively." This finding suggests although low soil nitrogen precluded a short-term CO₂-induced growth response in this tree species, it is possible the negative impact of nitrogen deficiency could be overcome in the course of much longer-term atmospheric CO₂ enrichment.

Liu *et al.* (2002) grew Sitka spruce seedlings in well-watered and -fertilized pots in open-top chambers maintained for three years at atmospheric CO₂ concentrations of either 350 or 700 ppm. They then planted the seedlings directly into native nutrient-deficient forest soil and maintained them at the same atmospheric CO₂ concentrations for two more years in larger open-top chambers either with or without extra nitrogen being supplied to the soil. After the first three years of the study, they determined the CO₂-enriched trees possessed 11.6% more total biomass than the ambient-treatment trees. At the end of the next two years, the CO₂-enriched trees supplied with extra nitrogen had 15.6% more total biomass than their similarly treated ambient-air counterparts, and the CO₂-enriched trees receiving no

extra nitrogen had 20.5% more biomass than their ambient-treatment counterparts.

Typically, the aerial fertilization effect of atmospheric CO₂ enrichment stimulates the growth of young spruce trees in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting. Evidence also suggests at some point the response to increasing soil nitrogen saturates, and beyond that point, higher N concentrations may reduce the growth response of young spruce trees to elevated CO₂.

References

Egli, P., Maurer, S., Gunthardt-Goerg, M.S., and Korner, C. 1998. Effects of elevated CO₂ and soil quality on leaf gas exchange and aboveground growth in beech-spruce model ecosystems. *New Phytologist* **140**: 185–196.

Liu, S.R., Barton, C., Lee, H., Jarvis, P.G., and Durrant, D. 2002. Long-term response of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) to CO₂ enrichment and nitrogen supply. I. Growth, biomass allocation and physiology. *Plant Biosystems* **136**: 189–198.

Murray, M.B., Smith, R.I., Friend, A., and Jarvis, P.G. 2000. Effect of elevated [CO₂] and varying nutrient application rates on physiology and biomass accumulation of Sitka spruce (*Picea sitchensis*). *Tree Physiology* **20**: 421–434.

3.7.4.4 Other

- Typically, the aerial fertilization effect of atmospheric CO₂ enrichment stimulates the growth of young tree species in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting.

Maillard *et al.* (2001) grew pedunculate oak seedlings for three to four months in greenhouses maintained at atmospheric CO₂ concentrations of either 350 or 700 ppm under conditions of either low or high soil nitrogen concentration. The elevated CO₂ of their study stimulated belowground growth in the seedlings growing in the nitrogen-poor soil, significantly increasing their root-to-shoot ratios. It increased both the below- and above-ground biomass of seedlings growing in nitrogen-rich soil. The CO₂-enriched seedlings growing in the nitrogen-rich soil produced 217 and 533% more stem and coarse-root biomass,

respectively, than their ambient-air counterparts growing in the same fertility treatment. Overall, the doubled CO₂ concentration of the air in their study enhanced total seedling biomass by approximately 30 and 140% under nitrogen-poor and nitrogen-rich soil conditions, respectively.

Schortemeyer *et al.* (1999) grew seedlings of *Acacia melanoxylon* (a leguminous nitrogen-fixing tree native to southeastern Australia) in hydroponic culture for six weeks in growth cabinets, where the air was maintained at CO₂ concentrations of either 350 or 700 ppm and the seedlings were supplied with water containing nitrogen in a number of concentrations ranging from 3 to 6,400 mmol m⁻³. In the two lowest of these nitrogen concentration treatments, final biomass was unaffected by atmospheric CO₂ enrichment; but it was increased by 5- to 10-fold at the highest nitrogen concentration.

Temperton *et al.* (2003) measured total biomass production in another N₂-fixing tree—*Alnus glutinosa* (the common alder)—seedlings of which had been grown for three years in open-top chambers in either ambient or elevated (ambient + 350 ppm) concentrations of atmospheric CO₂ and one of two soil nitrogen regimes (full nutrient solution or no fertilizer). The trees growing under low soil nutrient conditions exhibited essentially the same growth enhancement as the well-fertilized trees.

Gleadow *et al.* (1998) grew eucalyptus seedlings for six months in glasshouses maintained at atmospheric CO₂ concentrations of either 400 or 800 ppm, fertilizing them twice daily with low or high nitrogen solutions. Their doubling of the air's CO₂ concentration increased total seedling biomass by 134% in the low nitrogen treatment and 98% in the high nitrogen treatment. In addition, the elevated CO₂ led to greater root growth in the low nitrogen treatment, as indicated by a 33% higher root:shoot ratio.

Different species of young trees respond differently to atmospheric CO₂ enrichment under conditions of low vs. high soil nitrogen fertility. The most common response is for the growth-promoting effects of atmospheric CO₂ enrichment to be expressed to a greater degree when soil nitrogen fertility is optimal as opposed to less than optimal.

References

Gleadow, R.M., Foley, W.J., and Woodrow, I.E. 1998. Enhanced CO₂ alters the relationship between photosynthesis and defense in cyanogenic *Eucalyptus*

cladocalyx F. Muell. *Plant, Cell and Environment* **21**: 12–22.

Maillard, P., Guehl, J.-M., Muller, J.-F., and Gross, P. 2001. Interactive effects of elevated CO₂ concentration and nitrogen supply on partitioning of newly fixed ¹³C and ¹⁵N between shoot and roots of pedunculate oak seedlings (*Quercus robur* L.). *Tree Physiology* **21**: 163–172.

Schortemeyer, M., Atkin, O.K., McFarlane, N., and Evans, J.R. 1999. The impact of elevated atmospheric CO₂ and nitrate supply on growth, biomass allocation, nitrogen partitioning and N₂ fixation of *Acacia melanoxylon*. *Australian Journal of Plant Physiology* **26**: 737–774.

Temperton, V.M., Grayston, S.J., Jackson, G., Barton, C.V.M., Millard, P., and Jarvis, P.G. 2003. Effects of elevated carbon dioxide concentration on growth and nitrogen fixation in *Alnus glutinosa* in a long-term field experiment. *Tree Physiology* **23**: 1051–1059.

3.8 Ozone Pollution

3.8.1 Agricultural Species

- Atmospheric CO₂ enrichment typically reduces—and more often than not completely overrides—the negative effects of ozone pollution on the photosynthesis, growth, and yield of essentially all agricultural crops that have been experimentally evaluated.

3.8.1.1 Soybean

- The high ozone concentrations that will exist in many parts of the world in the future will have severe negative consequences for soybean production, all else being equal. However, the higher CO₂ concentration predicted for the future will have an important ameliorative effect on the adverse impact of this major air pollutant. It may compensate, or even more than compensate, for the potential negative consequences of elevated O₃.

Air pollution-induced productivity losses to agriculture are serious, especially to soybeans (*Glycine max* L.). Some appreciation for the magnitude of this problem can be gained by considering East Asia, which has 25% of the world's population but produces only 21% of humanity's cereal needs.

Wang and Mauzerall (2004) note air pollution, and especially that due to ozone (O₃), is an increasingly serious problem in this region, reducing agricultural productivity and exacerbating the problem of food security. The two researchers evaluate the impact of rising surface O₃ concentrations in East Asia on agricultural production in 1990 and its projected impact in 2020.

According to their “conservative estimates,” the two scientists write, “due to O₃ concentrations in 1990, China, Japan and south Korea lost ... 23–27% of their yield of soybeans,” and by 2020, the “loss due to increased levels of O₃ pollution is projected to increase to ... 28–35% for soybeans.” As a result of these and other O₃-induced crop losses, Wang and Mauzerall conclude, “East Asian countries are presently on the cusp of substantial reductions in grain production,” meaning they are also “on the cusp” of substantial reductions in food security.

Wahid *et al.* (2001) demonstrated the findings of Wang and Mauzerall are indeed “conservative.” In a study of the effects of ozone pollution in the Punjab region of Pakistan, Wahid *et al.* periodically applied a powerful ozone protectant to soybeans growing in three locations near the city of Lahore—a suburban site, a remote rural site, and a rural roadside site—throughout two growing seasons (one immediately post-monsoon and one the following spring or pre-monsoon).

At the suburban site, application of the ozone protectant increased the weight of soybean seeds produced per plant by 47% in the post-monsoon season and by 113% in the pre-monsoon season. At the remote rural site, the corresponding yield increases were 94% and 182%, and at the rural roadside site, they were 170% and 285%. Averaged across all three sites and both seasons of the year, the mean increase in yield caused by countering the deleterious effects of this major air pollutant was nearly 150%, and because they found “the impacts of ozone on the yield of soybean are larger in the rural areas around Lahore than in suburban areas of the city,” they conclude “there may be substantial impacts of oxidants on crop yield across large areas of the Punjab.”

Clearly, whatever can be done to reduce O₃-induced crop losses—or eliminate them altogether—would be considered a benefit in areas where such pollution is commonplace. Rising atmospheric CO₂ concentrations can help to alleviate this problem.

Miller *et al.* (1998) grew soybeans for one season in pots in open-top chambers maintained at atmos-

pheric CO₂ concentrations of 370, 482, 599, and 713 ppm in combination with atmospheric O₃ concentrations of 20, 50, and 79 ppb. By harvest time (113 days after planting), elevated CO₂ had significantly increased all biomass and growth variables measured, with the greatest enhancements occurring at the highest CO₂ and O₃ concentrations. Plants grown at 20 ppb O₃ and 713 ppm CO₂, for example, displayed total dry weights 48% greater than their ambient-air-grown counterparts, and plants grown at 79 ppb O₃ and 713 ppm CO₂ exhibited dry weights 53% greater than their ambient-air counterparts. Likewise, in the same experiment, Heagle *et al.* (1998) observed plants grown at 20 ppb O₃ and 713 ppm CO₂ displayed seed dry weights 20% greater than their ambient-air-grown counterparts, and plants grown at 79 ppb O₃ and 713 ppm CO₂ exhibited seed dry weights 74% greater.

Reid *et al.* (1998) grew soybeans in open-top chambers maintained at atmospheric CO₂ concentrations of 371 and 708 ppm and O₃ concentrations of 24 and 81 ppb. In the ambient-CO₂ air, the elevated O₃ exposure reduced the amount and activity of rubisco per unit leaf area, as well as leaf starch content. In the elevated-CO₂ air, elevated O₃ exposure had no effect on these three leaf parameters: the atmospheric CO₂ enrichment completely ameliorated potential O₃-induced damage.

Reid and Fiscus (1998) grew soybeans for a single season in pots placed in open-top chambers maintained at either ambient (365 ppm) or elevated (727 ppm) concentrations of atmospheric CO₂ and below-ambient (20 ppb) or 1.5 times ambient (74 ppb) levels of ozone. They found elevated CO₂ enhanced rates of photosynthesis regardless of the presence of ozone and typically ameliorated the negative effects of ozone on carbon assimilation.

In a literature review of O₃ and CO₂ effects on soybean photosynthesis, growth and yield, Morgan *et al.* (2003) write, “meta-analytic techniques were used to quantitatively summarize the response of soybean to an average, chronic ozone exposure of 70 ppb, from 53 peer-reviewed studies,” after which they similarly derived the net effect of concurrently elevated O₃ and CO₂ (to unspecified concentrations described as being “above 400 ppm”). They found “when both O₃ and CO₂ are elevated, the mean decrease in photosynthesis is 7%,” which “compares to a 20% loss for plants grown at elevated O₃ and the current ambient CO₂.” The three researchers also report, “at maturity, the average shoot biomass was decreased 34% and seed yield was 24% lower” in

response to elevated O₃ alone, but “seed yield decreases for plants grown in elevated O₃ and elevated CO₂ are only half of those for plants grown in current ambient CO₂ and elevated O₃.”

They also found “significant ozone responses in several plant parameters at low daily average concentrations (less than 60 ppb),” which is less than current concentrations in many locations. In studies where the O₃ treatment average was less than 60 ppb, they report, “seed yield, shoot and root dry weight were all significantly decreased by about 10%,” which suggests the atmospheric CO₂ enrichment employed in the joint O₃/CO₂ experiments likely would have completely eradicated the O₃-induced losses in plant production.

The findings of Booker *et al.* (2005a) suggest this conclusion is robust. They grew well-watered and well-fertilized soybeans from seeds sown either directly in the ground or in 15-liter pots out-of-doors in open-top chambers maintained at all combinations of low (24 ppb) or high (75 ppb) O₃ concentrations and ambient (373 ppm) or elevated (699 ppm) CO₂ concentrations in 1999, and in 21-liter pots maintained at all combinations of low (24 ppb) or high (75 ppb) O₃ concentrations and ambient (369 ppm) or elevated (717 ppm) CO₂ concentrations in 2000.

In 1999, in the pot-grown plants, the 212% increase in atmospheric O₃ concentration decreased net photosynthesis by approximately 21%. When the air’s CO₂ concentration was simultaneously increased by 87%, the negative impact of the O₃ increase was more than ameliorated, as the plants exposed to elevated concentrations of both gases exhibited net photosynthesis rates 26% greater than the plants growing in low O₃ and CO₂ air. Likewise, in the ground-grown plants, the 212% increase in atmospheric O₃ concentration decreased net photosynthesis by approximately 14%, but when the air’s CO₂ concentration was simultaneously increased by 87%, the negative impact of the O₃ increase was more than ameliorated, as the plants exposed to elevated concentrations of both gases exhibited net photosynthesis rates 40% greater than the plants growing in low O₃ and CO₂ air.

With respect to seed yield in 1999, in the pot-grown plants the 212% increase in atmospheric O₃ concentration decreased total seed biomass by approximately 27%, but when the air’s CO₂ concentration was boosted by 87%, the negative impact of the O₃ increase was also more than ameliorated, as the plants exposed to elevated concentrations of both gases produced 15% more total

seed biomass than those growing in low O₃ and CO₂ air. Likewise, in the ground-grown plants, the 212% increase in atmospheric O₃ concentration decreased total seed biomass by approximately 24%, but when the air's CO₂ concentration was boosted by 87%, the negative impact of the O₃ increase was more than ameliorated, as the plants exposed to elevated concentrations of both gases produced 15% more total seed biomass than those in low O₃ and CO₂ air.

With respect to seed yield in 2000, in the pot-grown plants the 212% increase in atmospheric O₃ concentration decreased total seed biomass by approximately 41%, but when the air's CO₂ concentration was simultaneously boosted by 94%, the negative impact of the O₃ increase was more than ameliorated, as the plants exposed to elevated concentrations of both gases produced 18% more total seed biomass than those in low O₃ and CO₂ air. Likewise, in the ground-grown plants, the 212% increase in atmospheric O₃ concentration decreased total seed biomass by approximately 39%, but when the air's CO₂ concentration was boosted by 94%, the negative impact of the O₃ increase was more than ameliorated, as the plants exposed to elevated concentrations of both gases produced 9% more total seed biomass than those in low O₃ and CO₂ air. In all of the many situations investigated by Booker *et al.*, slightly less than a doubling of the air's CO₂ concentration more than compensated for the deleterious effects of slightly more than a tripling of the atmosphere's O₃ concentration on both leaf net photosynthesis and total seed biomass production in soybeans.

In a similar two-year open-top chamber study of aboveground postharvest residue, Booker *et al.* (2005b) grew soybeans in reciprocal combinations of low and high atmospheric concentrations of O₃ (21 and 74 ppb, respectively) and CO₂ (370 and 714 ppm, respectively), finding residue mass input "is increased by elevated CO₂ and suppressed by O₃." They found elevated O₃ decreased aboveground postharvest residue by 15–46%, elevated CO₂ increased it by 28–56%, and in combination the CO₂ effect always predominated. In the case of leaves, for example, elevating the air's O₃ concentration dropped dry mass residue to only 54% of what it was under ambient conditions, and concurrently elevating the air's CO₂ concentration boosted it to 124% of what it was in ambient air. Corresponding results of 85% and 123% were obtained for petioles, 60% and 121% for stems, and 72% and 122% for husks. Consequently, as in the cases of net photosynthesis and seed yield investi-

gated by Booker *et al.* (2005a), the results of this study demonstrated a slightly less than doubling of the air's CO₂ concentration more than compensated for the deleterious effects of slightly more than a tripling of the air's O₃ concentration on the production of aboveground postharvest residue in soybeans.

Booker and Fiscus (2005) grew well-watered and well-fertilized soybean plants for two years (1998 and 1999) out-of-doors in 21-liter pots in open-top chambers from emergence to maturity and exposed them to either charcoal-filtered air, charcoal-filtered air plus an extra 336 ppm CO₂, charcoal-filtered air plus 1.5 times normal ambient O₃, or charcoal-filtered air plus an extra 336 ppm CO₂ and 1.5 times normal ambient O₃. They found the imposition of elevated CO₂ alone increased soybean pod biomass by 23.0%, the imposition of elevated O₃ alone decreased pod biomass by 13.3%, and the imposition of elevated CO₂ and O₃ together increased pod biomass by 23.0%.

Today's high ozone concentrations and the even-higher concentrations of the future have and will continue to have severe negative consequences for soybean production, all else being equal. But the atmosphere's current high CO₂ concentration, plus the higher concentration it will have in the future, ameliorates the adverse impacts of this major air pollutant and will continue to do so in the years to come. The anticipated concentrations of CO₂ may more than compensate for the negative effects of elevated O₃.

References

- Booker, F.L. and Fiscus, E.L. 2005. The role of ozone flux and antioxidants in the suppression of ozone injury by elevated CO₂ in soybean. *Journal of Experimental Botany* **56**: 2139–2151.
- Booker, F.L., Miller, J.E., Fiscus, E.L., Pursley, W.A., and Stefanski, L.A. 2005a. Comparative responses of container-versus ground-grown soybean to elevated carbon dioxide and ozone. *Crop Science* **45**: 883–895.
- Booker, F.L., Prior, S.A., Torbert, H.A., Fiscus, E.L., Pursley, W.A., and Hu, S. 2005b. Decomposition of soybean grown under elevated concentrations of CO₂ and O₃. *Global Change Biology* **11**: 685–698.
- Heagle, A.S., Miller, J.E., and Pursley, W.A. 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment: III. Yield and seed quality. *Crop Science* **38**: 128–134.

Miller, J.E., Heagle, A.S., and Pursley, W.A. 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment: II. Biomass and development. *Crop Science* **38**: 122–128.

Morgan, P.B., Ainsworth, E.A., and Long, S.P. 2003. How does elevated ozone impact soybean? A meta-analysis of photosynthesis, growth and yield. *Plant, Cell and Environment* **26**: 1317–1328.

Reid, C.D. and Fiscus, E.L. 1998. Effects of elevated [CO₂] and/or ozone on limitations to CO₂ assimilation in soybean (*Glycine max*). *Journal of Experimental Botany* **18**: 885–895.

Reid, C.D., Fiscus, E.L., and Burkey, K.O. 1998. Combined effects of chronic ozone and elevated CO₂ on rubisco activity and leaf components in soybean (*Glycine max*). *Journal of Experimental Botany* **49**: 1999–2011.

Wahid, A., Milne, E., Shamsi, S.R.A., Ashmore, M.R., and Marshall, F.M. 2001. Effects of oxidants on soybean growth and yield in the Pakistan Punjab. *Environmental Pollution* **113**: 271–280.

Wang, X. and Mauzerall, D.L. 2004. Characterizing distributions of surface ozone and its impact on grain production in China, Japan and South Korea: 1990 and 2020. *Atmospheric Environment* **38**: 4383–4402.

3.8.1.2 Wheat

- A number of studies conducted around the turn of the century demonstrate enriching the air with CO₂ substantially ameliorates a variety of negative influences of ozone pollution on the productivity of wheat plants.

Bender *et al.* (1999) analyzed the results of 13 open-top chamber studies in which spring wheat was grown at ambient and twice-ambient CO₂ concentrations in combination with ambient and elevated ozone (O₃) concentrations. They found the elevated O₃ treatment had little effect on growth and yield, suggesting either the O₃ concentrations employed in the studies were not high enough to elicit a negative response in the specific cultivar tested (Minaret) or the cultivar was highly tolerant of ozone. Consequently, elevated CO₂ was the primary variable influencing the growth and yield of the spring wheat. It proved very effective in this regard, increasing aboveground biomass by an average of 37% (with a range of 11 to 128%) and grain yield by an average of 35% (with a range of 11 to 121%).

Tiedemann and Firsching (2000) grew spring

wheat from germination to maturity in controlled-environment chambers maintained at ambient (377 ppm) and enriched (612 ppm) atmospheric CO₂ concentrations and ambient (20 ppb) and enriched (61 ppb) atmospheric O₃ concentrations. The extra CO₂ increased mean photosynthetic rates at both O₃ concentrations, with the greatest absolute photosynthetic rates and the largest CO₂-induced percentage increases in photosynthesis being observed in the elevated CO₂/elevated O₃ treatment. Total grain yield was also greatest in the high CO₂/high O₃ treatment, with the elevated CO₂ increasing total grain yield at high O₃ by 38% relative to that observed at ambient CO₂ and elevated O₃. Moreover, the absolute value of total grain yield in the high CO₂/high O₃ treatment was not significantly different from that produced at ambient O₃, regardless of the atmospheric CO₂ concentration. Atmospheric CO₂ enrichment completely ameliorated the deleterious effects of ozone on photosynthesis and yield in this study.

Pleijel *et al.* (2000) grew spring wheat in open-top chambers maintained at atmospheric CO₂ concentrations of 340 and 680 ppm for three consecutive years. They exposed some plants in each CO₂ treatment to ambient, 1.5 x ambient, and 2 x ambient O₃ concentrations. These elevated O₃ concentrations negatively influenced wheat yield at both atmospheric CO₂ concentrations. Grain yield was always higher for the plants grown in the CO₂-enriched air, averaging 13% greater over the three years of the study and leading the scientists who conducted the work to conclude “the positive effect of elevated CO₂ could compensate for the yield losses due to O₃.”

Vilhena-Cardoso and Barnes (2001) grew spring wheat for two months in environmental chambers fumigated with air containing atmospheric CO₂ concentrations of 350 and 700 ppm at ambient and elevated (75 ppb) O₃ concentrations in soils of low, medium, and high nitrogen content. The elevated O₃ treatment was shown to reduce photosynthetic rates in the ambient-CO₂-grown plants, but it had no effect on the CO₂-enriched plants, which maintained enhanced photosynthetic rates even in the high O₃ treatments. With respect to biomass production, elevated CO₂ increased total plant dry weight by 44, 29, and 12% at high, medium, and low soil nitrogen supply, respectively, and although elevated O₃ by itself reduced plant biomass, the simultaneous application of elevated CO₂ completely ameliorated this detrimental effect at all soil nitrogen concentrations.

Fangmeier and Bender (2002) analyzed mean

grain yields of spring wheat derived from the ESPACE-Wheat project of the European Stress Physiology and Climate Experiment—Project 1, which was conducted for three growing seasons at eight experimental field sites across Europe that employed atmospheric CO₂ concentrations of 380, 540, and 680 ppm and O₃ concentrations of 32.5 and 60.3 ppb for half-day periods (Jager *et al.*, 1999). They found the high O₃ stress reduced wheat yields by an average of about 12% at the ambient CO₂ concentration. As the air's CO₂ concentration was increased to 540 and 680 ppm, there were no longer any significant reductions in yield due to the high O₃ stress. Whereas wheat yield in ambient-O₃ air increased by 34% over the entire CO₂ enrichment range investigated (380 to 680 ppm), it increased by 46% in the high-O₃ air, once again more than compensating for the O₃-alone-induced yield losses.

The results described above indicate enriching the air with CO₂ substantially ameliorates a variety of negative influences of ozone pollution on the productivity of wheat plants.

References

Bender, J., Herstein, U., and Black, C.R. 1999. Growth and yield responses of spring wheat to increasing carbon dioxide, ozone and physiological stresses: a statistical analysis of 'ESPACE-wheat' results. *European Journal of Agronomy* **10**: 185–195.

Fangmeier, A. and Bender, J. 2002. Air pollutant combinations—Significance for future impact assessments on vegetation. *Phyton* **42**: 65–71.

Jager, H.-J., Hertstein, U., and Fangmeier, A. 1999. The European stress physiology and climate experiments—Project 1—Wheat. *European Journal of Agronomy* **10**: 153–260.

Pleijel, H., Gelang, J., Sild, E., Danielsson, H., Younis, S., Karlsson, P.-E., Wallin, G., Skarby, L., and Sellden, G. 2000. Effects of elevated carbon dioxide, ozone and water availability on spring wheat growth and yield. *Physiologia Plantarum* **108**: 61–70.

Tiedemann, A.V. and Firsching, K.H. 2000. Interactive effects of elevated ozone and carbon dioxide on growth and yield of leaf rust-infected versus non-infected wheat. *Environmental Pollution* **108**: 357–363.

Vilhena-Cardoso, J. and Barnes, J. 2001. Does nitrogen supply affect the response of wheat (*Triticum aestivum* cv. Hanno) to the combination of elevated CO₂ and O₃? *Journal of Experimental Botany* **52**: 1901–1911.

3.8.1.3 Other Species

- Atmospheric CO₂ enrichment typically reduces, and more often than not completely counteracts, the negative effects of ozone pollution on the photosynthesis, growth, and yield of almost all agricultural crops that have been experimentally evaluated.

In addition to soybean and wheat, several studies have examined the effects of elevated CO₂ and ozone on photosynthesis and growth in other agricultural crops. The main findings of some of these studies are described below.

Cotton plants grown by Booker (2000) at elevated ozone concentrations exhibited 25 and 48 percent reductions in leaf mass per unit area and foliar starch concentration, respectively, relative to control plants grown in ambient air. When the cotton plants were simultaneously exposed to twice-ambient CO₂ concentrations, the reductions in these parameters were only 5 and 7 percent, respectively.

Wolf and van Oijen (2002) used a validated potato model to predict increases in European tuber production ranging from 1,000 to 3,000 kg of dry matter per hectare in spite of concomitant increases in ozone concentrations and air temperatures. In a field-based study, Vandermeiren *et al.* (2005) studied the impact of future increases in atmospheric ozone (O₃) and carbon dioxide (CO₂) concentrations on yield and tuber quality in potato (*Solanum tuberosum* L.). This research endeavor, they write, was “the first large-scale open-top chamber project to provide field-based data spanning a wide range of European climatic conditions and ozone concentrations for a widely used cultivar, cv. Bintje.” After two years of intensive measurements made on potatoes growing throughout Europe—including Belgium, Finland, Germany, Ireland, Sweden, and the United Kingdom—they determined the relative yield losses expected to occur in response to O₃ concentrations projected to prevail in Europe at mid-century were a mere 5%. The four researchers also report “the prevailing conditions under climate scenarios for 2050 (including increases in temperature, solar radiation and CO₂ and O₃ concentrations) would increase the yield of irrigated potato crops by 2000–4000 kg ha⁻¹ in most regions in Europe, primarily because of the beneficial influence of increased atmospheric CO₂,” citing Wolf and Van Oijen (2003).

Plessl *et al.* (2005) grew well-watered and fertilized spring barley (*Hordeum vulgare* L. cv.

Scarlett) plants from seed for four weeks after emergence in containers located in controlled-environment chambers maintained at either ambient (400 ppm) or 1.75 x ambient (700 ppm) atmospheric CO₂ concentrations. They simultaneously exposed the plants to either ambient or 2 x ambient atmospheric O₃ concentrations, evaluating the individual and combined effects of the CO₂ and O₃ additions. The researchers report the “elevated CO₂ concentration significantly increased aboveground biomass [15%], root biomass [30%], and tiller number [41%], whereas double-ambient ozone significantly decreased these parameters.” When applied together, the “ozone-induced reductions in growth parameters were strongly overridden by 700 ppm CO₂.” In the doubled-ozone treatment, the 75% increase in the air’s CO₂ content increased the barley’s aboveground biomass by 42%, its root biomass by 75%, and its tiller number by 94%. Thus, a less than doubling of the air’s CO₂ concentration more than compensated for a full doubling of the air’s O₃ concentration, revealing the potential for the rise in the air’s CO₂ content to more than overcome the negative growth effects of elevated O₃ concentrations on spring barley.

Yonekura *et al.* (2005) grew komatsuna (*Brassica campestris* cv. Rakuten) and radish (*Raphanus sativus* cv. Akamaru) plants from seed (one to a pot) in 1.4-L pots filled with “black soil” in controlled-climate chambers for 30 days in air of one of four different daylight O₃ concentrations—0–5 (charcoal-filtered), 60, 90, or 120 ppb—after which they destructively harvested the plants and determined their final dry weights. In the case of komatsuna (Japanese mustard spinach), where the edible portion of the vegetable is produced aboveground, the mean aboveground dry weights of the plants at the end of their 30-day growth cycle were 0.76, 0.63, 0.53, and 0.39 g in the 0–5, 60, 90, and 120 ppb O₃ treatments, respectively, when grown in ambient air of 380 ppm CO₂. When grown in air of 760 ppm CO₂, aboveground weights for the same set of O₃ concentrations were 1.19, 1.10, 0.98, and 0.85 g, representing CO₂-induced growth enhancements of 57%, 75%, 85%, and 118%. The doubling of the air’s CO₂ concentration more than compensated for the negative impact caused by the highest of the four O₃ concentrations in ambient-CO₂ air, turning what would have been a 49% O₃-induced yield loss (from 0.76 to 0.39 g) into a 12% CO₂-induced yield gain (from 0.76 to 0.85 g).

In the case of radish, where the edible portion of the vegetable is produced belowground, the mean belowground dry weights of the plants at the end of

their 30-day growth cycle were 0.63, 0.59, 0.39, and 0.36 g in the 0–5, 60, 90, and 120 ppb O₃ treatments, respectively, when grown in ambient air of 380 ppm CO₂. When grown in air of 760 ppm CO₂, however, belowground weights for the same set of O₃ concentrations were 1.45, 1.34, 1.15, and 0.88 g, which represent CO₂-induced growth enhancements of 132%, 127%, 195%, and 144%. Once again, the doubling of the air’s CO₂ concentration more than compensated for the negative impact caused by the highest of the four O₃ concentrations in ambient-CO₂ air, turning what would have been a 43% O₃-induced yield loss (from 0.63 to 0.36 g) into a 40% CO₂-induced yield gain (from 0.63 to 0.88 g).

Burkey *et al.* (2007) grew peanuts (*Arachis hypogaea* L., cv NC-V11) in a field near Raleigh, North Carolina (USA) using standard agricultural practices for two years in open-top chambers maintained at all combinations of three CO₂ treatments (375, 548, and 730 ppm) and three O₃ treatments—charcoal-filtered air (CF, 22 ppb), non-filtered air (NF, 46 ppb), and O₃-enriched air (75 ppb)—after which they assessed peanut seed yields and qualities. They found “elevated CO₂ increased yield parameters 7 to 17% for plants grown in CF air and restored yield in NF air and elevated O₃ treatments to control or higher levels,” while “market grade characteristics and seed protein and oil contents were not affected by elevated O₃ and CO₂.”

The USDA Agricultural Research Service scientists conclude, in the case of peanuts, “the major impacts of rising atmospheric O₃ and CO₂ will be on productivity, not product quality,” and as to productivity, their data indicate the positive effects of the rise in the air’s CO₂ content should be able to compensate for concomitant future increases in tropospheric ozone concentrations. In fact, the continuing upward trend in atmospheric CO₂ concentration should more than compensate for any future increases in the air’s O₃ content, because the latter will likely be relatively small due to the strong negative influence of elevated atmospheric CO₂ concentrations on vegetative isoprene emissions (Monson *et al.*, 2007), which are responsible for increasing O₃ concentrations over land by perhaps 50% over what they would be in their absence (Poisson *et al.*, 2000). Similarly, Arneth *et al.* (2007) calculated that when the effect of CO₂ on vegetative isoprene emissions is included, a properly forced model “maintains global isoprene emissions in ± 15% of present values,” which should significantly temper the future rate-of-rise of the troposphere’s ozone

concentration.

Tu *et al.* (2009) grew *Arachis hypogaea* L. plants from seed to maturity out-of-doors near Raleigh, North Carolina (USA) in open-top chambers under adequately watered and fertilized conditions, exposing the plants to charcoal-filtered air, which was thus ozone-free, ambient air of unaltered ozone (O_3) concentration, and air containing 1.6 times the ambient O_3 concentration. All of these O_3 treatments were exposed to air of 376, 550, and 730 ppm CO_2 . At the end of this period they harvested the crop and measured its final stem, leaf, and pod biomass.

They found “elevated CO_2 generally increased biomass production while O_3 suppressed it, and CO_2 ameliorated the O_3 effect.” In terms of the season-long mean of midday net photosynthesis, for example, the 94% increase in the air’s CO_2 concentration experienced in going from the lowest to the highest CO_2 treatment resulted in a 25% increase in net photosynthesis in the charcoal-filtered air, a 50% increase in the non-filtered air, and a 104% increase in the ozone-polluted air. As to the final aboveground biomass produced, the corresponding CO_2 -induced increases were 10%, 41%, and 105%.

The four researchers also note “at mid-vegetative growth, elevated CO_2 significantly reduced leaf nitrogen concentrations by up to 44%,” but “plant nitrogen concentrations only differed by 8% among CO_2 treatments at harvest while N_2 fixation was increased.” They say their experiment suggests “symbiotic N_2 fixation is important for maintaining seed N concentrations and that CO_2 enhancement of symbiotic N_2 fixation may compensate for low soil N availability.”

Tu *et al.* state a number of experiments, like theirs, “have shown that elevated CO_2 can offset the adverse effects of O_3 on crop biomass production and yield,” citing Olszyk *et al.* (2000), Fuhrer (2003), and Fiscus *et al.* (2005). In addition, they note “the protective effect of elevated CO_2 against O_3 injury has been observed in a number of C_3 plant species, including cotton, peanut, rice, soybean, and wheat, due in large part to a reduction in O_3 uptake from reduced stomatal conductance and possibly from increases in photoassimilation rates and antioxidant metabolism,” citing McKee *et al.* (2000), Booker and Fiscus (2005), Fiscus *et al.* (2005), and Booker *et al.* (2007).

Kumari *et al.* (2013) studied Palak (*Beta vulgaris* L. var Allgreen), “a cheap and popular leafy vegetable preferred mainly for iron content in the diet,” which is “widely grown” and “suitable for all

seasons in north India.” Recognizing the global growth in both atmospheric CO_2 (an aerial fertilizer) and tropospheric ozone (O_3 , an aerial pollutant) over the past two centuries, plus their anticipated future increases, Kumari *et al.* examined the interactive effects of these contrasting atmospheric molecules on the growth of palak. The three Indian researchers utilized open-top chambers at the botanical garden of Banaras Hindu University in the eastern Gangetic plains of India during December 2008 and January 2009, measuring morphological, biochemical, and yield responses of palak to ambient (A) and elevated (E) levels of CO_2 and O_3 , alone and in combination. The atmospheric CO_2 concentrations employed in this study were ambient (normal air) and 570 ppm, and the O_3 concentrations utilized were ambient and ambient + 20 ppb, with the elevated values selected to match predicted concentrations at the end of the century under the A1B scenario of IPCC (2007).

Their analysis revealed elevated CO_2 enhanced various plant growth parameters in palak, including root length, shoot length, number of leaves, leaf area, root biomass, shoot biomass, total plant biomass, and yield (compare the ECO_2 values in Table 3.8.1.3.1 with the ACO_2 values), and elevated concentrations of ozone had a negative effect (compare the EO_3 values in Table 3.8.1.3.1 with the $ACO_2 + AO_3$ values). When enhanced ozone and enhanced carbon dioxide were tested together, the growth-enhancing effects of CO_2 were sufficient in every instance to overpower the growth-retarding effects of ozone for every plant parameter measured (compare the $ECO_2 + EO_3$ values in Table 3.8.1.3.1 with the $ACO_2 + AO_3$ values).

Kumari *et al.* conclude, for IPCC-predicted atmospheric concentrations of CO_2 and O_3 at the end of the century, “palak is going to be benefited as biomass enhancement was more under $ECO_2 + EO_3$ compared to $ACO_2 + AO_3$.”

These studies indicate atmospheric CO_2 enrichment reduces, and more often than not completely overrides, the negative effects of ozone pollution on plant photosynthesis, growth, and yield.

References

- Arneth, A., Miller, P.A., Scholze, M., Hickler, T., Schurgers, G., Smith, B., and Prentice, I.C. 2007. CO_2 inhibition of global terrestrial isoprene emissions: Potential implications for atmospheric chemistry. *Geophysical Research Letters* **34**: 10.1029/2007GL030615.
- Booker, F.L. 2000. Influence of carbon dioxide enrichment,

Parameters	50 DAG				
	ACO ₂	ACO ₂ + AO ₃	ECO ₂	EO ₃	ECO ₂ + EO ₃
Root length (cm)	9.6	7.6	10.6	6.4	8.7
Shoot length (cm)	36.5	32.0	39.7	28.7	32.3
Number of leaves	13.66	10.00	22.66	7.66	11.33
Leaf area (cm ²)	626	496	983	390	589
Root biomass (g plant ⁻¹)	0.36	0.22	0.53	0.14	0.34
Shoot biomass (g plant ⁻¹)	2.1	1.5	3.3	1.2	2.5
Total biomass (g plant ⁻¹)	2.5	1.7	3.8	1.3	2.8
Yield (g plant ⁻¹)	38.2	30.0	51.9	22.5	34.8

ACO₂ = Ambient CO₂, ACO₂ + AO₃ = Ambient CO₂ + Ambient O₃, ECO₂ = Elevated CO₂,
EO₃ = Elevated O₃ + Ambient CO₂, ECO₂ + EO₃ = Elevated CO₂ + Elevated O₃.

Table 3.8.1.3.1. Growth parameters of palak plants under different treatments of O₃ and CO₂, individually and in combination at 50 days after germination (DAG). Adapted from Kumari et al. (2013).

ozone and nitrogen fertilization on cotton (*Gossypium hirsutum* L.) leaf and root composition. *Plant, Cell and Environment* **23**: 573–583.

Booker, F.L., Burkey, K.O., Pursley, W.A., and Heagle, A.S. 2007. Elevated carbon dioxide and ozone effects on peanut: I. Gas-exchange, biomass, and leaf chemistry. *Crop Science* **47**: 1475–1487.

Booker, F.L. and Fiscus, E.L. 2005. The role of ozone flux and antioxidants in the suppression of ozone injury by elevated CO₂ in soybean. *Journal of Experimental Botany* **56**: 2139–2151.

Burkey, K.O., Booker, F.L., Pursley, W.A., and Heagle, A.S. 2007. Elevated carbon dioxide and ozone effects on peanut: II. Seed yield and quality. *Crop Science* **47**: 1488–1497.

Fiscus, E.L., Booker, F.L. and Burkey, K.O. 2005. Crop responses to ozone: Uptake, modes of action, carbon assimilation and partitioning. *Plant, Cell and Environment* **28**: 997–1011.

Fuhrer, J. 2003. Agroecosystem responses to combinations of elevated CO₂, ozone, and global climate change. *Agriculture, Ecosystems and Environment* **97**: 1–20.

IPCC. 2007. *Climate Change 2007. The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom.

Kumari, S., Agrawal, M., and Tiwari, S. 2013. Impact of elevated CO₂ and elevated O₃ on *Beta vulgaris* L.: Pigments, metabolites, antioxidants, growth and yield. *Environmental Pollution* **174**: 279–288.

McKee, I.F., Mulholland, B.J., Craigan, J., Black, C.R., and Long, S.P. 2000. Elevated concentrations of atmospheric CO₂ protect against and compensate for O₃ damage to photosynthetic tissues of field-grown wheat. *New Phytologist* **146**: 427–435.

Monson, R.K., Trahan, N., Rosenstiel, T.N., Veres, P., Moore, D., Wilkinson, M., Norby, R.J., Volder, A., Tjoelker, M.G., Briske, D.D., Karnosky, D.F., and Fall, R. 2007. Isoprene emission from terrestrial ecosystems in response to global change: minding the gap between models and observations. *Philosophical Transactions of the Royal Society A* **365**: 1677–1695.

Olszyk, D.M., Tingey, D.T., Watrud, L., Seidler, R., and Andersen, C. 2000. Interactive effects of O₃ and CO₂: Implications for terrestrial ecosystems. In Singh, S.N. (Ed.) *Trace Gas Emissions and Plants*. Kluwer Academic, Dordrecht, the Netherlands, pp. 97–136.

Plessl, M., Heller, W., Payer, H.-D., Elstner, E.F., Habermeyer, J., and Heiser, I. 2005. Growth parameters and resistance against *Drechslera teres* of spring barley (*Hordeum vulgare* L. cv. Scarlett) grown at elevated ozone and carbon dioxide concentrations. *Plant Biology* **7**: 694–705.

Poisson, N., Kanakidou, M., and Crutzen, P.J. 2000.

Impact of non-methane hydrocarbons on tropospheric chemistry and the oxidizing power of the global troposphere: 3-dimensional modeling results. *Journal of Atmospheric Chemistry* **36**: 157–230.

Tu, C., Booker, F.L., Burkey, K.O., and Hu, S. 2009. Elevated atmospheric carbon dioxide and O₃ differentially alter nitrogen acquisition in peanut. *Crop Science* **49**: 1827–1836.

Vandermeiren, K., Black, C., Pleijel, H., and De Temmerman, L. 2005. Impact of rising tropospheric ozone on potato: effects on photosynthesis, growth, productivity and yield quality. *Plant, Cell and Environment* **28**: 982–996.

Wolf, J. and van Oijen, M. 2002. Modelling the dependence of European potato yields on changes in climate and CO₂. *Agricultural and Forest Meteorology* **112**: 217–231.

Wolf, J. and van Oijen, M. 2003. Model simulation of effects of changes in climate and atmospheric CO₂ and O₃ on tuber yield potential of potato (cv. Bintje) in the European Union. *Agriculture, Ecosystems and Environment* **94**: 141–157.

Yonekura, T., Kihira, A., Shimada, T., Miwa, M., Aruzate, A., Izuta, T., and Ogawa, K. 2005. Impacts of O₃ and CO₂ enrichment on growth of Komatsuna (*Brassica campestris*) and radish (*Raphanus sativus*). *Phyton* **45**: 229–235.

3.8.2 Tree Species

3.8.2.1 Aspen

- Earth's aspen trees, like much of the rest of the biosphere, are better equipped to live long and productive lives in CO₂-enriched air, even when experiencing the generally negative influence of atmospheric ozone pollution.

Trees grown in CO₂-enriched air nearly always exhibit increased rates of photosynthesis and biomass production, and trees grown in ozone (O₃)-enriched air tend to experience the opposite effects. So what happens when both of these trace constituents of the atmosphere increase together? This question is explored below with respect to the most widely distributed tree species of North America: quaking aspen (*Populus tremuloides* Michx.).

Karnosky *et al.* (1999) describe how they grew O₃-sensitive and O₃-tolerant aspen clones in 30-m diameter plots at the Aspen FACE site near Rhinelander, Wisconsin (USA), where the young

trees were maintained at atmospheric CO₂ concentrations of either 360 or 560 ppm either with or without exposure to elevated O₃ (1.5 times the ambient ozone concentration). After one year of growth at ambient CO₂, the researchers found elevated O₃ caused visible injury to leaves of both types of aspen, with the average percent damage in O₃-sensitive clones more than three times as great as observed in O₃-tolerant clones (55% vs. 17%, respectively). In combination with elevated CO₂, the O₃-induced damage to the leaves of these same clones was only 38% and 3%, respectively. Thus elevated CO₂ prevented much of the foliar damage that otherwise would have been induced by the high O₃ concentrations.

King *et al.* (2001) studied the same young trees for two years, concentrating on belowground growth, where elevated O₃ alone had no effect on fine-root biomass. When the two aspen clones were simultaneously exposed to elevated CO₂ and O₃, there was an approximate 66% increase in the fine-root biomass of both. Wustman *et al.* (2001) found the aspen clones exposed to both elevated ozone and CO₂ had 40% fewer visible foliar injuries than clones exposed to elevated ozone and ambient CO₂.

Noormets *et al.* (2001) studied the interactive effects of O₃ and CO₂ on photosynthesis in the aspen trees at the same facility, finding elevated CO₂ increased rates of photosynthesis in both clones at all leaf positions. Maximum rates of photosynthesis increased in the O₃-tolerant clone by averages of 33 and 49% due to elevated CO₂ alone and in combination with elevated O₃, respectively, and in the O₃-sensitive clone they increased by 38% in both cases. Elevated-CO₂-induced increases in maximal rates of net photosynthesis were typically maintained, and sometimes even increased, during simultaneous exposure to elevated O₃.

In another phase of the same experiment, Oksanen *et al.* (2001) found, after three years of treatment, ozone exposure caused significant structural injuries to thylakoid membranes and the stromal compartments in the chloroplasts of the trees' leaves, but they note these injuries were largely ameliorated by atmospheric CO₂ enrichment. Likewise, leaf thickness, mesophyll tissue thickness, the amount of chloroplasts per unit cell area, and the amount of starch in the leaf chloroplasts were all decreased in the high ozone treatment, but simultaneous exposure of the ozone-stressed trees to elevated CO₂ more than compensated for the ozone-induced reductions.

After four years of growing five aspen clones with varying degrees of tolerance to ozone under the same experimental conditions, McDonald *et al.* (2002) developed what they term a “competitive stress index,” based on the heights of the four nearest neighbors of each tree, in order to study the influence of competition on the CO₂ growth response of the various clones as modified by ozone. This work showed elevated O₃ reduced aspen growth independent of competitive status, and the four researchers note an “apparent convergence of competitive performance responses in +CO₂ +O₃ conditions,” which suggests “stand diversity may be maintained at a higher level” in such circumstances.

Percy *et al.* (2002) utilized the same experimental setting to assess a number of the aspen trees’ growth characteristics and the responses of one plant pathogen and two insects with different feeding strategies that typically attack the trees. Of the plant pathogen studied, they write, “the poplar leaf rust, *Melampsora medusae*, is common on aspen and belongs to the most widely occurring group of foliage diseases.” As for the two insects, they note “the forest tent caterpillar, *Malacosoma disstria*, is a common leaf-chewing lepidopteran in North American hardwood forests” and “the sap-feeding aphid, *Chaitophorus stevensis*, infests aspen throughout its range.” Thus the rust and the two insect pests the scientists studied are widespread and have significant deleterious impacts on trembling aspen and other tree species. Percy *et al.* note “the forest tent caterpillar has defoliated more deciduous forest than any other insect in North America” and “outbreaks can reduce timber yield up to 90% in one year, and increase tree vulnerability to disease and environmental stress.”

Percy *et al.* found elevated O₃ by itself decreased tree height and trunk diameter, increased rust occurrence by nearly fourfold, improved tent caterpillar performance by increasing female pupal mass by 31%, and had a strong negative effect on the natural enemies of aphids. The addition of the extra CO₂ completely ameliorated the negative effects of elevated O₃ on tree height and trunk diameter, reduced the O₃-induced enhancement of rust development from nearly fourfold to just over twofold, completely ameliorated the enhancement of female tent caterpillar pupal mass caused by elevated O₃, and also completely ameliorated the reduction in the abundance of natural enemies of aphids caused by elevated O₃.

Also studying the Aspen FACE site, Holton *et al.* (2003) raised parasitized and non-parasitized forest

tent caterpillars on two quaking aspen genotypes (O₃-sensitive and O₃-tolerant) alone and in combination for one full growing season. They too found elevated O₃ improved tent caterpillar performance under ambient CO₂ conditions but not in CO₂-enriched air. Thus it is clear elevated ozone concentrations have significant negative impacts on the well-being of North America’s most widely distributed tree species, and elevated carbon dioxide concentrations have significant positive impacts that often completely override the negative impacts of elevated O₃. Therefore, if the tropospheric O₃ concentration rises as expected (Percy *et al.* note “damaging O₃ concentrations currently occur over 29% of the world’s temperate and subpolar forests but are predicted to affect fully 60% by 2100”), a concomitant rise in the air’s CO₂ content will help to prevent damage to the planet’s aspen trees.

Working at the same site, Oksanen *et al.* (2003) report they were able to “visualize and locate ozone-induced H₂O₂ [hydrogen peroxide] accumulation within leaf mesophyll cells, and relate oxidative stress with structural injuries in aspen.” They discovered “H₂O₂ accumulation was found only in ozone-exposed leaves and not in the presence of elevated CO₂,” leading them to conclude “CO₂ enrichment appears to alleviate chloroplastic oxidative stress.”

King *et al.* (2005) evaluated the effect of CO₂ enrichment alone, O₃ enrichment alone, and the net effect of CO₂ and O₃ enrichment together after seven years of treatment at the Aspen FACE site. Relative to the ambient-air treatment, they found elevated CO₂ increased total biomass by 25%, whereas elevated O₃ decreased it by 23%. The combination of elevated CO₂ and O₃ resulted in a total biomass response of -7.8% relative to the control. King *et al.* thus conclude “exposure to even moderate levels of O₃ significantly reduces the capacity of net primary productivity to respond to elevated CO₂ in some forests.” They suggest it makes sense to move forward with technologies that reduce anthropogenic precursors to photochemical O₃ formation, because their use would decrease an important constraint on the ability of forest ecosystems to benefit from the rise in the air’s CO₂ concentration.

Kubiske *et al.* (2006) found individual tree and stand growth at the Aspen FACE site were significantly increased by the elevated CO₂ treatment but decreased by the elevated O₃ treatment, and the two effects essentially negated each other for no net change in the combined CO₂ plus O₃ treatment. They also state “growth in elevated CO₂ continued to

increase each year but at a decreasing rate,” such that “the annual growth increases under elevated CO₂ became smaller with each successive year.” They examined several possible explanations for this phenomenon, including N limitations and water limitations.

The eight researchers write, “inter-annual variation in soil moisture did not modify the CO₂ or O₃ responses,” and “N limitations on growth did not differ among treatments.” In addition, they report “root-specific uptake of nitrate or ammonium was not affected by elevated CO₂ or O₃.” The growth response to elevated CO₂ “paralleled decreasing July PPF [photosynthetic photon flux] from 2001 through 2004, and decreasing previous October temperatures from 2001 to 2003.” Kubiske *et al.* conclude “a several-year trend of increasingly cloudy summers and cool autumns was responsible for the decrease in CO₂ growth response,” explaining, “July PPF directly influences the amount of photosynthate available for stem volume growth,” and “October temperature in the north-temperate latitudes is of major importance in the photosynthetic activity of trees before leaf senescence,” the stored products of which are used “to support the determinate growth phase the following year.”

Reporting the results of their study of the Wisconsin aspen trees during the eighth and ninth years of growing-season CO₂ enrichment, Riikonen *et al.* (2008) state elevated O₃ decreased net photosynthesis in aspen clone 42E by 30% and clone 271 by 13%, averaged over the growing season, and in aspen clone 216 by 42% in the late-season. Elevated CO₂ increased net photosynthesis in aspen clones 42E and 271 by 73 and 52%, respectively, averaged over the growing season, and in aspen clone 216, measured in the late-season only, elevated CO₂ enhanced net photosynthesis by 42%. They write, “elevated CO₂ delayed, and elevated O₃ tended to accelerate, leaf abscission in autumn.” When both treatments were applied together, they report, “elevated CO₂ generally ameliorated the effects of elevated O₃,” noting “leaf stomatal conductance was usually lowest in the combination treatment, which probably caused a reduction in O₃ uptake.”

Kostiainen *et al.* (2008) studied interactive effects of elevated concentrations of CO₂ and O₃ on radial growth, wood chemistry, and structure of five 5-year-old trembling aspen clones at the Wisconsin FACE facility, where they had been exposed to four treatments—control, elevated CO₂ (560 ppm), elevated O₃ (1.5 x ambient), and their combination—

for five full growing seasons. The researchers report, “elevated CO₂ in the presence of ambient O₃ tended to increase, and elevated O₃ in the presence of ambient CO₂ tended to decrease, stem radial growth,” whereas “stem radial growth of trees in the combined elevated CO₂ + O₃ treatment did not differ from controls.” None of the structural variables of the aspen wood was affected by the elevated CO₂ treatment, but elevated O₃ tended to decrease vessel lumen diameter.

Reporting on another aspect of the long-term aspen study at the Wisconsin FACE facility, Udling *et al.* (2008) investigated how a 40% increase above ambient values in CO₂ and O₃, alone and in combination, affected tree water use where “measurements of sap flux and canopy leaf area index (*L*) were made during two growing seasons, when steady-state *L* had been reached after more than 6 years of exposure to elevated CO₂ and O₃.” The 40% increase in atmospheric CO₂ increased tree size and *L* by 40%, and the 40% increase in O₃ concentration decreased tree size and *L* by 22%. The combined effect of the two trace gas increases was an 18% increase in maximum stand-level sap flux. In addition, elevated O₃ predisposed aspen stands to drought-induced sap flux reductions, whereas increased tree water use in response to elevated CO₂ did not result in lower soil water content in the upper soil or decreasing sap flux relative to control values during dry periods.

Thus the negative effects of O₃ enrichment on tree growth and leaf development were more than compensated by the positive effects of an equal percentage increase in atmospheric CO₂ concentration. And although the net effect on sap flux was positive (so that the trees transferred more water to the atmosphere), when the aspen stands needed moisture most (during times of drought), the water was available to them, possibly because they “were growing in soil with CO₂-induced increases in litter build-up and water-holding capacity of the upper soil,” as these latter two benefits and the extra water they could supply to the trees were lacking when the trees were exposed to elevated ozone.

Pregitzer *et al.* (2008) write, “all root biomass sampling previous to 2002 showed that O₃ exposure, alone or in combination with elevated CO₂, consistently resulted in lower coarse root biomass.” In analyzing more recent data, they determined the elevated O₃ treatment significantly increased fine-root biomass in the aspen trees and, in combination with elevated CO₂, increased coarse root biomass in them

as well. They conclude “the amount of carbon being allocated to aspen fine-root biomass under elevated O_3 is increasing over time relative to the control, especially in the elevated CO_2 and elevated O_3 treatment,” in contrast with most shorter-term results, including those of King *et al.* (2001). Consequently, they conclude “the positive effects of elevated CO_2 on belowground net primary productivity may not be offset by negative effects of O_3 .”

Andrew and Lilleskov (2009) note sporocarps (the reproductive structures of fungi) can be significant carbon sinks for the ectomycorrhizal fungi that develop symbiotic relationships with plants by forming sheaths around their root tips, where they are the last sinks for carbon in the long and winding pathway that begins at the source of carbon assimilation in plant leaves. The researchers say “it is critical to understand how ectomycorrhizal fungal sporocarps are affected by elevated CO_2 and O_3 ” because “sporocarps facilitate genetic recombination, permit long-distance dispersal and contribute to food webs.”

They sampled aboveground sporocarps for four years at the Aspen FACE site, which provided, they write, a “unique opportunity to examine the effects of both elevated CO_2 and O_3 on a forested ecosystem.” They conducted their examination during years 4 through 7 of the long-term study. They report total mean sporocarp biomass “was generally lowest under elevated O_3 with ambient CO_2 ,” and it “was greatest under elevated CO_2 , regardless of O_3 concentration.” They state there was “a complete elimination of O_3 effects on sporocarp production when [extra] CO_2 was added,” noting they “expect that the responses seen in the present study were conservative compared to those expected under regional to global changes in CO_2 and O_3 .”

By itself, or in combination with rising ozone concentrations, the rise in the air’s CO_2 content appears destined to enhance the genetic recombination and long-distance dispersal of the ectomycorrhizal fungi that form symbiotic relationships with the roots of aspen and other trees, thereby positively contributing to various food webs that will be found in Earth’s forests of the future.

Zak *et al.* (2011) noted how both insufficient soil nitrogen (N) and an overabundance of atmospheric ozone have been claimed to either partially or totally repress the many positive effects of elevated atmospheric CO_2 concentrations on plant growth and development, especially in the case of long-lived woody plants such as trees. However, they write, the

combined effects of elevated CO_2 and elevated O_3 (eCO_2 and eO_3) “remain undocumented in the context of long-term, replicated field experiments.” In 1997 the four researchers planted at the Rhinelander (Wisconsin, USA) FACE facility one-half of each of 12 FACE plots with various trembling aspen (*Populus tremuloides*) genotypes (8, 42, 216, 259, 271) of differing CO_2 and O_3 sensitivities. They planted one-quarter of each ring with a single aspen genotype (226) and paper birch (*Betula papyrifera*), and another quarter of each ring with the same single aspen genotype and sugar maple (*Acer saccharum*). The authors maintained each FACE plot for 12 years at either ambient CO_2 and O_3 (aCO_2 and aO_3), aCO_2 and eO_3 , eCO_2 and aO_3 , or eCO_2 and eO_3 —where eCO_2 was 560 ppm, and where eO_3 was in the range of 50–60 nmol/mol—while they collected numerous types of pertinent data.

In reference to the progressive nitrogen limitation hypothesis, Zak *et al.* (2011) say they “found no evidence of this effect after 12 years of eCO_2 exposure.” Relative to net primary production (NPP) under aCO_2 , they found a 26% increase in NPP in the eCO_2 treatment over the last three years of the study, which for a more standard 300-ppm increase in atmospheric CO_2 concentration equates to an approximate 42% increase in NPP. The increase “was sustained by greater root exploration of soil for growth-limiting N, as well as more rapid rates of litter decomposition and microbial N release during decay.”

With respect to the concomitant stress of O_3 pollution, the researchers report, “despite eO_3 -induced reductions in plant growth that occurred early in the experiment (i.e., after three years of exposure), eO_3 had no effect on NPP during the 10th–12th years of exposure.” This response, they write, “appears to result from the compensatory growth of eO_3 -tolerant genotypes and species as the growth of eO_3 -sensitive individuals declined over time (Kubiske *et al.*, 2007; Zak *et al.*, 2007), thereby causing NPP to attain equivalent levels under ambient O_3 and elevated O_3 .”

Zak *et al.* (2011) write, “NPP in the three plant communities responded similarly to the combined eCO_2 and eO_3 treatment.” And “given the degree to which eO_3 has been projected to decrease global NPP (Felzer *et al.*, 2005), the compensatory growth of eO_3 -tolerant plants in our experiment should be considered in future simulations and, depending on the generality of this response, could dramatically diminish the negative effect of eO_3 on NPP and carbon storage on land.”

The four researchers ultimately conclude if forests of similar composition growing throughout northeastern North America respond in the same manner as those in their experiment (Cole *et al.*, 2009), enhanced forest NPP under eCO₂ may be sustained for a longer duration than previously had been thought possible. They conclude, “the negative effect of eO₃ may be diminished by compensatory growth of eO₃-tolerant plants as they begin to dominate forest communities (Kubiske *et al.*, 2007; Zak *et al.*, 2007), suggesting that aspects of biodiversity like genetic diversity and species composition are important components of ecosystem response to this agent of global change.”

References

- Andrew, C. and Lilleskov, E.A. 2009. Productivity and community structure of ectomycorrhizal fungal sporocarps under increased atmospheric CO₂ and O₃. *Ecology Letters* **12**: 813–822.
- Cole, C.T., Anderson, J.E., Lindroth, R.L., and Waller, D.M. 2009. Rising concentrations of atmospheric CO₂ have increased growth of natural stands of quaking aspen (*Populus tremuloides*). *Global Change Biology* **16**: 2186–2197.
- Felzer, B., Reilly, J., Melillo, J., Kicklighter, D., Sarofim, M., Wang, C., Prinn, R., and Zhuang, Q. 2005. Future effects of ozone on carbon sequestration and climate change policy using a global biogeochemical model. *Climatic Change* **73**: 345–373.
- Holton, M.K., Lindroth, R.L., and Nordheim, E.V. 2003. Foliar quality influences tree-herbivore-parasitoid interactions: effects of elevated CO₂, O₃, and plant genotype. *Oecologia* **137**: 233–244.
- Karnosky, D.F., Mankovska, B., Percy, K., Dickson, R.E., Podila, G.K., Sober, J., Noormets, A., Hendrey, G., Coleman, M.D., Kubiske, M., Pregitzer, K.S., and Isebrands, J.G. 1999. Effects of tropospheric O₃ on trembling aspen and interaction with CO₂: results from an O₃-gradient and a FACE experiment. *Water, Air, and Soil Pollution* **116**: 311–322.
- King, J.S., Kubiske, M.E., Pregitzer, K.S., Hendrey, G.R., McDonald, E.P., Giardina, C.P., Quinn, V.S., and Karnosky, D.F. 2005. Tropospheric O₃ compromises net primary production in young stands of trembling aspen, paper birch and sugar maple in response to elevated atmospheric CO₂. *New Phytologist* **168**: 623–636.
- King, J.S., Pregitzer, K.S., Zak, D.R., Sober, J., Isebrands, J.G., Dickson, R.E., Hendrey, G.R., and Karnosky, D.F. 2001. Fine-root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO₂ and tropospheric O₃. *Oecologia* **128**: 237–250.
- Kostiainen, K., Kaakinen, S., Warsta, E., Kubiske, M.E., Nelson, N.D., Sober, J., Karnosky, D.F., Saranpaa, P., and Vapaavuori, E. 2008. Wood properties of trembling aspen and paper birch after 5 years of exposure to elevated concentrations of CO₂ and O₃. *Tree Physiology* **28**: 805–813.
- Kubiske, M.E., Quinn, V.S., Heilman, W.E., McDonald, E.P., Marquardt, P.E., Teclaw, R.M., Friend, A.L., and Karnosky, D.F. 2006. Interannual climatic variation mediates elevated CO₂ and O₃ effects on forest growth. *Global Change Biology* **12**: 1054–1068.
- Kubiske, M.E., Quinn, V.S., Marquardt, P.E., and Karnosky, D.F. 2007. Effects of elevated atmospheric CO₂ and/or O₃ on intra- and inter-specific competitive ability of aspen. *Plant Biology* **9**: 342–355.
- McDonald, E.P., Kruger, E.L., Riemenschneider, D.E., and Isebrands, J.G. 2002. Competitive status influences tree-growth responses to elevated CO₂ and O₃ in aggrading aspen stands. *Functional Ecology* **16**: 792–801.
- Noormets, A., Sober, A., Pell, E.J., Dickson, R.E., Podila, G.K., Sober, J., Isebrands, J.G., and Karnosky, D.F. 2001. Stomatal and non-stomatal limitation to photosynthesis in two trembling aspen (*Populus tremuloides* Michx.) clones exposed to elevated CO₂ and O₃. *Plant, Cell and Environment* **24**: 327–336.
- Oksanen, E., Haikio, E., Sober, J., and Karnosky, D.F. 2003. Ozone-induced H₂O₂ accumulation in field-grown aspen and birch is linked to foliar ultrastructure and peroxisomal activity. *New Phytologist* **161**: 791–799.
- Oksanen, E., Sober, J., and Karnosky, D.F. 2001. Impacts of elevated CO₂ and/or O₃ on leaf ultrastructure of aspen (*Populus tremuloides*) and birch (*Betula papyrifera*) in the Aspen FACE experiment. *Environmental Pollution* **115**: 437–446.
- Percy, K.E., Awmack, C.S., Lindroth, R.L., Kubiske, M.E., Kopper, B.J., Isebrands, J.G., Pregitzer, K.S., Hendrey, G.R., Dickson, R.E., Zak, D.R., Oksanen, E., Sober, J., Harrington, R., and Karnosky, D.F. 2002. Altered performance of forest pests under atmospheres enriched by CO₂ and O₃. *Nature* **420**: 403–407.
- Pregitzer, K.S., Burton, A.J., King, J.S., and Zak, D.R. 2008. Soil respiration, root biomass, and root turnover following long-term exposure of northern forests to elevated atmospheric CO₂ and tropospheric O₃. *New Phytologist* **180**: 153–161.
- Riikonen, J., Kets, K., Darbah, J., Oksanen, E., Sober, A.,

Vapaavuori, E., Kubiske, M.E., Nelson, N., and Karnosky, D.F. 2008. Carbon gain and bud physiology in *Populus tremuloides* and *Betula papyrifera* grown under long-term exposure to elevated concentrations of CO₂ and O₃. *Tree Physiology* **28**: 243–254.

Uddling, J., Teclaw, R.M., Kubiske, M.E., Pregitzer, K.S., and Ellsworth, D.S. 2008. Sap flux in pure aspen and mixed aspen-birch forests exposed to elevated concentrations of carbon dioxide and ozone. *Tree Physiology* **28**: 1231–1243.

Wustman, B.A., Oksanen, E., Karnosky, D.F., Noormets, A., Isebrands, J.G., Pregitzer, K.S., Hendrey, G.R., Sober, J., and Podila, G.K. 2001. Effects of elevated CO₂ and O₃ on aspen clones varying in O₃ sensitivity: Can CO₂ ameliorate the harmful effects of O₃? *Environmental Pollution* **115**: 473–481.

Zak, D.R., Holmes, W.E., Pregitzer, K.S., King, J.S., Ellsworth, D.S., and Kubiske, M.E. 2007. Belowground competition and the response of developing forest communities to atmospheric CO₂ and O₃. *Global Change Biology* **13**: 2230–2238.

Zak, D.R., Pregitzer, K.S., Kubiske, M.E., and Burton, A.J. 2011. Forest productivity under elevated CO₂ and O₃: positive feedbacks to soil N cycling sustain decade-long net primary productivity enhancement by CO₂. *Ecology Letters* **14**: 1220–1226.

3.8.2.2 Beech

- Even when faced with the generally negative influence of atmospheric ozone pollution on their leaves, shoot axes, coarse roots, and fine roots, as well as the carbohydrate (starch and soluble sugar) contents and concentrations of those plant parts, these adverse effects of ozone on beech trees are typically more than counteracted by atmospheric CO₂ enrichment.

In discussing the problem of elevated tropospheric ozone (O₃) concentrations, Liu *et al.* (2004) write, “ozone is considered to be one of the air pollutants most detrimental to plant growth and development in both urban and rural environments (Lefohn, 1992; Skarby *et al.*, 1998; Matyssek and Innes, 1999),” because it “reduces the growth and yield of numerous agronomic crops as well as fruit and forest trees (Retzlaff *et al.*, 1997; Fumagalli *et al.*, 2001; Matyssek and Sandermann, 2003).” In addition, they note ozone concentrations are “currently two to three times higher than in the early 1900s (Galloway, 1998;

Fowler *et al.*, 1999),” and likely “will remain high in the future (Elvingson, 2001).” This section addresses studies that have examined the effects of ozone on European beech (*Fagus sylvatica* L.) trees.

Liu *et al.* (2005) grew three- and four-year-old European beech seedlings for five months in well-watered and -fertilized soil in containers located in walk-in phytotrons maintained at either ambient or ambient + 300 ppm CO₂ (each subdivided into ambient and double-ambient O₃ concentration treatments, with maximum ozone levels restricted to <150 ppb), in both monoculture and in competition with Norway spruce. They examined the effects of each treatment on leaf non-structural carbohydrate levels (soluble sugars and starch), finding the effects of elevated O₃ alone on non-structural carbohydrate levels were small when the beech seedlings were grown in monoculture. When they were grown in mixed culture, the elevated O₃ slightly enhanced leaf sugar levels but reduced starch levels by 50%.

With respect to elevated CO₂ alone, for the beech seedlings grown in both monoculture and mixed culture, levels of sugar and starch were significantly enhanced. Thus, when elevated O₃ and CO₂ significantly affected non-structural carbohydrate levels, elevated CO₂ tended to enhance them, whereas elevated O₃ tended to reduce them. The combined effects of elevated CO₂ and O₃ acting together were such as to produce a significant increase in leaf non-structural carbohydrates in both mixed and monoculture conditions. The researchers conclude “since the responses to the combined exposure were more similar to elevated pCO₂ than to elevated pO₃, apparently elevated pCO₂ overruled the effects of elevated pO₃ on non-structural carbohydrates.”

Grams *et al.* (1999) grew European beech seedlings in glasshouses maintained at average atmospheric CO₂ concentrations of either 367 or 667 ppm for one year. Throughout the following year, in addition to being exposed to the same set of CO₂ concentrations, the seedlings were exposed to either ambient or twice-ambient levels of O₃. Elevated O₃ significantly reduced photosynthesis in beech seedlings grown at ambient CO₂ concentrations by a factor of approximately three. In the CO₂-enriched air, the seedlings did not exhibit any photosynthetic reduction due to the doubled O₃ concentration. The photosynthetic rates of the CO₂-enriched seedlings rose by 8% when simultaneously fumigated with elevated O₃, leading the five researchers to conclude long-term acclimation to elevated CO₂ supply does indeed counteract the O₃-induced decline of photosynthetic

light and dark reactions.

Liu *et al.* (2004) grew three- and four-year-old beech seedlings for two growing seasons under the same experimental conditions as Liu *et al.* (2005) after the seedlings had been pre-acclimated for one year to either the ambient or elevated CO₂ treatment. At the end of the study, the plants were harvested and fresh weights and dry biomass values were determined for leaves, shoot axes, coarse roots, and fine roots, as were carbohydrate (starch and soluble sugar) contents and concentrations for the same plant parts. The results falsified the hypothesis that “prolonged exposure to elevated CO₂ does not compensate for the adverse ozone effects on European beech,” instead revealing all “adverse effects of ozone on carbohydrate concentrations and contents were counteracted when trees were grown in elevated CO₂.”

These results add more evidence of the ability of increased CO₂ concentrations to fight—and overpower—the deleterious consequences of one of the world’s most devastating air pollutants.

References

Elvingson, P. 2001. For the most parts steadily down. *Acid News* 3: 20–21.

Fowler, D., Cape, J.N., Coyle, M., Flechard, C., Kuylenstierna, J., Hicks, K., Derwent, D., Johnson, C., and Stevenson, D. 1999. The global exposure of forests to air pollutants. In: Sheppard, L.J. and Cape, J.N. (Eds.) *Forest Growth Responses to the Pollution Climate of the 21st Century*. Kluwer Academic Publisher, Dordrecht, The Netherlands.

Fumagalli, I., Gimeno, B.S., Velissariou, D., De Temmerman, L., and Mills, G. 2001. Evidence of ozone-induced adverse effects on crops in the Mediterranean region. *Atmospheric Environment* 35: 2583–2587.

Galloway, J.N. 1998. The global nitrogen cycle: changes and consequences. *Environmental Pollution* 102: 15–24.

Grams, T.E.E., Anegg, S., Haberle, K.-H., Langebartels, C., and Matyssek, R. 1999. Interactions of chronic exposure to elevated CO₂ and O₃ levels in the photosynthetic light and dark reactions of European beech (*Fagus sylvatica*). *New Phytologist* 144: 95–107.

Lefohn, A.S. 1992. *Surface Level Ozone Exposure and Their Effects on Vegetation*. Lewis Publishers, Chelsea, UK.

Liu, X.-P., Grams, T.E.E., Matyssek, R., and Rennenberg, H. 2005. Effects of elevated pCO₂ and/or pO₃ on C-, N-, and S-metabolites in the leaves of juvenile beech and

spruce differ between trees grown in monoculture and mixed culture. *Plant Physiology and Biochemistry* 43: 147–154.

Liu, X., Kozovits, A.R., Grams, T.E.E., Blaschke, H., Rennenberg, H., and Matyssek, R. 2004. Competition modifies effects of ozone/carbon dioxide concentrations on carbohydrate and biomass accumulation in juvenile Norway spruce and European beech. *Tree Physiology* 24: 1045–1055.

Matyssek, R. and Innes, J.L. 1999. Ozone—a risk factor for trees and forests in Europe? *Water, Air and Soil Pollution* 116: 199–226.

Matyssek, R. and Sandermann, H. 2003. Impact of ozone on trees: an ecophysiological perspective. *Progress in Botany* 64: 349–404.

Retzlaff, W.A., Williams, L.E., and DeJong, T.M. 1997. Growth and yield response of commercial bearing-age “Casselman” plum trees to various ozone partial pressures. *Journal of Environmental Quality* 26: 858–865.

Skarby, L., Ro-Poulsen, H., Wellburn, F.A.M., and Sheppard, L.J. 1998. Impacts of ozone on forests: a European perspective. *New Phytologist* 139: 109–122.

3.8.2.3 Birch

- Birch trees are generally harmed by rising ozone concentrations, but when the air’s CO₂ concentration is also rising, these negative effects are generally eliminated and replaced by positive responses.

At the free-air CO₂ enrichment (FACE) facility located near Rhinelander, Wisconsin (USA), King *et al.* (2001) grew a mixture of paper birch and quaking aspen trees in 30-m-diameter plots maintained at atmospheric CO₂ concentrations of 360 and 560 ppm with and without exposure to elevated O₃ (1.5 times the ambient O₃ concentration) for two years. The extra O₃ had no effect on the growth of fine roots over that period, but elevated O₃ and CO₂ together increased the fine-root biomass of the mixed stand by 83%.

At the same FACE facility, Oksanen *et al.* (2001) observed O₃-induced injuries in the thylakoid membranes of the chloroplasts of the birch trees’ leaves, but the injuries were partially ameliorated in the elevated CO₂ treatment. And in a study conducted two years later, Oksanen *et al.* (2003) “were able to visualize and locate ozone-induced H₂O₂ accumu-

lation within leaf mesophyll cells, and relate oxidative stress with structural injuries.” They report “H₂O₂ accumulation was found only in ozone-exposed leaves and not in the presence of elevated CO₂,” adding “CO₂ enrichment appears to alleviate chloroplastic oxidative stress.”

In Finland, Kull *et al.* (2003) constructed open-top chambers around two clones (V5952 and K1659) of silver birch saplings rooted in the ground and growing there for the past seven years. These chambers were then fumigated with air containing 360 and 720 ppm CO₂ in combination with 30 and 50 ppb O₃ for two growing seasons, after which it was reported the extra O₃ had significantly decreased branching in the trees’ crowns. This effect was almost completely ameliorated by a doubling of the air’s CO₂ content. In addition, after one more year of study, Eichelmann *et al.* (2004) report the increase in the air’s CO₂ content by itself increased the average net photosynthetic rates of both clones by approximately 16%, whereas the increased O₃ by itself caused a 10% decline in the average photosynthetic rate of clone V5952, although not of clone K1659. When both gases were simultaneously increased, the photosynthetic rate of clone V5952 once again experienced a 16% increase in net photosynthesis, as if the extra O₃ had had no effect when applied in the presence of the extra CO₂.

Riikonen *et al.* (2004) harvested the same trees and reported “the negative effects of elevated O₃ were found mainly in ambient CO₂, not in elevated CO₂.” Doubling the air’s O₃ concentration decreased total biomass production by 13% across both clones, but simultaneously doubling the air’s CO₂ concentration increased total biomass production by 30%, more than compensating for the deleterious consequences of doubling the atmospheric ozone concentration.

The Finnish scientists say this ameliorating effect of elevated CO₂ “may be associated with either increased detoxification capacity as a consequence of higher carbohydrate concentrations in leaves grown in elevated CO₂, or decreased stomatal conductance and thus decreasing O₃ uptake in elevated CO₂ conditions (e.g., Rao *et al.*, 1995).” They also note “the ameliorating effect of elevated CO₂ is in accordance with the results of single-season open-top chamber and growth chamber studies on small saplings of various deciduous tree species (Mortensen 1995; Dickson *et al.*, 1998; Loats and Rebeck, 1999) and long-term open-field and open-OTC studies with aspen and yellow-poplar (Percy *et al.*, 2002; Rebeck and Scherzer, 2002).”

Peltonen *et al.* (2005) evaluated the impacts of doubled atmospheric CO₂ and O₃ concentrations on the accumulation of 27 phenolic compounds in the leaves of the silver birch trees, finding elevated CO₂ increased the concentration of phenolic acids (+25%), myricetin glycosides (+18%), catechin derivatives (+13%), and soluble condensed tannins (+19%). Elevated O₃ increased the concentration of one glucoside by 22%, chlorogenic acid by 19%, and flavone aglycons by 4%. Peltonen *et al.* say this O₃-induced production of antioxidant phenolic compounds “did not seem to protect the birch leaves from detrimental O₃ effects on leaf weight and area, but may have even exacerbated them.” In the combined elevated CO₂ and O₃ treatment, they write, “elevated CO₂ did seem to protect the leaves from elevated O₃ because all the O₃-derived effects on the leaf phenolics and traits were prevented by elevated CO₂.”

At the Rhinelander, Wisconsin (USA) FACE facility, Agrell *et al.* (2005) examined the effects of ambient and elevated concentrations of atmospheric CO₂ and O₃ on the foliar chemistry of birch and aspen trees, plus the consequences of these effects for host plant preferences of forest tent caterpillar larvae. They note “the only chemical component showing a somewhat consistent co-variation with larval preferences was condensed tannins,” and they report “the tree becoming relatively less preferred as a result of CO₂ or O₃ treatment was in general also the one for which average levels of condensed tannins were most positively (or least negatively) affected by that treatment.”

The researchers found the mean condensed tannin concentration of birch leaves was 18% higher in the elevated CO₂ and O₃ treatment. Consequently, as atmospheric concentrations of CO₂ and O₃ continue to rise, the increases in condensed tannin concentrations likely to occur in the foliage of birch trees should lead to their leaves becoming less preferred for consumption by the forest tent caterpillar, which according to Agrell *et al.* is “an eruptive generalist defoliator in North American hardwood forests, causing extensive damage during outbreak years (Fitzgerald, 1995).”

King *et al.* (2005) evaluated the effect of CO₂ enrichment alone, O₃ enrichment alone, and the net effect of both CO₂ and O₃ enrichment together on the growth of the Rhinelander birch trees. In the ambient-air control treatment, elevated CO₂ increased total biomass by 45% in the aspen-birch community; elevated O₃ caused a 13% reduction in total biomass relative to the control. The combination of elevated

CO₂ and O₃ resulted in a total biomass increase of 8.4% relative to the control aspen-birch community. King *et al.* conclude “exposure to even moderate levels of O₃ significantly reduces the capacity of net primary productivity to respond to elevated CO₂ in some forests.”

Kostiainen *et al.* (2006) studied the effects of elevated CO₂ and O₃ on various wood properties of silver birch. They found the elevated CO₂ treatment had no effect on wood structure but increased annual ring width by 21%, woody biomass by 23%, and trunk starch concentration by 7%. Elevated O₃ decreased stem vessel percentage in one of the clones by 10% but had no effect on vessel percentage in the presence of elevated CO₂.

Kostiainen *et al.* note, “in the xylem of angiosperms, water movement occurs principally in vessels (Kozlowski and Pallardy, 1997),” and “the observed decrease in vessel percentage by elevated O₃ may affect water transport.” They continue, “elevated CO₂ ameliorated the O₃-induced decrease in vessel percentage.” In addition, they note “the concentration of nonstructural carbohydrates (starch and soluble sugars) in tree tissues is considered a measure of carbon shortage or surplus for growth (Korner, 2003).” They conclude “starch accumulation observed under elevated CO₂ in this study indicates a surplus of carbohydrates produced by enhanced photosynthesis of the same trees (Riikonen *et al.*, 2004).” In addition, they report, “during winter, starch reserves in the stem are gradually transformed to soluble carbohydrates involved in freezing tolerance (Bertrand *et al.*, 1999; Piispanen and Saranpää, 2001),” so “the increase in starch concentration may improve acclimation in winter.”

At the Rhinelander FACE studies of paper birch, Darbah *et al.* (2007) found the total number of trees that flowered increased by 139% under elevated CO₂ but only 40% under elevated O₃. With respect to the quantity of flowers produced, elevated CO₂ led to a 262% increase and elevated O₃ led to only a 75% increase. They also determined elevated CO₂ had significant positive effects on birch catkin size, weight, and germination success rate, with elevated CO₂ increasing the germination rate of birch by 110%, decreasing seedling mortality by 73%, increasing seed weight by 17%, and increasing new seedling root length by 59%. Just the opposite was true of elevated O₃, as it decreased the germination rate of birch by 62%, decreased seed weight by 25%, and increased new seedling root length by only 15%.

Darbah *et al.* report “the seeds produced under

elevated O₃ had much less stored carbohydrate, lipids, and proteins for the newly developing seedlings to depend on and, hence, the slow growth rate.” They conclude, “seedling recruitment will be enhanced under elevated CO₂ but reduced under elevated O₃,” another important reason to hope the atmosphere’s CO₂ concentration continues to climb as long as the air’s O₃ content is doing so as well.

Riikonen *et al.* (2008) studied physiological consequences of increases in the atmospheric concentrations of CO₂ (+36%) and O₃ (+39%)—both alone and in combination—in paper birch trees during the eighth and ninth years of growing-season CO₂ enrichment at the Rhinelander FACE site. They determined elevated O₃ decreased net photosynthesis in birch short-shoot leaves by 27%, averaged over the growing season, and in birch long-shoot leaves by 23% in the late season, whereas elevated CO₂ increased net photosynthesis in birch short-shoot leaves by 49% averaged over the growing season. They also report, for birch long-shoot leaves, measured in the late-season only, elevated CO₂ enhanced net photosynthesis by 42%. In addition, “elevated CO₂ delayed, and elevated O₃ tended to accelerate, leaf abscission in autumn.” When both treatments were applied together, the scientists note, “elevated CO₂ generally ameliorated the effects of elevated O₃,” adding “leaf stomatal conductance was usually lowest in the combination treatment, which probably caused a reduction in O₃ uptake.”

Darbah *et al.* (2008) at various times over the 2004–2007 growing seasons collected many types of data pertaining to flowering, seed production, seed germination, and new seedling growth and development of young paper birch trees at the Rhinelander FACE site. Giving results for O₃ elevation first and CO₂ enrichment second (as best can be determined from Darbah *et al.*’s graphs and text), the following percentage changes were derived for:

- number of trees producing male flowers: (+86%, +140%) in 2006, (+70%, +70%) in 2007,
- total number of male flowers produced (+58%, +260%) in 2006, (+68%, +82%) in 2007,
- mean catkin or flower cluster mass (-8%, +12%) in 2004,
- mean seed mass (-22%, +10%) in 2004, (-24%, +17%) in 2005, (-22%, -2%) in 2006,

Climate Change Reconsidered II: Biological Impacts

- mean seed germination success (-70%, +70%) in 2004, (-60%, +110%) in 2005, (-50%, +20%) in 2006,
- mean seedling mortality, where the greatest reductions represent the greatest benefits, (-9%, -73%) in 2004,
- mean seedling root length (+15%, +59%) in 2004,
- mean seedling shoot length (-7%, +21%) in 2004,
- mean seedling cotyledon length (-5%, +13%) in 2004, and
- mean seedling dry mass after approximately five months growth in ambient air (-38%, +69%) in 2004.

Summarizing their findings, the six researchers write, “in this study, we found that elevated CO₂ enhances and elevated O₃ decreases birch reproduction and early seedling growth,” while in the concluding sentence of their abstract, they write, “the evidence from this study indicates that elevated CO₂ may have a largely positive impact on forest tree reproduction and regeneration while elevated O₃ will likely have a negative impact.”

Kostiainen *et al.* (2008) investigated the interactive effects of elevated concentrations of CO₂ and O₃ on the wood chemistry of paper birch saplings at the FACE facility in Rhineland, where the saplings had been exposed to four treatments—control, elevated CO₂ (560 ppm), elevated O₃ (1.5 x ambient), and their combination—for five growing seasons. They found the paper birch saplings exhibited a tendency for increased stem diameter in elevated CO₂, that also caused “an increase in extractives,” such as fats, waxes, triterpenoids, and steroids, that have important roles to play in defense against pathogens and other biotic attacks. The nine researchers conclude the increased growth they observed in response to elevated CO₂ “can be foreseen to shorten rotation lengths, with only moderate changes in wood properties,” which is good. However, “in response to elevated O₃, stem wood production decreased and was accompanied by changes in vessel properties, which may indicate decreasing efficiency of water and nutrient transport,” which is not good. Here, too, the major negative effects of the elevated O₃ concentration were reversed by the positive effects of the elevated CO₂ concentration.

Uddling *et al.* (2008) studied how a 40% increase in CO₂ and O₃, alone and in combination, affected tree water use of mixed aspen-birch forests in the Rhineland FACE study, where sap flux and canopy leaf area index (*L*) were measured during two growing seasons, when steady-state *L* had been reached after more than six years of exposure to elevated CO₂ and O₃. The 40% increase in atmospheric CO₂ concentration increased tree size and *L* by 40%, and the 40% increase in O₃ concentration decreased tree size and *L* by 22%. The combined effect of the two trace gas increases was an 18% increase in maximum stand-level sap flux in the mixed tree stands.

Pregitzer *et al.* (2008) write, “all root biomass sampling [at the Rhineland FACE facility] previous to 2002 showed that O₃ exposure, alone or in combination with elevated CO₂, consistently resulted in lower coarse root biomass for all plant communities.” In their analysis of subsequent data, however, they found +O₃ in combination with +CO₂ increased coarse root biomass in birch/aspen communities, leading them to conclude the amount of carbon being allocated to fine-root biomass under elevated O₃ was increasing over time relative to the control, especially in the +CO₂ +O₃ treatment, in contrast with most shorter-term results. They conclude, “the positive effects of elevated CO₂ on belowground net primary productivity may not be offset by negative effects of O₃.”

For three years (1999–2001) Vapaavuori *et al.* (2009) grew 20 initially seven-years-old individual trees of each of two different silver birch (*Betula pendula* Roth) clones—4 and 80 (V5952 and K1659, respectively, in the Finnish forest genetic register)—out-of-doors at the Suonenjoki Research Unit site of the Finnish Forest Research Institute in individual open-top chambers maintained at all combinations of ambient CO₂ and ambient O₃, ambient CO₂ and double O₃, double CO₂ and ambient O₃, and double CO₂ and double O₃, where CO₂ treatments were imposed 24 hours per day and O₃ treatments were imposed for 12, 12, and 14 hours per day in 1999, 2000, and 2001, respectively. Throughout the course of the experiment they measured a variety of plant physiological responses to the four treatments, including net photosynthesis, leaf stomatal conductance, leaf soluble proteins, leaf phenolic compounds, leaf nutrient concentrations, trunk and branch growth, physiology of the foliage and root systems, crown structure, wood properties, and interactions with folivorous insects.

The 12 scientists report the negative effects of elevated O₃ on the various growth parameters and properties of the trees “were mainly found in ambient CO₂,” noting elevated CO₂ typically “reversed or diminished the effects of elevated O₃.”

References

- Agrell, J., Kopper, B., McDonald, E.P., and Lindroth, R.L. 2005. CO₂ and O₃ effects on host plant preferences of the forest tent caterpillar (*Malacosoma disstria*). *Global Change Biology* **11**: 588–599.
- Bertrand, A., Robitaille, G., Nadeau, P., and Castonguay, Y. 1999. Influence of ozone on cold acclimation in sugar maple seedlings. *Tree Physiology* **19**: 527–534.
- Darbah, J.N.T., Kubiske, M.E., Nelson, N., Oksanen, E., Vapaavuori, E., and Karnosky, D.F. 2007. Impacts of elevated atmospheric CO₂ and O₃ on paper birch (*Betula papyrifera*): Reproductive fitness. *The Scientific World Journal* **7**(S1): 240–246.
- Darbah, J.N.T., Kubiske, M.E., Nelson, N., Oksanen, E., Vapaavuori, E., and Karnosky, D.F. 2008. Effects of decadal exposure to interacting elevated CO₂ and/or O₃ on paper birch (*Betula papyrifera*) reproduction. *Environmental Pollution* **155**: 446–452.
- Dickson, R.E., Coleman, M.D., Riemenschneider, D.E., Isebrands, J.G., Hogan, G.D., and Karnosky, D.F. 1998. Growth of five hybrid poplar genotypes exposed to interacting elevated [CO₂] and [O₃]. *Canadian Journal of Forest Research* **28**: 1706–1716.
- Eichelmann, H., Oja, V., Rasulov, B., Padu, E., Bichele, I., Pettai, H., Mols, T., Kasparova, I., Vapaavuori, E., and Laisk, A. 2004. Photosynthetic parameters of birch (*Betula pendula* Roth) leaves growing in normal and in CO₂- and O₃-enriched atmospheres. *Plant, Cell and Environment* **27**: 479–495.
- Fitzgerald, T.D. 1995. *The Tent Caterpillars*. Comstock Publishing, Ithaca, New York, USA.
- King, J.S., Kubiske, M.E., Pregitzer, K.S., Hendrey, G.R., McDonald, E.P., Giardina, C.P., Quinn, V.S., and Karnosky, D.F. 2005. Tropospheric O₃ compromises net primary production in young stands of trembling aspen, paper birch and sugar maple in response to elevated atmospheric CO₂. *New Phytologist* **168**: 623–636.
- King, J.S., Pregitzer, K.S., Zak, D.R., Sober, J., Isebrands, J.G., Dickson, R.E., Hendrey, G.R., and Karnosky, D.F. 2001. Fine-root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO₂ and tropospheric O₃. *Oecologia* **128**: 237–250.
- Korner, C. 2003. Carbon limitation in trees. *Journal of Ecology* **91**: 4–17.
- Kostiainen, K., Jalkanen, H., Kaakinen, S., Saranpaa, P., and Vapaavuori, E. 2006. Wood properties of two silver birch clones exposed to elevated CO₂ and O₃. *Global Change Biology* **12**: 1230–1240.
- Kostiainen, K., Kaakinen, S., Warsta, E., Kubiske, M.E., Nelson, N.D., Sober, J., Karnosky, D.F., Saranpaa, P., and Vapaavuori, E. 2008. Wood properties of trembling aspen and paper birch after 5 years of exposure to elevated concentrations of CO₂ and O₃. *Tree Physiology* **28**: 805–813.
- Kozłowski, T.T. and Pallardy, S.G. 1997. *Physiology of Woody Plants*. Academic Press, San Diego, CA, USA.
- Kull, O., Tulva, I., and Vapaavuori, E. 2003. Influence of elevated CO₂ and O₃ on *Betula pendula* Roth crown structure. *Annals of Botany* **91**: 559–569.
- Loats, K.V. and Rebeck, J. 1999. Interactive effects of ozone and elevated carbon dioxide on the growth and physiology of black cherry, green ash, and yellow-poplar seedlings. *Environmental Pollution* **106**: 237–248.
- Mortensen, L.M. 1995. Effects of carbon dioxide concentration on biomass production and partitioning in *Betula pubescens* Ehrh. seedlings at different ozone and temperature regimes. *Environmental Pollution* **87**: 337–343.
- Oksanen, E., Haikio, E., Sober, J., and Karnosky, D.F. 2003. Ozone-induced H₂O₂ accumulation in field-grown aspen and birch is linked to foliar ultrastructure and peroxisomal activity. *New Phytologist* **161**: 791–799.
- Oksanen, E., Sober, J., and Karnosky, D.F. 2001. Impacts of elevated CO₂ and/or O₃ on leaf ultrastructure of aspen (*Populus tremuloides*) and birch (*Betula papyrifera*) in the Aspen FACE experiment. *Environmental Pollution* **115**: 437–446.
- Peltonen, P.A., Vapaavuori, E., and Julkunen-Tiitto, R. 2005. Accumulation of phenolic compounds in birch leaves is changed by elevated carbon dioxide and ozone. *Global Change Biology* **11**: 1305–1324.
- Percy, K.E., Awmack, C.S., Lindroth, R.L., Kubiske, M.E., Kopper, B.J., Isebrands, J.G., Pregitzer, K.S., Hendrey, G.R., Dickson, R.E., Zak, D.R., Oksanen, E., Sober, J., Harrington, R., and Karnosky, D.F. 2002. Altered performance of forest pests enriched by CO₂ and O₃. *Nature* **420**: 403–407.
- Piispanen, R. and Saranpaa, P. 2001. Variation of non-structural carbohydrates in silver birch (*Betula pendula* Roth) wood. *Trees* **15**: 444–451.

Pregitzer, K.S., Burton, A.J., King, J.S., and Zak, D.R. 2008. Soil respiration, root biomass, and root turnover following long-term exposure of northern forests to elevated atmospheric CO₂ and tropospheric O₃. *New Phytologist* **180**: 153–161.

Rao, M.V., Hale, B.A., and Ormrod, D.P. 1995. Amelioration of ozone-induced oxidative damage in wheat plants grown under high carbon dioxide. *Plant Physiology* **109**: 421–432.

Rebbeck, J. and Scherzer, A.J. 2002. Growth responses of yellow-poplar (*Liriodendron tulipifera* L.) exposed to 5 years of [O₃] alone or combined with elevated [CO₂]. *Plant, Cell and Environment* **25**: 1527–1537.

Riikonen, J., Kets, K., Darbah, J., Oksanen, E., Sober, A., Vapaavuori, E., Kubiske, M.E., Nelson, N., and Karnosky, D.F. 2008. Carbon gain and bud physiology in *Populus tremuloides* and *Betula papyrifera* grown under long-term exposure to elevated concentrations of CO₂ and O₃. *Tree Physiology* **28**: 243–254.

Riikonen, J., Lindsberg, M.-M., Holopainen, T., Oksanen, E., Lappi, J., Peltonen, P., and Vapaavuori, E. 2004. Silver birch and climate change: variable growth and carbon allocation responses to elevated concentrations of carbon dioxide and ozone. *Tree Physiology* **24**: 1227–1237.

Uddling, J., Teclaw, R.M., Kubiske, M.E., Pregitzer, K.S., and Ellsworth, D.S. 2008. Sap flux in pure aspen and mixed aspen-birch forests exposed to elevated concentrations of carbon dioxide and ozone. *Tree Physiology* **28**: 1231–1243.

Vapaavuori, E., Holopainen, J.K., Holopainen, T., Julkunen-Titto, R., Kaakinen, S., Kasurien, A., Kontunen-Soppela, S., Kostianen, K., Oksanen, E., Peltonen, P., Riikonen, J., and Tulva, I. 2009. Rising atmospheric CO₂ concentration partially masks the negative effects of elevated O₃ in silver birch (*Betula pendula* Roth). *Ambio* **38**: 418–424.

3.8.2.4 Yellow Poplar

- As the air's CO₂ content rises, yellow-poplar trees likely will display substantial increases in photosynthetic rate and biomass production, even under conditions of elevated O₃ concentrations, and the soils in which the trees grow should therefore sequester increasing quantities of carbon.

Scherzel *et al.* (1998) grew yellow-poplar seedlings in open-top chambers for four years at three combinations of atmospheric O₃ and CO₂—ambient O₃ and ambient CO₂, doubled O₃ and ambient CO₂, and

doubled O₃ and doubled CO₂—to study the interactive effects of these gases on leaf-litter decomposition. This experiment revealed decomposition rates of yellow-poplar leaves were similar for all three treatments for nearly five months, after which time litter produced in the elevated O₃ and elevated CO₂ air decomposed at a significantly slower rate, such that even after two years of decomposition, litter from the elevated O₃ and elevated CO₂ treatment still contained about 12% more biomass than litter produced in the other two treatments. This reduced rate of decomposition under elevated O₃ and CO₂ conditions likely will result in greater carbon sequestration in soils supporting yellow-poplar trees in the future.

Loats and Rebbeck (1999) grew yellow-poplar seedlings for 10 weeks in pots placed in growth chambers filled with ambient air, air with twice the ambient CO₂ concentration, air with twice the ambient O₃ concentration, and air with twice the ambient CO₂ and O₃ concentrations, to determine the effects of elevated CO₂ and O₃ on photosynthesis and growth in this deciduous tree species. They found doubling the air's CO₂ concentration increased the rate of net photosynthesis by 55% in ambient O₃ air; at twice the ambient level of O₃ it stimulated net photosynthesis by an average of 50%. The doubled CO₂ concentration significantly increased total biomass by 29%, and the doubled O₃ concentration had little impact on growth.

Rebbeck *et al.* (2004) grew yellow poplar seedlings for five years in open-top chambers in a field plantation at Delaware, Ohio (USA), exposing them continuously from mid-May through mid-October of each year to charcoal-filtered air to remove ambient O₃, ambient O₃, 1.5 times ambient O₃, or 1.5 times ambient O₃ plus 350 ppm CO₂ above ambient CO₂. The trees were never fertilized during the study, and they received no supplemental water beyond some given in the first season.

Averaged over the experiment's five growing seasons, the midseason net photosynthetic rate of upper canopy foliage at saturating light intensities declined by 10% when the trees were grown in ambient O₃-air and by 14% when grown in elevated O₃-air, compared to the trees grown in the charcoal-filtered air. Seasonal net photosynthesis of foliage grown in the combination of elevated O₃ and elevated CO₂ was 57–80% higher than it was in the trees exposed to elevated O₃ alone. There was no evidence of any photosynthetic down-regulation in the trees exposed to the elevated O₃ and CO₂ air, with some of

the highest rates being observed during the final growing season. Rebbeck *et al.* conclude “elevated CO₂ may ameliorate the negative effects of increased tropospheric O₃ on yellow-poplar.” Their results suggest a nominally doubled atmospheric CO₂ concentration more than compensates for the deleterious effects of a 50% increase in ambient O₃ levels, and by several times over.

References

Loats, K.V. and Rebbeck, J. 1999. Interactive effects of ozone and elevated carbon dioxide on the growth and physiology of black cherry, green ash, and yellow-poplar seedlings. *Environmental Pollution* **106**: 237–248.

Rebbeck, J., Scherzer, A.J., and Loats, K.V. 2004. Foliar physiology of yellow-poplar (*Liriodendron tulipifera* L.) exposed to O₃ and elevated CO₂ over five seasons. *Trees* **18**: 253–263.

Scherzel, A.J., Rebbeck, J., and Boerner, R.E.J. 1998. Foliar nitrogen dynamics and decomposition of yellow-poplar and eastern white pine during four seasons of exposure to elevated ozone and carbon dioxide. *Forest Ecology and Management* **109**: 355–366.

3.8.2.5 Miscellaneous

- The positive effects of atmospheric CO₂ enrichment generally more than compensate for the negative effects of elevated ozone concentrations on tree growth.

Ozone (O₃) is the primary air pollutant responsible for visible foliar injury and reduced growth in trees the world over. Most studies of the subject suggest it gains entrance to leaves through their stomata, where it interferes with the process of photosynthesis and thereby reduces plant productivity. Fowler *et al.* (1999) described the global significance of the phenomenon in some detail by estimating O₃ to have been negatively affecting a quarter of Earth’s forests at the close of the twentieth century, and calculating it to have the potential to negatively affect one-half of the planet’s forests by 2100.

In one of the earlier studies of the subject, Kainulainen *et al.* (1998) constructed open-top chambers around Scots pine (*Pinus sylvestris* L.) trees about 20 years old and fumigated them with combinations of ambient or CO₂-enriched air (645 ppm) and ambient or twice-ambient (20 to

40 ppb) ozone-enriched air for three growing seasons, to study the interactive effects of these gases on starch and secondary metabolite production. They discovered elevated CO₂ and O₃ had no significant impact on the trees’ starch production, even after two years of treatment exposure. Near the end of the third year, elevated CO₂ alone significantly enhanced starch production in current-year needles. But neither elevated CO₂ nor O₃, acting alone or together, had any significant effects on the concentrations of the secondary metabolites the researchers investigated.

Kainulainen *et al.*’s paper made clear the need for long-term studies of tree responses to atmospheric CO₂ enrichment. Whereas no effects of elevated CO₂ on starch production were found after two years of treatment exposure, starch concentrations in needles ultimately increased significantly in the CO₂-enriched trees late into the third year of the study. It’s hardly surprising that long-lived perennial plants, such as trees, require long-term CO₂-enrichment studies to reveal how they will respond to the rising concentration of atmospheric CO₂. This study suggests over time, Scots pine trees may respond to the rising CO₂ content of the air with increases in starch concentration, which can be mobilized to provide carbohydrates for active plant sinks to increase total tree size and biomass. In addition, if ozone continues to accumulate in the lower atmosphere, Scots pine may not display any adverse response to it, as atmospheric CO₂ enrichment seems able to protect against O₃-induced harm.

Broadmeadow *et al.* (1999) studied several species of young trees, including sessile oak (*Quercus petraea*), European beech (*Fagus sylvatica*), and sweet chestnut (*Castanea sativa*), to determine how their responses to ozone exposure are affected by elevated CO₂ and other environmental variables. They found elevated CO₂ generally reduced the amount of ozone damage by inducing stomatal closure, which decreased the uptake of this air pollutant. This study suggests, as the air’s CO₂ concentration continues to rise, many tree species likely will exhibit reductions in stomatal conductance, which should reduce the negative effects of tropospheric ozone on their growth and development.

Herman *et al.* (2001) note air pollution by SO₂, Pb, NO_x, and NH₃ had been significantly reduced in central Europe over the two decades prior to their study, but ozone levels were still on the rise, based on trends derived from European databases that included ozone measurements from about 100 stations in Austria and Germany. The parameter Herman *et al.*

used to express the significance of these ozone trends was the AOT40 Critical Level set by the UN-ECE (1994), which had a value of 10 ppm.h and was defined as accumulated ozone exposure above a threshold of 40 ppb 24 hours per day over the six-month growing season of April–September, which in controlled experiments had been documented to cause approximate 10% reductions in tree biomass production.

As a measure of how bad ozone pollution had become in central Europe, in most of the grid plots of the Austrian Forest Inventory Grid, and based on 1993 ozone data, Herman *et al.* report “the Critical Level of 10 ppm.h had been exceeded up to sevenfold,” and “where standards had been exceeded to such an alarming extent, serious damage of forest trees should be expected.”

So what did the trees in these highly ozone-polluted grid plots look like? Were they absolutely devastated? Or dead? Herman *et al.* report, “the results of the Austrian monitoring surveys did not reflect such damage.” They note, for example, “neither the general evaluation of the foliage losses in the context of the crown condition inventories nor the development of the growing stock reflect a dramatic situation.” Not only were there no “dramatic” reductions in tree health and productivity, there were typically none at all, and in many areas there were actually improvements, such as crown conditions in Austria looking slightly better and the growing stock increasing.

Herman *et al.* acknowledge that although ozone-related losses of biomass could not be confirmed on old trees, under the ozone levels of that day they did show some reductions in photosynthetic CO₂ uptake. This phenomenon was particularly evident in old trees at high altitudes, where AOT40 values were much more extreme, and in trees experiencing “additional climatic stress.” But the researchers were careful to add “the reductions of the CO₂ uptake were in no proportion to the massive excess of the AOT40.”

Ozone exposures more than sevenfold greater than the Critical Level (which Critical Level alone should have decreased tree productivity by 10%) were occurring all across the Austrian Forest Inventory Grid, and such conditions could have been expected to reduce the growth rates of the exposed trees by 70% or more. Yet there was no evidence of any widespread damage or productivity reduction. In fact, growth conditions seemed to have improved almost everywhere, except at high altitudes and under conditions of more-than-usual climatic stress.

Herman *et al.* suggest these observations imply the once-adequate Critical Level of ozone exposure was no longer suitable for application. Why? Because “the significant parameter for the assessment of the risk” is not the atmospheric concentration of ozone, but “the absorbed dose.” Therefore, they advise the creation of a new Critical Level that “takes into account leaf conductance and the environmental parameters influencing it.”

This latter statement is an example of the proper approach to risk assessment, for there are many concurrent and ongoing changes in Earth’s atmosphere and the net result of all of them acting in concert must be considered when predicting the consequences of changes in any individual factor. In the case of Earth’s climate, for example, the surface air temperature effects of an increase in the air’s CO₂ content cannot be adequately evaluated without considering the effects of concurrent changes in atmospheric aerosol quantities and properties. Likewise, in the case of ozone and forest health, the biological consequences of rising tropospheric ozone concentrations cannot be adequately evaluated without considering the effects of the concurrent rise in the air’s CO₂ content, which is known to have a significant impact on leaf conductance and, hence, largely determines a tree’s critical “absorbed dose” of ozone. When this more rational approach has been followed, numerous laboratory and field experiments have shown realistically scaled concurrent increases in atmospheric CO₂ and ozone concentrations typically lead to very little change in plant net productivity. The lack of substantial negative ozone-induced impacts on the forests of central Europe, as described by Herman *et al.*, may have been the result of the compensatory beneficial impacts of the historical and still-ongoing rise in the air’s CO₂ content.

King *et al.* (2005) note preindustrial concentrations of tropospheric O₃ were estimated to have been less than 10 ppb, but subsequently rose to the 30–40 ppb background levels of their day, referencing Levy *et al.* (1997). In addition, they report the rising boundary-layer O₃ concentration caused by increasing industrialization around the globe has had negative continent-scale implications for carbon sequestration (Felzer *et al.*, 2004). Thus they sought to evaluate the net effect of the positive CO₂ and negative O₃ impacts of possible future increases in these trace atmospheric gases on the productivity of the most widespread tree species found in North America—trembling aspen (*Populus tremuloides* Michx.)—and two-member

mixed communities of trembling aspen-paper birch (*Betula papyrifera* Marsh.) and trembling aspen-sugar maple (*Acer saccharum* Marsh.).

Working at the Aspen FACE site (Dickson *et al.*, 2000) near Rhinelander, Wisconsin (USA), King *et al.* allowed pure stands of aspen and mixed stands of aspen-birch and aspen-maple to grow for seven years in ambient air, air enriched with an extra 200 ppm of CO₂, air enriched with an extra 50% O₃, or air thus enriched by both CO₂ and O₃. Relative to the ambient-air control treatment, the eight researchers found elevated CO₂ increased “total biomass 25, 45, and 60% in the aspen, aspen-birch and aspen-maple communities, respectively,” while elevated O₃ “caused 23, 13, and 14% reductions in total biomass relative to the control in the respective communities.” The combination of elevated CO₂ and O₃ “resulted in total biomass responses of -7.8, +8.4, and +24.3% relative to the control in the aspen, aspen-birch and aspen-sugar maple communities, respectively.”

King *et al.* conclude “exposure to even moderate levels of O₃ significantly reduces the capacity of net primary productivity to respond to elevated CO₂ in some forests.”

Gardner *et al.* (2005) grew pre-flushed hardwood stem cuttings of the inter-American (*Populus trichocarpa* Torr. & Gray ex Hook. x *P. deltoides* Bartr. ex Marsh) hybrid poplar clone ‘Boelare’ out-of-doors in eight open-top chambers for two growing seasons of 132 and 186 days (first and second years, respectively), measuring a number of plant properties and physiological processes. Two of the eight chambers were maintained at ambient carbon dioxide (350 ppm) and ozone concentrations (A), two at ambient CO₂ with daily O₃ episodes rising to a mid-day peak of 100 ppb (AO), two at elevated CO₂ (700 ppm) and ambient O₃ (E), and two at elevated CO₂ and O₃ (EO) throughout the first year of the study. Only CO₂ was elevated during the second year.

With respect to the effect of CO₂ alone, Gardner *et al.* write mainstem dry weight “was increased by 38% in 700-ppm CO₂ compared with that in 350-ppm CO₂ at the end of the first growing season,” and “during year 2 mainstem dry weight increased by about 5-fold and the relative effect of elevated CO₂ remained similar in magnitude (32%) to that seen in the first year.” During the first season of exposure, mainstem dry mass was decreased by 45% in the O₃-episode treatment in 350-ppm CO₂, and by 34% in the O₃-episode treatment in 700-ppm CO₂. Because of the strong growth-promoting effect of the extra CO₂, the O₃-induced change in growth when going from the

ambient-CO₂-ambient-O₃ treatment to the elevated-CO₂-elevated-O₃ treatment was only a reduction of 10%, as compared to the O₃-induced reduction of 45% when CO₂ was not increased concurrently.

The British researchers conclude “elevated levels of CO₂ can play a key role in ameliorating the worst effects of severe ozone episodes on a relatively sensitive tree species,” and “O₃ episodes are less likely to be detrimental to *P. trichocarpa* x *P. deltoides* in the CO₂ concentrations of the future.”

Noting the “detrimental effects of ozone on plants are well known” and “CO₂ generally affects trees in opposite ways to ozone,” Valkama *et al.* (2007) conducted a literature review they describe as “the first quantitative analysis of the interactive effects of elevated O₃ and elevated CO₂ on tree chemistry and herbivore performance,” based on the results of 63 studies conducted on 22 tree species and 10 insect herbivore species published between 1990 and 2005.

With respect to the ways elevated O₃ may benefit insect herbivores that tend to damage trees, Valkama *et al.* write, “elevated O₃ significantly shortened development time of insect herbivores [when they are exposed and vulnerable to attack by various enemies] and increased their pupal mass in the overall dataset.” In addition, the “relative growth rate of chewers was significantly increased by 3.5% under elevated O₃.” They report “these effects were counteracted by elevated CO₂,” such that “elevated O₃ in combination with CO₂ had no effect on herbivore performance,” with the exception that when elevated CO₂ was added to the O₃-enriched air, it not only counteracted the O₃-induced increase in pupal biomass, but reduced it below what it was in ambient air by 7%. This analysis of the vast majority of experimental data obtained prior to 2006 suggests in the interaction between insect herbivores and trees, the rise in the air’s CO₂ content likely plays an extremely important role in negating, and in some cases even more than negating, the damage insect pests would otherwise do to forests.

Wittig *et al.* (2007) calculated the increase in the atmosphere’s O₃ concentration since the start of the Industrial Revolution had caused a mean decrease of 11% in the leaf photosynthetic CO₂ uptake of temperate and boreal forests. Based on projections derived from the A2 storyline of the *Special Report on Emissions Scenarios* included in IPCC’s Fourth Assessment Report (which indicate atmospheric O₃ concentrations could rise 20–25% between 2015 and 2050, and could further increase by 40–60% by 2100 if current emission trends continue), they calculate temperate and boreal forest photosynthetic rates could

decline by an additional 8–16% by the end of the century.

Fortunately, the stomatal-aperture-constricting effect of concomitant past increases and anticipated future increases in the air's CO₂ content tend to counter the negative influence of rising O₃ concentrations by retarding O₃ entry into plant leaves. In addition, the CO₂-induced increase in leaf photosynthesis (its "aerial fertilization effect") has been shown to often more than compensate for the negative influence of ozone on leaf photosynthesis rates. These welcome findings comprise only half of the good news about rising CO₂ concentrations and their impact on the ozone problem.

It is a well-established fact that vegetative isoprene emissions are responsible for the production of vast amounts of tropospheric ozone (Chameides *et al.*, 1988; Harley *et al.*, 1999). Poisson *et al.* (2000) calculated current levels of non-methane hydrocarbon (NMHC) emissions (the vast majority of which are isoprene, accounting for more than twice as much as all other NMHCs combined) likely increase surface ozone concentrations from what they would be in their absence by up to 50–60% over land. In addition, although little appreciated, it has been known for some time that atmospheric CO₂ enrichment typically leads to large reductions in isoprene emissions from plants. This phenomenon typically has not been factored into projections of future atmospheric O₃ concentrations.

Arneth *et al.* (2007) addressed this issue, noting future vegetative isoprene emissions typically have been modeled to rise in tandem with projected increases in vegetative biomass and productivity driven by projected changes in various environmental factors. This protocol, in an anticipated warmer and CO₂-enriched environment, generally has led to predictions of significant increases in isoprene emissions and, therefore, significant increases in future atmospheric O₃ concentrations, as Wittig *et al.* predicted. However, Arneth *et al.* convincingly demonstrate "a quite different result is obtained when the direct CO₂ effect on isoprene emissions is included," noting in this more-realistic situation a properly forced model "maintains global isoprene emissions within $\pm 15\%$ of present values."

The seven Swedish and UK researchers thus conclude "predictions of high future tropospheric O₃ concentrations partly driven by isoprene emissions may need to be revised."

Xu *et al.* (2012) report "levels of atmospheric CO₂ and O₃ have increased rapidly in the last five

decades," and "it is predicted that at the end of this century, the average levels of CO₂ and O₃ in Earth's atmosphere are going to reach 700 ppm and 80 ppb, respectively (IPCC, 2007)." Thus, in an experiment designed to evaluate the opposing effects of these two atmospheric trace gases on Chinese pine (*Pinus tabulaeformis*) trees at the year AD 2100, they grew four-year-old trees in loamy soil with no extra fertilizer in 12 open-top chambers in May 2006 in the populated central area of Shenyang city in northeastern China, where the trees were exposed to either current ambient air of about 400 ppm CO₂ and 40 ppb O₃ or 700 ppm CO₂ and 80 ppm O₃, plus all combinations thereof.

This study revealed elevated CO₂ by itself increased growth but "did not significantly affect net photosynthetic rate, stomatal conductance, chlorophyll content, the maximum quantum yield of photosystem II, or the effective quantum yield of photosystem II electron transport after 90 days of gas exposure." Elevated O₃ by itself "decreased growth, net photosynthetic rate and stomatal conductance after 90 days of exposure," but Xu *et al.* note "its negative effects were alleviated by elevated CO₂."

References

- Arneth, A., Miller, P.A., Scholze, M., Hickler, T., Schurgers, G., Smith, B., and Prentice, I.C. 2007. CO₂ inhibition of global terrestrial isoprene emissions: Potential implications for atmospheric chemistry. *Geophysical Research Letters* **34**: 10.1029/2007GL030615.
- Broadmeadow, M.S.J., Heath, J., and Randle, T.J. 1999. Environmental limitations to O₃ uptake—Some key results from young trees growing at elevated CO₂ concentrations. *Water, Air, and Soil Pollution* **116**: 299–310.
- Chameides, W.L., Lindsay, R.W., Richardson, J., and Kiang, C.S. 1988. The role of biogenic hydrocarbons in urban photochemical smog: Atlanta as a case study. *Science* **241**: 1473–1475.
- Dickson, R.E., Lewin, K.F., Isebrands, J.G., Coleman, M.D., Heilman, W.E., Riemenschneider, D.E., Sober, J., Host, G.E., Zak, D.R., Hendrey, G.R., Pregitzer, K.S., and Karnosky, D.F. 2000. *Forest Atmosphere Carbon Transfer and Storage (FACTS-II): The Aspen Free-Air CO₂ and O₃ Enrichment (FACE) Project: An Overview*. USDA Forest Service NCRS, St. Paul, Minnesota, USA.
- Felzer, B., Kicklighter, D., Mellilo, J., Wang, C., Zhuang, Q., and Prinn, R. 2004. Effects of ozone on net primary production and carbon sequestration in the conterminous United States using a biogeochemistry model. *Tellus* **56B**: 230–248.

Fowler, D., Cape, J.N., Coyle, M., Flechard, C., Kuylensstierna, J., Hicks, K., Derwent, D., Johnson, C., and Stevenson, D. 1999. The global exposure of forests to air pollutants. *Water, Air & Soil Pollution* **116**: 5–32.

Gardner, S.D.L., Freer-Smith, P.H., Tucker, J., and Taylor, G. 2005. Elevated CO₂ protects poplar (*Populus trichocarpa* × *P. deltoides*) from damage induced by O₃: identification of mechanisms. *Functional Plant Biology* **32**: 221–235.

Harley, P.C., Monson, R.K., and Lerda, M.T. 1999. Ecological and evolutionary aspects of isoprene emission from plants. *Oecologia* **118**: 109–123.

Herman, F., Smidt, S., Huber, S., Englisch, M., and Knoflacher, M. 2001. Evaluation of pollution-related stress factors for forest ecosystems in central Europe. *Environmental Science & Pollution Research* **8**: 231–242.

IPCC. 2007. *Climate Change 2007*. Working Group I Report: The Physical Basis of Climate Change. IPCC, Geneva, Switzerland.

Kainulainen, P., Holopainen, J.K., and Holopainen, T. 1998. The influence of elevated CO₂ and O₃ concentrations on Scots pine needles: Changes in starch and secondary metabolites over three exposure years. *Oecologia* **114**: 455–460.

King, J.S., Kubiske, M.E., Pregitzer, K.S., Hendrey, G.R., McDonald, E.P., Giardina, C.P., Quinn, V.S., and Karnosky, D.F. 2005. Tropospheric O₃ compromises net primary production in young stands of trembling aspen, paper birch and sugar maple in response to elevated atmospheric CO₂. *New Phytologist* **168**: 623–636.

Levy, H.I.I., Kasibhatla, P.S., Moxim, W.J., Klonecki, A.A., Hirsch, A.I., Oltmans, S.J., and Chameides, W.L. 1997. The global impact of human activity on tropospheric ozone. *Geophysical Research Letters* **24**: 791–794.

Poisson, N., Kanakidou, M., and Crutzen, P.J. 2000. Impact of non-methane hydrocarbons on tropospheric chemistry and the oxidizing power of the global troposphere: 3-dimensional modeling results. *Journal of Atmospheric Chemistry* **36**: 157–230.

UN-ECE. 1994. *Critical Levels for Ozone*. A UN-ECE Workshop Report. Fuhrer, J. and Achermann, B. (Eds.) Swiss Federal Research Station of Agricultural Chemistry and Environmental Health, No. 16. ISSN-1013-154X.

Valkama, E., Koricheva, J., and Oksanen, E. 2007. Effects of elevated O₃, alone and in combination with elevated CO₂, on tree leaf chemistry and insect herbivore performance: a meta-analysis. *Global Change Biology* **13**: 184–201.

Wittig, V.E., Ainsworth, E.A., and Long, S.P. 2007. To

what extent do current and projected increases in surface ozone affect photosynthesis and stomatal conductance of trees? A meta-analytic review of the last 3 decades of experiments. *Plant, Cell and Environment* **30**: 1150–1162.

Xu, S., Chen, W., Huang, Y., and He, X. 2012. Responses of growth, photosynthesis and VOC emissions of *Pinus tabulaeformis* Carr. exposure to elevated CO₂ and/or elevated O₃ in an urban area. *Bulletin of Environmental Contamination and Toxicology* **88**: 443–448.

3.9 Non-Ozone Air Pollutants

- Despite being labeled by the United Nations and U.S. Environmental Protection Agency as a dangerous air pollutant, not only is CO₂ not a “pollutant,” as those entities claim it is; it is actually an anti-pollutant that helps plants overcome the negative effects of real air and soil pollutants and better enables their removal from polluted areas.

In addition to ozone, many other airborne substances can damage plant life. This section explores the scientific literature pertaining to the negative effects of some of these other harmful components of the planet’s atmosphere and how these negative effects can be alleviated by atmospheric CO₂ enrichment.

Lee *et al.* (1997) note, “several studies using controlled-environment chambers have shown that CO₂ may compensate for sulfur dioxide (SO₂)-induced leaf injury (Black, 1982; Carlson and Bazzaz, 1982; Darrall, 1989; Sandhu *et al.*, 1992; Rao and De Kok, 1994; Niewiadomska and Miszalski, 1995; Tausz *et al.*, 1996).” They conducted a similar study out-of-doors using open-top chambers placed over soybeans (*Glycine max* L. Merr. cv. Essex) growing in a typical field situation, to determine whether the positive effects of atmospheric CO₂ enrichment would compensate for the negative effects of elevated SO₂ concentrations on soybean photosynthetic rates. They exposed the soybeans to either ambient (350 ppm) or elevated (500 ppm) atmospheric CO₂ concentrations in combination with atmospheric SO₂ concentrations of either 0.00 or 0.12 ppm. They describe the latter concentration as being sufficient to produce “potentially toxic effects over long term exposure.”

They found, throughout the period of pod filling, the mean photosynthetic rate of plants growing in ambient-CO₂ but elevated-SO₂ air was 17.2% lower than the mean rate of plants growing in ambient-CO₂ and SO₂-free air, and the mean photosynthetic rate of

plants growing in CO₂-enriched but SO₂-free air was 25.1% higher than the mean rate of plants growing in ambient-CO₂ and SO₂-free air. The mean photosynthetic rate of plants growing in CO₂-enriched and elevated-SO₂ air was 33.4% greater than the mean rate of plants growing in ambient-CO₂ and SO₂-free air. Enriching the air with CO₂ more than compensated for the negative effects of the elevated SO₂ on the photosynthetic rates of the soybeans the five researchers studied.

Deepak and Agrawal (2001) grew two cultivars of soybeans (*Glycine max* L. Merr. Cv. PK472 and Bragg) in open-top chambers at atmospheric CO₂ concentrations of either 350 or 600 ppm, both alone and in combination with 60 ppb SO₂, to determine the individual and interactive effects of elevated CO₂ and SO₂ on the growth and yield of this important crop. Exposure to the elevated SO₂ significantly reduced total plant biomass and grain yield by approximately 18% in both cultivars. In contrast, elevated CO₂ significantly increased total plant biomass and grain yield in both cultivars by averages of 30 and 34%, respectively. When the plants were exposed simultaneously to elevated SO₂ and CO₂, the negative effects of SO₂ were completely ameliorated.

Agrawal and Deepak (2003) conducted a similar study of two cultivars of wheat (*Triticum aestivum* L. cv. Malviya 234 and HP1209) in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 600 ppm both alone and in combination with 60 ppb SO₂, to study the individual and interactive effects of elevated CO₂ and SO₂ on another of the world's major crops. They found exposure to elevated CO₂ boosted photosynthetic rates by 58 and 48% in M234 and HP1209, respectively, and fumigation with elevated SO₂ had no significant impact on rates of photosynthesis in either cultivar. Plants grown in the combined treatment of elevated CO₂ and elevated SO₂ displayed slightly lower photosynthetic rates, but they were still 42 and 38% greater than those measured in control plants for M234 and HP1209, respectively.

The plants grown in elevated CO₂ in this experiment also displayed an approximate 20% reduction in stomatal conductance, and those grown in elevated SO₂ exhibited an average conductance increase of 15%. When exposed simultaneously to both gases, the plants displayed an average 11% reduction in stomatal conductance. This phenomenon contributed to an approximate 32% increase in water-use efficiency (plant growth per unit of water used) for plants simultaneously exposed to increased concentrations of both gases, whereas plants exposed

to elevated SO₂ alone displayed an average decrease in water-use efficiency of 16%. In addition, plant exposure to elevated SO₂ caused an average 13% decrease in foliar protein concentrations in both cultivars, but when the plants were concurrently exposed to an atmospheric CO₂ concentration of 600 ppm, leaf protein levels decreased by only 3% in HP1209 and increased by 4% in M234.

As the air's CO₂ content rises, it likely will reduce the stress and growth reductions of these specific wheat cultivars and others as a consequence of SO₂ pollution. Agrawal and Deepak's study demonstrates CO₂-induced increases in photosynthesis will be only partially offset by elevated SO₂ concentrations, which should allow greater wheat yields to be produced in the future under similar conditions. In addition, since SO₂-induced reductions in plant water-use efficiency were essentially eliminated by concurrent plant exposure to elevated CO₂, these cultivars should be able to grow better in areas with limited water availability and in areas close to industrial complexes emitting large quantities of SO₂. Also, wheat plants growing in SO₂-polluted air should not suffer as large a reduction in foliar protein content in a future high-CO₂ world as they do today.

Izrael *et al.* (2002) evaluated the effects of sulfur dioxide pollution on Russian forests. Among other things, the five researchers report "sulfur dioxide (SO₂) causes widespread damage to plants, because it can spread through large distances, and its emissions into the atmosphere are large." In 1996, for example, they found "total SO₂ emission from the industrial areas of Russia comprised 5866.76 thousand tons, or 42.2% of the total emission of liquid and gaseous pollutants." They determined 1.3 million hectares of Russian forest land had been adversely affected by SO₂ pollution. They estimated total forest destruction occurs on 2–5% of this area, and heavy, moderate, and slight damage occur on 10–15%, 30–40%, and 40–50% of this area, respectively.

These results indicate the seriousness of SO₂ pollution for forest health, and they highlight the fact that atmospheric CO₂ enrichment can significantly alleviate SO₂'s adverse biological consequences. Hallgren (1984), for example, demonstrated a 300 ppm increase in the air's CO₂ concentration stimulated the photosynthetic rate of Scots pine trees by 64% in unpolluted air and by 77% in air with abnormally high SO₂ concentrations. Hallgren also found a 600-ppm increase in atmospheric CO₂ stimulated photosynthetic rates in this important forest species by 85% in unpolluted air and 110% in

air of high SO₂ concentration. Similarly, Carlson (1983) found a 900-ppm increase in the air's CO₂ concentration boosted photosynthetic rates of soybeans by 87% in unpolluted air and 715% in high-SO₂ air. Thus the rise in the air's CO₂ content can do much to prevent or significantly alleviate the adverse consequences of SO₂ pollution.

Several studies have been conducted at naturally occurring CO₂ springs in Tuscany, Italy, providing a unique opportunity to examine the effects of long-term atmospheric CO₂ enrichment on plant growth and development. These springs also emit elevated concentrations of the major phytotoxic air pollutants H₂S and SO₂ (Schulte *et al.*, 1999). Consequently, the springs provide a suitable setting in which to study the relative strengths of two competing phenomena: the growth-promoting effect of elevated CO₂ and the growth-retarding effects of elevated H₂S and SO₂.

Grill *et al.* (2004) analyzed various properties of leaves and acorns produced on two species of oak tree (*Quercus ilex* L. and *Quercus pubescens* L.) growing in air of double-to-triple the normal atmospheric CO₂ concentration near the CO₂ springs, and the same characteristics of leaves and acorns growing on similar trees located some distance away in ambient-CO₂ air. They also analyzed several characteristics of seedlings they sprouted from acorns produced by the CO₂-enriched and ambient-treatment trees, and they used chromosome stress tests “to investigate whether alterations in sulfur-regime have negative consequences for seedlings.”

The six scientists report “acorns from CO₂ springs contained significantly higher sulphur concentrations than controls (0.67 vs. 0.47 mg g⁻¹ dry weight in *Q. ilex* cotyledons and 1.10 vs. 0.80 in *Q. pubescens*),” indicating the trees were indeed significantly affected by the H₂S- and SO₂-enriched air in the vicinity of the CO₂-emitting springs. They also note *Q. ilex* seedlings grown from CO₂-spring acorns showed elevated rates of chromosomal aberrations in root tips, suggestive of a permanent stress. Nevertheless, as demonstrated by the results of several studies conducted on mature trees from these sites, the CO₂-enriched air—even in the presence of significantly elevated concentrations of phytotoxic H₂S and SO₂—significantly enhanced the trees’ photosynthetic capacity: by 26–69% (Blaschke *et al.*, 2001), 36–77% (Stylinski *et al.*, 2000), and 175–510% (Tognetti *et al.*, 1998).

Jia *et al.* (2010) note “mining and smelting, disposal of sewage sludge and the use of cadmium rich phosphate fertilizers (Wagner, 1993; Liu *et al.*,

2007) have contaminated a large proportion of the agricultural land throughout the world, causing an increase in the soil concentration of many heavy metals.” They further note, “as one of the most toxic environmental pollutants (Zhang *et al.*, 2009) cadmium (Cd) has a strong influence on metabolic activities of crop plants by inducing a number of physiological changes, such as growth inhibition, changes in water and ion metabolism, photosynthesis inhibition, enzyme activity changes, and free radical formation (Ekmekci *et al.*, 2008),” stating “even at relatively low concentrations cadmium can exert strong toxic effects on crops (Seregin and Ivanov, 2001).”

The seven scientists grew Italian and perennial ryegrass (*Lolium multiflorum* and *L. perenne*) in pots filled with soil from a long-term experimental rice field in Guangdong Province, China, which they treated to contain either 0, 25, or 100 mg Cd per kg soil. They fertilized the soils to contain 150 mg N/kg, 100 mg P/kg, and 150 mg K/kg, after which (once the ryegrass seeds had sprouted) the pots were taken outdoors and distributed among six open-top chambers. Three of these (one each for the three soil cadmium concentrations) were maintained at the ambient atmospheric CO₂ concentration of 375 ppm, and three were maintained at an elevated CO₂ concentration of 810 ppm from 0800 to 1700 hours throughout all 58 days of the summer study. During this time and at the conclusion of the study, they measured a number of plant physiological processes and parameters.

Jia *et al.* found elevated CO₂ significantly increased both net photosynthesis and plant water use efficiency, which led to increases in both shoot and root biomass at harvest. “When compared with the ambient CO₂ control, the increase in total biomass due to elevated CO₂ was about 32 and 31% for *L. multiflorum* and *L. perenne*, respectively, grown on the control soil; 37 and 45% on soil amended with 25 mg/kg Cd; [and] 46 and 52% on soil spiked with 100 mg/kg Cd, respectively.” In addition to these very positive results, compared to the ambient CO₂ control, under elevated CO₂ both *Lolium* species had decreased Cd concentrations in their shoots and roots, where “the decreased magnitude of Cd concentration in *L. multiflorum* and *L. perenne* grown on soil spiked with 25 mg/kg Cd was 10.3 and 3.8% for the shoots, and 18.6 and 14.7% for the roots, respectively; for those [plants] grown on soil spiked with 100 mg/kg Cd, it was 8.4 and 8.9% for the shoots, and 12.5 and 13.9% for the roots, respectively.”

Thus atmospheric CO₂ enrichment not only spurred both ryegrass species to produce more root and shoot biomass, but this greater amount of plant material contained reduced concentrations of a toxic soil pollutant. Jia *et al.* conclude, “given expected global increases in CO₂ concentration, elevated CO₂ may help plants better survive in contaminated soil and reduce the food safety risk due to CO₂-induced reduction and dilution in heavy metal concentration.”

Not only is carbon dioxide not a “pollutant,” as the United Nations and U.S. Environmental Protection Agency claim, it is actually an *anti*-pollutant that helps plants overcome the negative effects of real air and soil pollutants and remove them from polluted areas.

References

- Agrawal, M. and Deepak, S.S. 2003. Physiological and biochemical responses of two cultivars of wheat to elevated levels of CO₂ and SO₂, singly and in combination. *Environmental Pollution* **121**: 189–197.
- Black, V.J. 1982. Effects of sulphur dioxide on physiological processes in plants. In: Unsworth, M.H. and Ormrod, O.P. (Eds.) *Effects of Gaseous Pollution in Agriculture and Horticulture*, Butterworth, London, UK, pp. 67–91.
- Blaschke, L., Schulte, M., Raschi, A., Slee, N., Rennenberg, H., and Polle, A. 2001. Photosynthesis, soluble and structural carbon compounds in two Mediterranean oak species (*Quercus pubescens* and *Q. ilex*) after lifetime growth at naturally elevated CO₂ concentrations. *Plant Biology* **3**: 288–297.
- Carlson, R.W. 1983. The effect of SO₂ on photosynthesis and leaf resistance at varying concentrations of CO₂. *Environmental Pollution Series A* **30**: 309–321.
- Carlson, R.W. and Bazzaz, F.A. 1982. Photosynthetic and growth responses to fumigation with SO₂ at elevated CO₂ for C₃ and C₄ plants. *Oecologia* **54**: 50–54.
- Darrall, N.M. 1989. The effect of air pollutants on physiological processes in plants. *Plant, Cell and Environment* **12**: 1–30.
- Deepak, S.S. and Agrawal, M. 2001. Influence of elevated CO₂ on the sensitivity of two soybean cultivars to sulphur dioxide. *Environmental and Experimental Botany* **46**: 81–91.
- Ekmekci, Y., Tanyolac, D., and Ayhan, B. 2008. Effects of cadmium on antioxidant enzyme and photosynthetic activities in leaves of two maize cultivars. *Journal of Plant Physiology* **165**: 600–611.
- Grill, D., Muller, M., Tausz, M., Strnad, B., Wonisch, A., and Raschi, A. 2004. Effects of sulphurous gases in two CO₂ springs on total sulphur and thiols in acorns and oak seedlings. *Atmospheric Environment* **38**: 3775–3780.
- Hallgren, J.-E. 1984. Photosynthetic gas exchange in leaves affected by air pollutants. In: Koziol, M.J. and Whatley, F.R. (Eds.) *Gaseous Air Pollutants and Plant Metabolism*. Butterworths, London, UK, pp. 147–159.
- Izrael, Y.A., Gytarsky, M.L., Karaban, R.T., Lelyakin, A.L., and Nazarov, I.M. 2002. Consequences of climate change for forestry and carbon dioxide sink in Russian forests. *Izvestiya, Atmospheric and Oceanic Physics* **38**: S84–S98.
- Jia, Y., Tang, S., Wang, R., Ju, X., Ding, Y., Tu, S., and Smith, D.L. 2010. Effects of elevated CO₂ on growth, photosynthesis, elemental composition, antioxidant level, and phytochelatin concentration in *Lolium mutiflorum* and *Lolium perenne* under Cd stress. *Journal of Hazardous Materials* **180**: 384–394.
- Lee, E.H., Pausch, R.C., Rowland, R.A., Mulchi, C.L., and Rudorff, B.F.T. 1997. Responses of field-grown soybean (cv. Essex) to elevated SO₂ under two atmospheric CO₂ concentrations. *Environmental and Experimental Botany* **37**: 85–93.
- Liu, Y., Wang, X., Zeng, G., Qu, D., Gu, J., Zhou, M., and Chai, L. 2007. Cadmium-induced oxidative stress and response of the ascorbate-glutathione cycle in *Beckmeria nivea* (L.), Gaud. *Chemosphere* **69**: 99–107.
- Niewiadomska, E. and Misalski, Z. 1995. Does CO₂ modify the effect of SO₂ on variegated leaves of *Chlorophytum comosum* (Thunb) Bak? *New Phytologist* **130**: 461–466.
- Rao, M.V. and De Kok, L.J. 1994. Interactive effects of high CO₂ and SO₂ on growth and antioxidant levels in wheat. *Phyton (Horn)* **34**: 279–290.
- Sandhu, R., Li, Y., and Gupta, G. 1992. Sulphur dioxide and carbon dioxide induced changes in soybean physiology. *Plant Science* **83**: 31–34.
- Schulte, M., Raiesi, F.G., Papke, H., Butterbach-Bahl, K., van Breemen, N., and Rennenberg, H. 1999. CO₂ concentration and atmospheric trace gas mixing ratio around natural CO₂ vents in different Mediterranean forests in central Italy. In: Raschi, A., Vaccori, F.P., and Miglietta, F. (Eds.) *Ecosystem Response to CO₂: The Maple Project Results*. European Communities, Brussels, Belgium, pp. 168–188.
- Seregin, I.V. and Ivanov, V.B. 2001. Physiological aspects of cadmium and lead toxic effects on higher plants. *Russian Journal of Plant Physiology* **48**: 523–544.

Stylinski, C.D., Oechel, W.C., Gamon, J.A., Tissue, D.T., Miglietta, F., and Raschi, A. 2000. Effects of lifelong [CO₂] enrichment on carboxylation and light utilization of *Quercus pubescens* Willd. examined with gas exchange, biochemistry and optical techniques. *Plant, Cell and Environment* **23**: 1353–1362.

Tausz, M., De Kok, L., Stulen, I., and Grill, D. 1996. Physiological responses of Norway spruce trees to elevated CO₂ and SO₂. *Journal of Plant Physiology* **148**: 362–376.

Tognetti, R., Johnson, J.D., Michelozzi, M., and Raschi, A. 1998. Response of foliar metabolism in mature trees of *Quercus pubescens* and *Quercus ilex* to long-term elevated CO₂. *Environmental and Experimental Botany* **39**: 233–245.

Wagner, G.J. 1993. Accumulation of cadmium in crop plants and its consequences to human health. *Advances in Agronomy* **51**: 173–212.

Zhang, F.Q., Zhang, H.X., Wang, G.P., Xu, L.L., and Shen, Z.G. 2009. Cadmium-induced accumulation of hydrogen peroxide in the leaf apoplast of *Phaseolus aureus* and *Vicia sativa* and the roles of different antioxidant enzymes. *Journal of Hazardous Materials* **168**: 76–84.

3.10 Phosphorus Insufficiency

- Plants growing in CO₂-enriched air typically respond by increasing their biomass production, even under conditions of low soil phosphorus content, especially if the plants possess the ability to increase root phosphatase activity.

Under current ambient conditions, plant growth and development are typically carbon-limited, which is why plants generally exhibit increased growth and biomass production in response to atmospheric CO₂ enrichment. Next to carbon, nitrogen is usually the second-most-limiting nutrient to plant growth, followed by phosphorus. Although it is a less-significant component of plant tissues than carbon and nitrogen, phosphorus is still required for successful life-cycle completion in many plant species. It is thus important to investigate aspects of plant phosphorus acquisition and biomass production in response to atmospheric CO₂ enrichment when phosphorus concentrations in soils are less than optimal.

In an early study of the subject, Barrett *et al.* (1998) demonstrated a doubling of the air's CO₂ content under continuous phosphorus deficiency increased wheat root phosphatase activity by 30 to

40%, thus increasing the inorganic phosphorus supply available for plant utilization. As phosphatase is the primary enzyme responsible for the mineralization of organic phosphate, which thereby makes phosphorus available for plant use, an increase in its activity with elevated CO₂ could facilitate sustained plant growth responses to the rise in the air's CO₂ content, even in areas where growth is currently limited by phosphorous deficiencies. And because these increases in phosphatase activity also were observed under sterile growing conditions, this response can be mediated directly by plant roots without involving soil micro-organisms, which are known to aid in phosphorus mineralization.

As the air's CO₂ content continues to rise, phosphatase activity in wheat roots should increase, increasingly converting organic phosphorus into inorganic forms that support the increased plant growth and development stimulated by higher CO₂ concentrations. As a similar increase in phosphatase activity at elevated CO₂ already has been reported for a native Australian pasture grass, these results may be applicable to most of the planet's vegetation. If that turns out to be true, plants that are currently phosphorus-limited in their growth might increase their phosphorous acquisition from soil organic supplies as the atmosphere's CO₂ concentration rises, and this phenomenon, in turn, may allow them to sequester even greater amounts of carbon from the air.

Other studies also have investigated plant biomass responses to atmospheric CO₂ enrichment under conditions of limiting phosphorus supply. Staddon *et al.* (1999), for example, found *Plantago lanceolata* and *Trifolium repens* effectively increased their phosphorus-use efficiency under elevated CO₂ conditions by reducing shoot phosphorus content as a component of CO₂-induced photosynthetic acclimation. Walker *et al.* (1998) found ponderosa pine seedlings grown for a year at atmospheric CO₂ concentrations of 525 and 700 ppm exhibited significantly greater root, shoot, and total dry weights than control plants grown at ambient CO₂, with little influence of a superimposed phosphorus treatment (low vs. high).

Niklaus *et al.* (1998) explored the effects of elevated CO₂, nitrogen, and phosphorus supply on calcareous grassland communities. At low phosphorus concentrations, biomass nitrogen contents were unaffected by elevated CO₂ (600 ppm), whereas at high phosphorus concentrations, community biomass-nitrogen increased by 28%, suggesting

community biomass nitrogen will increase in the future if soil phosphorus contents are increased. A companion study of these grasslands published by Stocklin and Korner (1999) showed community total biomass (the actual dry weight of plant material, not the amount of nitrogen in the plant material) increased with atmospheric CO₂ enrichment even under low phosphorus concentrations, with or without nitrogen-fixing legumes present in the grassland swards.

Nguyen *et al.* (2006) grew seedlings of two N-fixing woody plants (*Acacia auriculiformis* Cunn. ex Benth and *Acacia mangium* Willd) well irrigated and fertilized—except for phosphorus (P), of which there were three treatments (low, medium, and high) composing 10, 50, and 100 mg P/liter of soil mixture—in growth chambers maintained at atmospheric CO₂ concentrations of either ambient or ambient + 800 ppm. They found plant biomass of *A. auriculiformis* was enhanced by 19%, 21%, and 57%, respectively, at high, medium, and low P. Biomass in *A. mangium* was enhanced by 5%, 32%, and 47%, respectively. Nguyen *et al.* also note, “in both species the increase in plant growth [caused] by elevated CO₂ was accompanied by increased P use efficiency,” “increased N use efficiency[,] and total N accumulation.” In addition, they write, “elevated CO₂ also increased P use efficiency for N₂ fixation.” Consequently, under ambient CO₂, “plant growth and the amount of N fixed symbiotically in N₂-fixing seedlings decreased with the decrease of supplied P,” but “this relationship did not occur under elevated CO₂,” because “elevated CO₂ alleviated [the] low P-induced reduction in plant growth,” mainly by “increasing the use efficiency of internal P for plant growth and N₂ fixation.”

Nguyen *et al.* note in many parts of the world “*Acacia* species are grown for environmental protection and energy plantations on degraded soils,” and their findings indicate these soils’ low nutrient levels may not impede the growth of these important plants.

Khan *et al.* (2008) note the faster and more vigorous plant growth typically observed in CO₂-enriched air “has to be sustained by a sufficient nutrient supply,” because “if increased biomass production is to continue, [nutrient] availability in the soil has to match increasing demand for major nutrients,” such as nitrogen (N) and phosphorus (P), two of the elements “often considered to limit productivity in terrestrial ecosystems.” Khan *et al.* set out to test this hypothesis as it pertains to phosphorus

at the EuroFACE facility near Viterbo in central Italy. They grew three genotypes of *Populus*—*P. alba*, *P. nigra*, and *P. x euroamericana*—under ambient and elevated (ambient + 200 ppm) atmospheric CO₂ concentrations for five years.

The four UK researchers report “increased tree growth under elevated CO₂ has not resulted in the depletion of phosphorus pools in soils as originally hypothesized, but rather in the replenishment and increased storage of P in the rooting zone,” and thus “P may not, therefore, limit tree growth in a high CO₂ world.” Kahn *et al.* conclude “biogenically driven weathering of primary minerals in the rooting zone is sufficient to maintain the replenishment of plant available inorganic P,” and “since future levels of elevated CO₂ may stimulate biomass production in a diverse range of forests (Norby *et al.*, 2005), this increase of P availability is of global consequence.”

Kahn *et al.* (2010) report similar findings in the same EuroFACE experiment, writing, “the availability of P can actually increase in elevated CO₂, forming a positive feedback with increased biomass production on P limited soils.” They conclude “phosphorus limitation may therefore not reduce tree growth in a high CO₂ world.”

Plants growing in CO₂-enriched air likely will respond by increasing their biomass production, even under conditions of low soil phosphorus concentration, especially if plants have the ability to increase root phosphatase activity, as Barrett *et al.* (1998) observed regarding wheat.

References

- Barrett, D.J., Richardson, A.E., and Gifford, R.M. 1998. Elevated atmospheric CO₂ concentrations increase wheat root phosphatase activity when growth is limited by phosphorus. *Australian Journal of Plant Physiology* 25: 87–93.
- Khan, F.N., Lukac, M., Miglietta, F., Khalid, M., and Godbold, D.L. 2010. Tree exposure to elevated CO₂ increases availability of soil phosphorus. *Pakistan Journal of Botany* 42: 907–916.
- Khan, F.N., Lukac, M., Turner, G., and Godbold, D.L. 2008. Elevated atmospheric CO₂ changes phosphorus fractions in soils under a short rotation poplar plantation (EuroFACE). *Soil Biology & Biochemistry* 40: 1716–1723.
- Nguyen, N.T., Mohapatra, P.K., and Fujita, K. 2006. Elevated CO₂ alleviates the effects of low P on the growth of N₂-fixing *Acacia auriculiformis* and *Acacia mangium*. *Plant and Soil* 285: 369–379.

Niklaus, P.A., Leadley, P.W., Stocklin, J., and Korner, C. 1998. Nutrient relations in calcareous grassland under elevated CO₂. *Oecologia* **116**: 67–75.

Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King J.S., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., Angelis, P.D., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarascia-Mugnozza, G.E., Schlesinger, W.H., and Oren, R. 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences USA* **102**: 18,052–18,056.

Staddon, P.L., Fitter, A.H., and Graves, J.D. 1999. Effect of elevated atmospheric CO₂ on mycorrhizal colonization, external mycorrhizal hyphal production and phosphorus inflow in *Plantago lanceolata* and *Trifolium repens* in association with the arbuscular mycorrhizal fungus *Glomus mosseae*. *Global Change Biology* **5**: 347–358.

Stocklin, J. and Korner, Ch. 1999. Interactive effects of elevated CO₂, P availability and legume presence on calcareous grassland: results of a glasshouse experiment. *Functional Ecology* **13**: 200–209.

Walker, R.F., Johnson, D.W., Geisinger, D.R., and Ball, J.T. 1998. Growth and ectomycorrhizal colonization of ponderosa pine seedlings supplied different levels of atmospheric CO₂ and soil N and P. *Forest Ecology and Management* **109**: 9–20.

3.11 The Progressive Nitrogen Limitation Hypothesis

The progressive nitrogen limitation hypothesis suggests low concentrations of soil nitrogen will impede the productivity-enhancing and carbon-sequestering effects of rising atmospheric CO₂ concentrations over the long term. The following three sections explore this possibility as it pertains to Earth's grasslands, loblolly pine trees, and other types of vegetation.

3.11.1 Grasslands

- Real-world data from several multiyear experiments indicate CO₂-induced increases in carbon input to the soil stimulate microbial decomposition and thus lead to more available soil nitrogen, contrary to the progressive nitrogen limitation hypothesis.

Richter *et al.* (2003) measured gross rates of N mineralization, NH₄⁺ consumption, and N immobil-

ization in soils on which monocultures of *Lolium perenne* and *Trifolium repens* had been exposed to ambient (360 ppm) and elevated (600 ppm) concentrations of atmospheric CO₂ for seven years in the Swiss FACE study conducted near Zurich. After seven years of exposure to elevated CO₂, “gross mineralization, NH₄⁺ consumption and N immobilization in both the *L. perenne* and the *T. repens* swards did not show significant differences,” and the size of the microbial N pool and immobilization of applied mineral ¹⁵N were not significantly affected by elevated CO₂. The five researchers conclude their observations “did not support the initial hypothesis,” which was “that increased below-ground translocation of photoassimilates at elevated pCO₂ would lead to an increase in immobilization of N due to an excess supply of energy to the roots and rhizosphere” and would ultimately lead to a reduction in the size of the growth-promoting effect of elevated atmospheric CO₂.

After five years of exposure of a nutrient-poor low-productivity calcareous grassland in northwestern Switzerland to atmospheric CO₂ concentrations of 360 and 660 ppm via screen-aided CO₂ control or SACC technology (Leadley *et al.*, 1997), Thurig *et al.* (2003) measured the vegetative and reproductive responses of the plants comprising the ecosystem. They write, “the effect of elevated CO₂ on the number of flowering shoots (+24%, *P* < 0.01) and seeds (+29%, *P* = 0.06) at the community level was similar to [the] above ground biomass response.” They also found a 42% (*P* < 0.01) increase in the mean seed number of graminoids and a 33% (*P* = 0.07) increase in the mean seed number of forbs, and in most species mean seed weight also tended to be greater (+12%, *P* < 0.01). Atmospheric CO₂ enrichment significantly increased both vegetative and reproductive biomass production. The researchers note many studies have shown heavier seeds result in seedlings that “are more robust than seedlings from lighter seeds (Baskin and Baskin, 1998).” Thus the continued rise of the air's CO₂ content would bode well for these and other nutrient-poor, low-productivity grasslands.

Reich *et al.* (2006) described the first six years' results of a FACE study of perennial grassland species conducted at the Cedar Creek Natural History Area in central Minnesota (USA). On natural ambient-N soil (where N limits growth) or natural soil receiving an extra 4 g N m⁻² yr⁻¹ (applied as NH₄NO₃), they planted 296 field plots to support the growth of either 1, 4, 9, or 16 grassland species (four C₃ grasses, four C₄ grasses, four N-fixing legumes,

and four non-leguminous forbs). The plots were fumigated with either ambient air of ~370 ppm CO₂ or air enriched to a CO₂ concentration of 560 ppm throughout each year's growing season. The nine researchers conclude "low availability of N progressively suppresses the positive response of plant biomass to elevated CO₂."

Their data, however, do not support this conclusion. As best as can be determined from their graph of total plant biomass vs. time in their ambient-N plots (see Figure 3.11.1.1), the percent increase in plant biomass production induced by the extra ~190 ppm of CO₂ supplied to the CO₂-enriched plots progressed from 15% in year 1 to 16% in year 2, 13% in year 3, 0% in year 4, 8% in year 5, and 12% in year 6. Over the first three years of the study, it is difficult to claim there is any meaningful trend in the data, but in year 4 it is clear something happened, as the CO₂-induced growth stimulation dropped to zero. The CO₂-induced growth stimulation reappeared in year 5, rising from 0% to 8%, and it continued its upward climb in year 6, rising from 8% to 12%. The latter value is probably not significantly different from the 13% biomass stimulation recorded in year 3.

The behavior illustrated in Figure 3.11.1.1 is not a low-soil-N-induced "progressive limitation" of the aerial fertilization effect of elevated CO₂. The percent

growth enhancement experienced in year 6 of Reich *et al.*'s study was essentially the same as that experienced in year 3, and the record ends with the aerial fertilization effect in a strong ascending mode. As for years 1 and 2, where the CO₂-induced growth stimulation was slightly higher, Reich *et al.* state, "the positive response to CO₂ enrichment observed under ambient N during the first two years of the experiment may also be more characteristic of seedlings or juvenile plants than of mature well-established plants." This phenomenon (initial large CO₂-induced growth stimulation in the juvenile plant stage which subsequently decreases with time) has been observed in a number of experiments, indicating just how risky it is to predict the course of the CO₂-induced aerial fertilization effect of atmospheric CO₂ enrichment on the basis of even multiple years of data.

These observations indicate there is no compelling reason to believe, as Reich *et al.* concluded, "low availability of N progressively suppresses the positive response of plant biomass to elevated CO₂." There is not even a weak reason for doing so, as their data depict no such phenomenon. And even if the trend they postulate were apparent, the long-term sour orange tree study of Idso and Kimball (2001; see section 1.1.3.2.3 Sour Orange,

this volume) shows six years of data are simply not sufficient to predict the ultimate equilibrium response of a long-lived plant or ecosystem to a large step-increase in atmospheric CO₂ concentration in either N-limiting or non-N-limiting situations. In addition, in the real world of nature the air's CO₂ concentration rises gradually, by only a ppm or two per year, a much easier situation for plants to cope with than that employed in essentially all CO₂ enrichment experiments that have been conducted to date, where a CO₂ concentration increase fully two orders of magnitude greater than that experienced each year in nature is typically imposed on the plants being studied. Thus it is important to

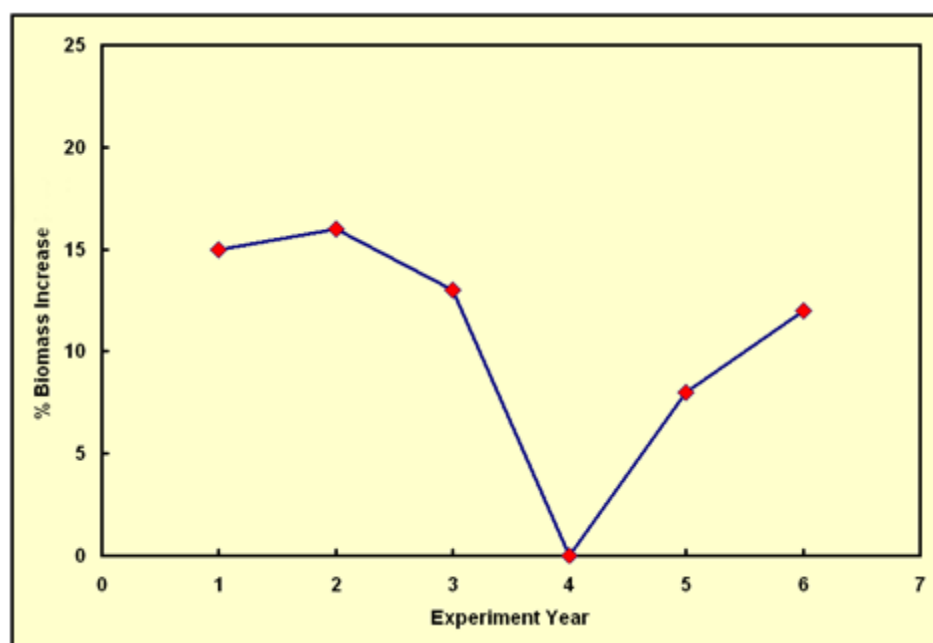


Figure 3.11.1.1. Percent increase in biomass production by the plants in the ambient-N soil plots of Reich *et al.* since the start of their long-term experiment, as a result of enriching the CO₂ concentration of the air above the plots by 190 ppm. Adapted from Reich *et al.* (2006)

conduct experiments for as long a period of time as possible—the answer is out there, but it could be far out there, several years in the future.

Zavaleta and Kettley (2006) studied an annual grassland at the Jasper Ridge Biological Preserve in the interior foothills of the central coast mountain range south of San Francisco, California (USA). They examined patterns of production, standing biomass, carbon and nitrogen storage, community composition, and soil moisture along a 25-year chronosequence of sites in various stages of invasion by the woody shrub *Baccharis pilularis*. They sought evidence for the hypothesis “*Baccharis*-invaded sites would experience increasing nitrogen limitation as nitrogen was immobilized in biomass and litter,” and whether this phenomenon would preclude further increases in ecosystem biomass.

In progressing from initial grassland conditions to conditions that prevailed 25 years after shrub invasion began, the two researchers report, “net increases in biomass and tissue and soil C:N [carbon to nitrogen ratio] contributed to increases in total ecosystem carbon storage of over 125%.” Even more stunning was their discovery the increases in ecosystem biomass “drove increases in ecosystem nitrogen sequestration of ~700%.” In the soil alone, nitrogen content also “increased rapidly with shrub age,” as the increase in soil nitrogen “was much larger than the increase in nitrogen immobilization in biomass and litter over time.”

What was the source of the extra nitrogen? The two researchers mention several possibilities but say they could not be sure of them. Nevertheless, their observations repudiate the progressive nitrogen limitation hypothesis, making it clear a soil of low initial nitrogen status need not constrain long-term positive ecosystem responses to biomass-enhancing phenomena such as woody plant invasions and atmospheric CO₂ enrichment. Zavaleta and Kettley state, “while many climate models now incorporate the effects of short-term energy and resource exchanges between the atmosphere and the biosphere, most do not consider feedbacks associated with long-term vegetation changes.” They also say their findings “illustrate the potential for important vegetation-mediated ecosystem responses and feedbacks to atmospheric CO₂ and climate change,” while additionally noting many of the changes they observed “were progressive and did not saturate with time.”

Drissner *et al.* (2007) measured soil microbial biomass and the activities of associated enzymes

covering cycles of the most important elements (C, N, and P) for nine years in a FACE study conducted near Zurich, Switzerland, on three types of grassland (monocultures and mixed cultures of *Trifolium repens* L. and *Lolium perenne* L.) under two nitrogen treatments (low N = 14 g N m⁻² year⁻¹; high N = 56 g N m⁻² year⁻¹) and maintained at atmospheric CO₂ concentrations of either 350 or 600 ppm. They write, “the enrichment in CO₂ increased soil microbial biomass (+48.1%) as well as activities of invertase (+36.2%), xylanase (+22.9%), urease (+23.8%), protease (+40.2%) and alkaline phosphomonoesterase (+54.1%) in spring,” and “in autumn, the stimulation of microbial biomass was 25% less and that of enzymes 3–12% less than in spring.” All of these increases, the researchers write, “were most likely stimulated by increase in roots under enriched CO₂.”

Drissner *et al.* report in their nine-year-long FACE experiment, “stimulation of enzyme activities in the enriched CO₂ indicated enhanced C, N and P cycling and greater availabilities of nutrients for microbial and plant growth.” They conclude their results “support the hypothesis of positive feedback proposed by Zak *et al.* (1993), who stated that additional C stimulates microbial decomposition and thus leads to more available N under enriched CO₂.” Their results and others thus contradict periodic claims that the future availability of nitrogen will be too low to support large CO₂-induced increases in plant growth over the long term.

References

- Baskin, C.C. and Baskin, J.M. 1998. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, CA.
- Drissner, D., Blum, H., Tscherko, D., and Kandeler, E. 2007. Nine years of enriched CO₂ changes the function and structural diversity of soil microorganisms in a grassland. *European Journal of Soil Science* **58**: 260–269.
- Hungate, B.A., Dukes, J.S., Shaw, M.R., Luo, Y., and Field, C.B. 2003. Nitrogen and climate change. *Science* **302**: 1512–1513.
- Idso, S.B. and Kimball, B.A. 2001. CO₂ enrichment of sour orange trees: 13 years and counting. *Environmental and Experimental Botany* **46**: 147–153.
- Leadley, P.W., Niklaus, P.A., and Stocker, R., *et al.* 1997. Screen-aided CO₂ control (SACC): a middle ground between FACE and open-top chambers. *Acta Oecologica* **18**: 39–49.

Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R.E., Oren, R., Parton, W.J., Pataki, D.E., Shaw, M.R., Zak, D.R., and Field, C.B. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* **54**: 731–739.

Reich, P.B., Hobbie, S.E., Lee, T., Ellsworth, D.S., West, J.B., Tilman, D., Knops, J.M.H., Naeem, S., and Trost, J. 2006. Nitrogen limitation constrains sustainability of ecosystem response to CO₂. *Nature* **440**: 922–925.

Richter, M., Hartwig, U.A., Frossard, E., Nosberger, J., and Cadisch, G. 2003. Gross fluxes of nitrogen in grassland soil exposed to elevated atmospheric pCO₂ for seven years. *Soil Biology & Biochemistry* **35**: 1325–1335.

Thurig, B., Korner, C., and Stocklin, J. 2003. Seed production and seed quality in a calcareous grassland in elevated CO₂. *Global Change Biology* **9**: 873–884.

Zak, D.R., Pregitzer, K.S., Curtis, P.S., Teeri, J.A., Fogel, R., and Randlett, D.L. 1993. Elevated atmospheric CO₂ and feedback between carbon and nitrogen cycles. *Plant and Soil* **151**: 105–117.

Zavaleta, E.S. and Kettley, L.S. 2006. Ecosystem change along a woody invasion chronosequence in a California grassland. *Journal of Arid Environments* **66**: 290–306.

3.11.2 Loblolly Pine

- Extensive experimentation on loblolly pine trees (plus several understory species) at the Duke Forest long-term free-air CO₂ enrichment (FACE) site has conclusively disproven the progressive nitrogen limitation hypothesis, instead suggesting the growth-enhancing benefits of atmospheric CO₂ enrichment should continue as the air's CO₂ content rises.

The progressive nitrogen limitation (PNL) hypothesis posits low concentrations of soil nitrogen will inhibit the productivity-enhancing effect of atmospheric CO₂ enrichment, meaning increases in plant growth and ecosystem carbon sequestration rates will not be sustained over long periods of time. In this section this possibility is explored as it pertains to loblolly pine (*Pinus taeda* L.) trees.

Finzi and Schlesinger (2003) measured and analyzed pool sizes and fluxes of inorganic and organic nitrogen in the forest floor and top 30 cm of mineral soil during the first five years of differential atmospheric CO₂ treatment of a stand of initially 13-year-old loblolly pine trees at the Duke Forest FACE

facility in the Piedmont region of North Carolina (USA), where half of the experimental plots were maintained at an atmospheric CO₂ concentration approximately 200 ppm above ambient. The extra CO₂ significantly increased the input of carbon (C) and nitrogen (N) to the forest floor, as well as to the mineral soil in which the trees were growing. Finzi and Schlesinger report “there was no statistically significant change in the cycling rate of N derived from soil organic matter under elevated CO₂,” and “neither the rate of net N mineralization nor gross ¹⁵NH₄⁺ dynamics were significantly altered by elevated CO₂.” They found “no statistically significant difference in the concentration or net flux of organic and inorganic N in the forest floor and top 30-cm of mineral soil after 5 years of CO₂ fumigation,” adding, “microbial biomass was not a larger sink for N.” Based on these findings, they rejected their original hypothesis, which was essentially the PNL hypothesis: that the extra CO₂ provided to the experimental plots would significantly increase the rate of nitrogen immobilization by the soil microbial communities found in the CO₂-enriched FACE arrays and thereby lead to a reduction in the magnitude of the growth stimulation initially manifest in the CO₂-enriched treatment.

Schafer *et al.* (2003) measured net ecosystem exchange (NEE) and net ecosystem production (NEP) at the Duke Forest FACE facility during the third and fourth years of the long-term CO₂ enrichment study conducted there. They found the extra 200 ppm of CO₂ supplied to the loblolly pine trees in the CO₂-enriched FACE arrays increased the entire canopy's net uptake of CO₂ (NEE) by 41%, and canopy NEP was increased by 44%. They note 87% of the extra NEP “was sequestered in a moderately long-term C pool in wood.” This large increase in solidly sequestered carbon is remarkable, especially given that, as noted by Finzi and Schlesinger (2003), the soil at the Duke Forest FACE site at that time was in “a state of acute nutrient deficiency that can only be reversed with fertilization,” which was not provided.

Finzi *et al.* (2006) again tested the PNL concept “using data on the pools and fluxes of C and N in tree biomass, microbes and soils” obtained from the first six years of the Duke Forest FACE study. As was the case three years earlier, “there was no reduction in the average stimulation of net primary production by elevated CO₂,” even though “significantly more N was immobilized in tree biomass and in the O [soil] horizon under elevated CO₂.” Also, and “in contrast to the PNL hypothesis,” they write, “microbial-N

immobilization did not increase under elevated CO₂, and although the rate of net N mineralization declined through time, the decline was not significantly more rapid under elevated CO₂.” The 12 researchers also report, “mass balance calculations demonstrated a large accrual of ecosystem N capital,” and the rate of the extra N accrual was “much greater than the estimated rate of N input via atmospheric deposition or heterotrophic N fixation.” Noting “there are no plant species capable of symbiotic N fixation in this ecosystem,” they say some other mechanism enabled the loblolly pine trees to obtain the extra N they needed to stave off the negative effects predicted by the PNL hypothesis; possibly, Finzi *et al.* write, by roots “actively taking up N and redistributing N from deeper in the soil profile.”

Moore *et al.* (2006) report finding “a sustained increase in basal area increment over the first 8 years of [their] experiment,” which varied between 13 and 27% in harmony with variations in weather and the timing of growth. They also report, “there was no evidence of a decline in the relative enhancement of tree growth by elevated CO₂ as might be expected if soil nutrients were becoming progressively more limiting,” which normally would be expected, considering the unfertilized state of the soil in which the experiment was conducted.

Pritchard *et al.* (2008a) published the results they obtained from minirhizotrons employed to characterize the influence of the extra 200 ppm of CO₂ on the fine roots of the Duke Forest loblolly pines over the six-year period 1998–2004. Averaged over all six years, they found the extra CO₂ increased average fine-root standing crop by 23%, which compared well with the overall stimulation of tree net primary productivity of 18–24% observed over the period 1996–2002. They noted “the positive effects of CO₂ enrichment on fine root growth persisted 6 years following minirhizotron tube installation (8 years following initiation of the CO₂ fumigation),” finding no evidence of progressive nitrogen limitation to the stimulatory effect of atmospheric CO₂ enrichment. As a possible explanation for their findings, Pritchard *et al.* point out the distal tips of fine roots are “the primary site for initiation of mycorrhizal partnerships which are critical for resource acquisition and could also influence whether or not forests can sustain higher productivity in a CO₂-enriched world.”

Pritchard *et al.* (2008b) focused their attention on the role played by ectomycorrhizal (ECM) fungi over five years, based on minirhizotron observations of fungal dynamics at the Duke Forest FACE site.

Summed across all years of the study, the five researchers found the extra 200 ppm of CO₂ provided to the trees in the high-CO₂ treatment did not influence mycorrhizal production in the top 15 cm of the forest soil, but it increased mycorrhizal root-tip production by 194% throughout the 15–30 cm depth interval. Production of soil rhizomorph length was 27% greater in the CO₂-enriched plots than in the ambient-air plots.

Pritchard *et al.* state the CO₂-induced “stimulation of carbon flow into soil has increased the intensity of root and fungal foraging for nutrients,” and “the shift in distribution of mycorrhizal fungi to deeper soils may enable perennial plant systems to acquire additional soil nitrogen to balance the increased availability of ecosystem carbohydrates in CO₂-enriched atmospheres.” This additional acquisition of nitrogen in the CO₂-enriched plots of the Duke Forest FACE study was determined to be approximately 12 g N per m² per year.

Pritchard *et al.* also write, “the notion that CO₂ enrichment expands the volume of soil effectively explored by roots and fungi, and that foraging in a given volume of soil also seems to intensify, provides compelling evidence to indicate that CO₂ enrichment has the potential to stimulate productivity (and carbon sequestration) in N-limited ecosystems more than previously expected.” While they also speculate “it is unlikely that ecosystem productivity will be stimulated by CO₂ enrichment indefinitely,” nature had to this point in time proven such speculations invalid.

Summarizing their nine years of work at the Duke Forest FACE facility, Lichter *et al.* (2008) once again warn progressive nitrogen limitation may “accompany carbon sequestration in plants and soils stimulated by CO₂ fertilization, gradually attenuating the CO₂ response.” They describe what they had learned about the PNL hypothesis over the prior nine years.

The nine scientists first note their data pertaining to forest-floor carbon pools indicate the existence of “a long-term steady-state sink” of about 30 g C per m² per year, which represents, they write, “a substantial increase in forest-floor C storage under elevated CO₂ (i.e. 29%),” which they attribute to “increased litter-fall and root turnover during the first 9 years of the study.” Second, below the forest floor, they say, “approximately 20% [of the mineral soil carbon formed during the prior nine years] has been allocated to stable pools that will likely remain protected from microbial activity and associated release as CO₂.”

A third important finding was “a significant

widening of the C/N ratio of soil organic matter in the upper mineral soil under both elevated and ambient CO₂,” which suggests, as they describe it, “enhanced rates of soil organic matter decomposition are increasing mineralization and uptake to provide the extra N required to support the observed increase in primary productivity under elevated CO₂.” And at the Duke Forest FACE site, Pritchard *et al.* (2008b) say this CO₂-induced increase in productivity amounted to approximately 30% annually, adding there is “little evidence to indicate a diminished response through time.” They cite Finzi *et al.* (2007), who found the same to be true at the long-term forest FACE studies at Rhinelander, Wisconsin (USA), Oak Ridge National Laboratory (USA), and Tuscania (Italy).

Contrary to the early expectations of many scientists, many forests thought to have had access to less-than-adequate soil nitrogen supplies appear to be able to acquire the extra nitrogen they need to maintain the sizable increases in their growth rates driven by elevated concentrations of atmospheric CO₂. In North Carolina’s Duke Forest, for example, “even after nine years of experimental CO₂ fertilization,” as Lichter *et al.* (2008) note, “attenuation of the CO₂-induced productivity enhancement has not been observed,” as Finzi *et al.* (2006) also found. This finding at this location is extremely significant because the growth of pine-hardwood forests in the southeastern United States often removes so much nitrogen from the soil they induce what Finzi and Schlesinger (2003) describe as “a state of acute nutrient deficiency that can only be reversed with fertilization,” which, as noted earlier in this section, was not employed at the Duke Forest FACE study.

Jackson *et al.* (2009) describe new belowground data they obtained at the Duke Forest Face site, then present a synthesis of these and other results obtained from 1996 through 2008 to determine which variables may have shown a decrease in their response to atmospheric CO₂ enrichment during that period. Among many other things, they found, “on average, in elevated CO₂, fine-root biomass in the top 15 cm of soil increased by 24%,” and in recent years the fine-root biomass increase “grew stronger, averaging ~30% at high CO₂.” Regarding coarse roots with diameters greater than 2 mm and extending to a soil depth of 32 cm, they report, biomass sampled in 2008 was “twice as great in elevated CO₂.” The graphical representation of their results indicates the coarse-root biomass was 130% greater, quite extraordinary given that the extra 200 ppm of CO₂ supplied to the air

surrounding the CO₂-enriched trees represented an enhancement of only about 55% above ambient conditions. They conclude, “overall, the effect of elevated CO₂ belowground shows no sign of diminishing.”

The four researchers also remark, “if progressive nitrogen limitation were occurring in this system, we would expect differences in productivity to diminish for trees in the elevated vs. ambient CO₂ plots,” but “there is little evidence from estimates of aboveground or total net primary productivity in the replicated Duke experiment that progressive nitrogen limitation is occurring there or at other forest FACE experiments,” citing Finzi *et al.* (2007).

McCarthy *et al.* (2010) analyzed data from the Duke Forest FACE experiment for the years 1996–2004, calculating the net primary productivity (NPP) of the entire ecosystem—including the loblolly pines’ understory of various broadleaf species (*Liriodendron tulipifera*, *Liquidambar styraciflua*, *Acer rubrum*, *Ulmus alata*, *Cornus florida*) plus various other trees, shrubs, and vines—as “the sum of the production of coarse wood (stems, branches, coarse roots), leaf litter (lagged for pines), fine roots and reproductive structures.”

They report “elevated CO₂ increased pine biomass production, starting in 1997 and continuing every year thereafter”; “the CO₂-induced enhancement remained fairly consistent as the stand developed”; and “elevated CO₂ increased stand (pine plus all other species) biomass production every year from 1997 onwards with no trend over time.” They also noted the average yearly increase in NPP caused by the approximate 54% increase in the air’s CO₂ content was 28%. In contradiction of the PNL hypothesis, the trees, bushes, and shrubs constituting the Duke Forest has continued to maintain the extra CO₂-enabled vitality it exhibited from the start of the study, with no subsequent sign of it tapering off.

Drake *et al.* (2011) described how the CO₂-induced enhanced rates of net primary production at the Duke Forest FACE site likely were sustained by a carbon cascade through the root-microbe-soil system. They write, “increases in the flux of carbon belowground under elevated CO₂ stimulated microbial activity” that in turn “accelerated the rate of soil organic matter decomposition and stimulated tree uptake of nitrogen bound to this soil organic matter.” This process “set into motion a positive feedback maintaining greater carbon gain under elevated CO₂ as a result of increases in canopy nitrogen content and higher photosynthetic nitrogen-use efficiency,” the

consequence of which was “the dominance of carbon storage in tree biomass.”

Drake *et al.* write, “the long-term increase in forest productivity under elevated CO₂ at the Duke FACE site appears to be maintained by a belowground exchange of tree carbon for soil nitrogen, with the quantity of carbon allocated belowground set by the availability of nitrogen in the soil and the demand for nitrogen to meet growth requirements.” They note, “all of the belowground carbon fluxes thought to increase decomposition rates increased under elevated CO₂, including root production and mortality (Pritchard *et al.*, 2008a), root exudation (Phillips *et al.*, 2011), fungal rhizomorph production (Pritchard *et al.*, 2008b) and allocation of carbon to mycorrhizal fungi (Garcia *et al.*, 2008).” They conclude, “the preponderance of the evidence points to increased decomposition [of organic matter] in surface soils as the primary source of additional nitrogen taken up by the trees growing under elevated CO₂.”

Phillips *et al.* (2011) opine “increased root exploration alone is unlikely to sustain plant nitrogen requirements under rising CO₂ unless accompanied by the concomitant stimulation of soil microbial activity and the release of nutrients from soil organic matter.” Despite the presumed importance of root exudates in this scenario, they note no studies had yet quantified the effects of CO₂ enrichment on exudation by mature trees. They set out to do so in order to understand why progressive nitrogen limitation was not observed in some long-term studies of trees growing on nutrient-poor soil (Langley *et al.*, 2009; McCarthy *et al.*, 2010). Working at the Duke Forest FACE facility, the three researchers examined plant-microbe interactions in the rhizospheres and bulk soils of the various treatments, measuring differences in rhizosphere microbial activity and root exudation rates.

On an annual basis, Phillips *et al.* state, “exudation increased by c. 50% for trees enriched with CO₂ in non-fertilized plots,” but trees were unaffected in this manner by CO₂ enrichment in fertilized plots, demonstrating “increased root carbon efflux from CO₂-enriched trees stimulates rhizosphere N cycling in low fertility soils.” Their work provides additional evidence that “rhizosphere microbes such as actinomycetes, which produce NAGase enzymes and respond strongly to CO₂ at this site (Billings and Ziegler, 2008), are using energy derived from exudates to synthesize enzymes that release nitrogen from soil organic matter (Cheng and Kuzyakov,

2005).” They emphasize “this dramatic contrast between the fertilized and unfertilized treatments provides evidence that enhanced exudation is a mechanism trees employ for increasing nitrogen availability.”

Phillips *et al.* write “the enhanced carbon flux from roots to soil in low fertility forests exposed to elevated CO₂ creates hotspots for microbial activity that are associated with faster rates of soil organic matter turnover and N cycling.” This phenomenon provides the trees the extra nitrogen they need to take full advantage of the enhanced potential for growth provided by atmospheric CO₂ enrichment, contrary to the incorrect implications of the progressive nitrogen limitation hypothesis. Phillips *et al.* state their results “provide field-based empirical support suggesting that sustained growth responses of forests to elevated CO₂ in low fertility soils are maintained by enhanced rates of microbial activity and N cycling fueled by inputs of root-derived carbon.”

Hofmockel *et al.* (2011) write, “several free-air CO₂ enrichment (FACE) experiments in North America have shown a continual stimulation in forest productivity under elevated CO₂ over time scales nearly reaching a decade (Finzi *et al.*, 2006; Norby and Iversen, 2006; Zak *et al.*, 2007; McCarthy *et al.*, 2010).” In their own examination of the effects of elevated CO₂ on nitrogen (N) cycling in the Duke Forest, where elevated atmospheric CO₂ concentrations “consistently stimulated forest productivity” throughout the decade-long experiment being conducted there, Hofmockel *et al.* provide “an integrated understanding” of this phenomenon that serves as “a basis for inferring how C and N cycling in this forest may respond to elevated CO₂ beyond the decadal time scale.”

“Using natural-abundance measures of nitrogen isotopes together with an ecosystem-scale ¹⁵N tracer experiment,” as the six scientists describe it, they “quantified the cycling of ¹⁵N in plant and soil pools under ambient and elevated CO₂ over three growing seasons to determine how elevated CO₂ changed nitrogen cycling between plants, soil and micro-organisms,” after having first measured natural abundances of ¹⁵N in plant and soil pools in the two CO₂ treatments over the prior year. They discovered “at the Duke FACE site, the rate at which N is being sequestered in plant biomass is greater than the rate of atmospheric deposition and heterotrophic N fixation,” a finding also established by Finzi *et al.* (2002), Hofmockel and Schlesinger (2007), and Sparks *et al.* (2008). These findings suggest, they write, “soil

organic matter decomposition supplies a significant fraction of plant N in both ambient and elevated-CO₂ conditions, but that this is greater under elevated CO₂.”

Hofmockel *et al.* conclude, “in pine forests of the southeastern United States, rising CO₂ may elicit shifts in the mechanisms by which plants acquire nitrogen, allowing a sustained increase in net primary productivity for decades,” further stating, “increased mineralization of nitrogen in the organic and 0–15 cm mineral horizon and deeper rooting are likely sustaining the elevated CO₂ enhancement of net primary productivity.”

Ellsworth *et al.* (2012) “compiled a comprehensive dataset measured over ten years for a temperate pine forest of *Pinus taeda*, but also including deciduous species, primarily *Liquidambar styraciflua*,” derived from “over one thousand controlled-response curves of photosynthesis as a function of environmental drivers (light, atmospheric CO₂ concentration [Ca] and temperature) measured at canopy heights up to 20 meters over eleven years (1996–2006).” From that data they generated “parameterizations for leaf-scale models for the Duke free-air CO₂ enrichment (FACE) experiment.”

They found the enhancement of light-saturated leaf net photosynthesis (Anet) in *P. taeda* trees produced by an elevated Ca of +200 ppm was 67% for current-year needles in the upper crown of the trees in summer conditions over the 10-year period, and previous-year foliage Anet was enhanced by 30%. They note “the mean stimulation in light-saturated Anet averaged over the growing season of all years and across canopy positions and needle age classes was $53 \pm 7\%$.” In addition, “the photosynthetic enhancement responses to elevated Ca are mirrored in part by the pine biomass accumulation responses to elevated Ca across different years.”

The eight researchers also report “co-dominant and sub-canopy *L. styraciflua* trees showed Anet enhancement of 62%,” and “various understory deciduous tree species showed an average Anet enhancement of 42%.” In addition, “the photosynthetic responses of shaded, understory leaves suggest a capacity to increase photosynthetic carbon capture in elevated Ca in shade-grown plants when measured in sunflecks,” citing DeLucia and Thomas (2000). They note this response suggests “a competitive advantage to shade-tolerant species adapted for carbon capture in high sunlight or sunflecks in the understory over less shade-tolerant species.”

This comprehensive set of photosynthesis mea-

surements compiled over the course of the Duke Forest FACE study rebuts the progressive nitrogen limitation hypothesis, which posits the initial growth stimulation of atmospheric CO₂ enrichment will dwindle away as time progresses, especially in the case of the pine-hardwood forests of the southeastern United States, which often remove so much nitrogen from the soils in which they grow as to induce what Finzi and Schlesinger (2003) once described as “a state of acute nutrient deficiency that can only be reversed with fertilization.” Ellsworth *et al.*’s work demonstrates this is simply not true. In another implication of their findings, the eight researchers conclude the observed “differences in photosynthetic responses between the over-story pines and deciduous tree sub-canopy suggest that increased Ca may have the potential to enhance the mixed-species composition of planted pine stands,” and, by extension, “naturally regenerating pine-dominated stands.”

Rounding out this review of the progressive nitrogen limitation hypothesis are Phillips *et al.* (2012), who write, “after nearly two decades of research on forest ecosystem responses to global change, uncertainty about the role of roots and rhizosphere processes in soil C and N retention and loss has limited our ability to predict biogeochemical feedbacks to long-term forest productivity.” Working at the Duke Forest FACE site, where eight 30-meter-diameter plots of loblolly pine (*Pinus taeda* L.) trees were enriched with an extra 200 ppm of CO₂ from 1996 to 2010, and four similar plots were maintained under then-current ambient-air conditions, Phillips *et al.* measured root-induced changes in soil C dynamics of trees exposed to CO₂ and nitrogen enrichment by combining stable isotope analyses, molecular characterizations of soil organic matter, and microbial assays.

The six scientists conclude the CO₂-enriched trees “may be both enhancing the availability of N by stimulating microbial decomposition of soil organic matter via priming and increasing the rate at which N cycles through the microbial pools owing to the rapid turnover of N-rich fungal tissues,” noting “the accelerated turnover of hyphal tissues under elevated CO₂ may represent an important source of N to plants and microbes.” Referring to this CO₂-induced phenomenon as the Rhizo-Accelerated Mineralization and Priming, or RAMP, hypothesis, Phillips *et al.* suggest it may have “important consequences for N availability and forest productivity,” which could be expected to sustain CO₂-enhanced tree growth over their lifetimes.

References

- Billings, S.A. and Ziegler, S.E. 2008. Altered patterns of soil carbon substrate usage and heterotrophic respiration in a pine forest with elevated CO₂ and N fertilization. *Global Change Biology* **14**: 1025–1036.
- Cheng, W. and Kuzyakov, Y. 2005. Root effects on soil organic matter decomposition. In: Zobel, R. and Wright, S. (Eds.) *Roots and Soil Management: Interactions Between Roots and the Soil*. American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, Wisconsin, USA, pp. 119–143.
- DeLucia, E.H. and Thomas, R.B. 2000. Photosynthetic responses to CO₂ enrichment of four hardwood species in a forest understory. *Oecologia* **122**: 11–19.
- Drake, J.E., Gallet-Budynek, A., Hofmockel, K.S., Bernhardt, E.S., Billings, S.A., Jackson, R.B., Johnsen, K.S., Lichter, J., McCarthy, H.R., McCormack, M.L., Moore, D.J.P., Oren, R., Palmroth, S., Phillips, R.P., Pippen, J.S., Pritchard, S.G., Treseder, K.K., Schlesinger, W.H., DeLucia, E.H., and Finzi, A.C. 2011. Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO₂. *Ecology Letters* **14**: 349–357.
- Ellsworth, D.S., Thomas, R., Crous, K.Y., Palmroth, S., Ward, E., Maier, C., DeLucia, E., and Oren, R. 2012. Elevated CO₂ affects photosynthetic responses in canopy pine and subcanopy deciduous trees over 10 years: a synthesis from Duke FACE. *Global Change Biology* **18**: 223–242.
- Finzi, A.C., Delucia, E.H., Hamilton, J.G., Richter, D.D., and Schlesinger, W.H. 2002. The nitrogen budget of a pine forest under free air CO₂ enrichment. *Oecologia* **132**: 567–578.
- Finzi, A.C., Moore, D.J.P., DeLucia, E.H., Lichter, J., Hofmockel, K.S., Jackson, R.B., Kim, H.-S., Matamala, R., McCarthy, H.R., Oren, R., Pippen, J.S., and Schlesinger, W.H. 2006. Progressive nitrogen limitation of ecosystem processes under elevated CO₂ in a warm-temperate forest. *Ecology* **87**: 15–25.
- Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., and Ceulemans, R. 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂. *Proceedings of the National Academy of Sciences, USA* **104**: 14,014–14,019.
- Finzi, A.C. and Schlesinger, W.H. 2003. Soil-nitrogen cycling in a pine forest exposed to 5 years of elevated carbon dioxide. *Ecosystems* **6**: 444–456.
- Garcia, M.O., Ovaspyan, T., Greas, M., and Treseder, K.K. 2008. Mycorrhizal dynamics under elevated CO₂ and nitrogen fertilization in a warm temperate forest. *Plant and Soil* **303**: 301–310.
- Hofmockel, K.S., Gallet-Budynek, A., McCarthy, H.R., Currie, W.S., Jackson, R.B., and Finzi, A. 2011. Sources of increased N uptake in forest trees growing under elevated CO₂: results of a large-scale ¹⁵N study. *Global Change Biology* **17**: 3338–3350.
- Hungate, B.A., Dukes, J.S., Shaw, M.R., Luo, Y., and Field, C.B. 2003. Nitrogen and climate change. *Science* **302**: 1512–1513.
- Jackson, R.B., Cook, C.W., Pippen, J.S., and Palmer, S.M. 2009. Increased belowground biomass and soil CO₂ fluxes after a decade of carbon dioxide enrichment in a warm-temperate forest. *Ecology* **90**: 3352–3366.
- Langley, J.A., McKinley, D.C., Wolf, A.A., Hungate, B.A., Drake, B.G., and Megonigal, J.P. 2009. Priming depletes soil carbon and releases nitrogen in a scrub-oak ecosystem exposed to elevated CO₂. *Soil Biology and Biochemistry* **41**: 54–60.
- Lichter, J., Billings, S.A., Ziegler, S.E., Gaindh, D., Ryals, R., Finzi, A.C., Jackson, R.B., Stemmmer, E.A., and Schlesinger, W.H. 2008. Soil carbon sequestration in a pine forest after 9 years of atmospheric CO₂ enrichment. *Global Change Biology* **14**: 2910–2922.
- McCarthy, H.R., Oren, R., Johnsen, K.H., Gallet-Budynek, A., Pritchard, S.G., Cook, C.W., LaDeau, S.L., Jackson, R.B., and Finzi, A.C. 2010. Re-assessment of plant carbon dynamics at the Duke free-air CO₂ enrichment site: interactions of atmospheric [CO₂] with nitrogen and water availability over stand development. *New Phytologist* **185**: 514–528.
- Moore, D.J.P., Aref, S., Ho, R.M., Pippen, J.S., Hamilton, J.G., and De Lucia, E.H. 2006. Annual basal area increment and growth duration of *Pinus taeda* in response to eight years of free-air carbon dioxide enrichment. *Global Change Biology* **12**: 1367–1377.
- Norby, R.J. and Iversen, C.M. 2006. Nitrogen uptake, distribution, turnover, and efficiency of use in a CO₂-enriched sweetgum forest. *Ecology* **87**: 5–14.
- Phillips, R.P., Finzi, A.C., and Bernhardt, E.S. 2011. Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO₂ fumigation. *Ecology Letters* **14**: 187–194.
- Phillips, R.P., Meier, I.C., Bernhardt, E.S., Grandy, A.S., Wickings, K., and Finzi, A.C. 2012. Roots and fungi accelerate carbon and nitrogen cycling in forests exposed to elevated CO₂. *Ecology Letters* **15**: 1042–1049.

Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., Finzi, A.C., Jackson, R.B., Matamala, R., Rogers, H.H., and Oren, R. 2008a. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO₂-enrichment: a six-year-minirhizotron study. *Global Change Biology* **14**: 588–602.

Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., and Oren, R. 2008b. Mycorrhizal and rhizomorph dynamics in a loblolly pine forest during 5 years of free-air-CO₂-enrichment. *Global Change Biology* **14**: 1–13.

Schafer, K.V.R., Oren, R., Ellsworth, D.S., Lai, C.-T., Herrick, J.D., Finzi, A.C., Richter, D.D., and Katul, G.G. 2003. Exposure to an enriched CO₂ atmosphere alters carbon assimilation and allocation in a pine forest ecosystem. *Global Change Biology* **9**: 1378–1400.

Sparks, J.P., Walker, J., Turnipseed, A., and Guenther, A. 2008. Dry nitrogen deposition estimates over a forest experiencing free air CO₂ enrichment. *Global Change Biology* **14**: 768–781

Zak, D.R., Holmes, W.E., and Pregitzer, K.S. 2007. Atmospheric CO₂ and O₃ alter the flow of N-15 in developing forest ecosystems. *Ecology* **88**: 2630–2639.

3.11.3 Other Plants

- Although the progressive nitrogen limitation hypothesis initially was embraced by many scientists, a vast array of observational data has subsequently shown it does not explain changes in real ecosystems.

The progressive nitrogen limitation (PNL) hypothesis—which contends low concentrations of soil nitrogen will gradually inhibit the aerial fertilization effect of atmospheric CO₂ enrichment—had its origins in the writings of Hungate *et al.* (2003) and Luo *et al.* (2004). Interestingly, the first of these papers contains considerable evidence that argues against its authors' contentions, as does a subsequent publication (Luo *et al.*, 2006), the senior author of which was also senior author of the second paper.

Hungate *et al.* (2003) report the C:N ratio of tree biomass increases with increases in the air's CO₂ concentration, citing Hungate (1999) and Rastetter *et al.* (1992). This indicates increasing amounts of carbon can be stored in tree tissues per unit of nitrogen stored therein as the air's CO₂ content rises; as Hungate and his coauthors state, "soil C:N could also increase with rising atmospheric CO₂ concentration, allowing soil carbon accumulation without

additional nitrogen."

Lou *et al.* (2006) conducted a meta-analysis of various C and N processes in plants and soils in response to atmospheric CO₂ enrichment based on experimentally derived data contained in 104 scientific publications. In response to atmospheric CO₂ enrichment, the carbon and nitrogen contents in all the plant and soil pools studied significantly increased, "leading to more net C and N accumulations in ecosystems at elevated than ambient CO₂." They found the mean CO₂-induced increases in C pools of shoot, root, whole plant, litter, and soil were 22.4%, 31.6%, 23.0%, 20.6%, and 5.6%, respectively, and the corresponding CO₂-induced increases in N pools were 4.6%, 10.0%, 10.2%, 25.4%, and 11.2%. In addition, "N accumulations in ecosystems have long been documented in association with C accumulations during both primary and secondary successions (Crocker and Major, 1955; Binkley *et al.*, 2000; Vitousek, 2004)." They conclude, "the net C and N accumulations revealed in this study," which were produced by atmospheric CO₂ enrichment, "together with studies of C and N dynamics during succession over hundreds to millions of years, suggest that ecosystems may have intrinsic capabilities to stimulate N accumulation by C input," which is typically increased by atmospheric CO₂ enrichment. They further conclude "net N accumulation likely supports long-term C sequestration in response to rising atmospheric CO₂ concentration." They state "concomitant increases in C and N contents in plant and soil pools at elevated CO₂ as shown in this study point toward a long-term trend of terrestrial C sequestration in response to rising atmospheric CO₂ concentration," just the opposite of what the PNL hypothesis predicts.

Norby and Iverson (2006) reviewed what they had learned about the PNL hypothesis from "a six-year record of N dynamics of a sweetgum (*Liquidambar styraciflua*) stand exposed to elevated CO₂ in the free-air CO₂ enrichment (FACE) experiment at Oak Ridge, Tennessee, USA," focusing on N uptake, content, distribution, turnover, and N-use efficiency. They write, "net primary productivity in this stand has been significantly higher in CO₂-enriched plots, and the response has been sustained through time, thereby meeting one of the criteria for the development of PNL." They further report, "none of the measured responses of plant N dynamics in this ecosystem indicated the occurrence of PNL."

Hungate *et al.* (2006) tested the PNL hypothesis against what they had observed over seven years in an

open-top chamber study of a scrub oak woodland dominated by *Quercus myrtifolia*, *Q. geminate*, and *Q. chapmanii* on an island in NASA's Kennedy Space Center on the coast of central Florida (USA). Their experiment commenced just a few months after a complete burning of the ecosystem located on well-drained but nutrient-poor soil. They report "litterfall production (one measure of aboveground primary productivity) increased initially in response to elevated CO₂, but the CO₂ stimulation declined during years five through seven, concurrent with the accumulation of N in the O [soil] horizon and the apparent restriction of plant N availability." They state these changes in N cycling were "likely to reduce the response of plant production to elevated CO₂." However, they acknowledge, "at the level of aboveground plant biomass (estimated by allometry), progressive N limitation was less apparent." In fact, there was a persistent CO₂-induced increase in aboveground plant carbon, which led them to conclude "some mechanisms are partially alleviating progressive N limitation," as Finzi *et al.* (2006) also concluded in their study of loblolly pines, where by some unknown means the pines obtained the extra nitrogen they needed.

Idso and Kimball (2001) also observed a large initial CO₂-induced increase in aboveground biomass production, followed by a rapid but slowing decline in this parameter, in their long-term sour orange tree study. Because the trees of their experiment were periodically fertilized so as never to lack nitrogen, the similar productivity vs. time pattern Hungate *et al.* observed may have had nothing to do with "restriction of plant N availability," which they characterized as being merely "apparent." It is also important to note the slow decline in the CO₂-induced growth stimulation of the sour orange trees came to a halt at the ten-year point of the experiment, when the declining growth stimulation finally leveled out at an essentially constant value that was maintained to the end of the 17-year study—a 69% increase in yearly total biomass production in response to a 75% increase in the air's CO₂ content (Kimball *et al.*, 2007).

Consequently, as Norby and Iverson (2006) and Finzi *et al.* (2006) both found, the pattern of CO₂-induced growth stimulation in the scrub oak ecosystem Hungate *et al.* studied provides no evidence for the PNL hypothesis. In fact, it and others of their observations point to one or more unknown means of ecosystem N acquisition that allow the aerial fertilization effect of atmospheric CO₂

enrichment to continue, albeit at a level of impact lower than its peak manifestation, even with "apparent" N limitations.

Johnson *et al.* (2006) studied the effects of elevated CO₂ (ambient, +175, +350 ppm) and N fertilization (unfertilized, +100, +200 kg N ha⁻¹ yr⁻¹, provided as ammonium sulfate) on C and N accumulations in the biomass of ponderosa pines (*Pinus ponderosa* Laws, grown from seed) and the soils that supported them, in a six-year open-top chamber experiment conducted near Placerville, California (USA). This study, like several others according to Johnson *et al.*, "showed that growth response to elevated CO₂ more than offset declines in tissue N concentrations, necessitating increased N uptake by trees," which led them to ask, "How did the trees manage to obtain this 'extra' N in an N-limited environment?"

In the fertilized treatments, the four researchers suggest, the extra N could readily have been supplied by the added fertilizer, but in the unfertilized treatments they opine a substantial amount of the N uptake "probably came from the soil," as both wet and dry deposition were not great enough to have supplied all of the extra N, and "no symbiotic N fixer was present in the study plots." Citing other investigators' results as supplying circumstantial evidence for what they finally concluded, they write, "the additional N needed to respond to elevated CO₂ came from the soil and was facilitated by greater root exploration under elevated CO₂." Acknowledging they could not "provide an accurate prediction from the results of this study," Johnson *et al.* nevertheless state they could "see no evidence that either growth or additional N uptake at the +350 ppm CO₂ level are being inhibited by PNL as of year 6 in this study."

Studying the same trees, Phillips *et al.* (2006) collected video images every two months of roots growing against the surfaces of three minirhizotron tubes installed in each chamber. Yearly values of fine-root standing crop, production, and mortality were consistently higher in the elevated CO₂ treatments throughout the study, and they write, "in this same study, Johnson *et al.* (2000) found that elevated CO₂ increased fine-root life span." Because elevated CO₂ also increased fine-root length, Phillips *et al.* note, "the amount of root length dying per year was actually greater." Therefore, they write, "the higher rates of mortality in absolute terms for elevated CO₂ are driven by increased standing crop and not reduced life spans." In addition, they report Tingey *et al.* (2005) found "in the elevated CO₂

treatments, fine roots explored the soil more extensively and deeper, and filled in the explored areas more intensively.” With respect to the PNL hypothesis, therefore, Phillips *et al.* state “the increased fine-root length reported here explains how additional N was provided to support the increased whole plant growth in elevated CO₂ treatments, and corresponds with the increased extent and intensity of the root system architecture discussed by Tingey *et al.* (2005).” This “mining of soil N,” they continue, “can in some cases go on for substantial lengths of time, and there is no evidence that PNL occurred during the course of this study.”

Barnard *et al.* (2006) injected ¹⁵N-labelled NH₄ into the soil of mesocosms of *Holcus lanatus* (L.) grown for more than 15 months at either ambient or elevated atmospheric CO₂ concentrations to determine whether the uptake capacity of soil micro-organisms had remained higher at elevated CO₂, and to shed further light on the short-term (48 hours) partitioning of N between plants and soil micro-organisms. Their results and data from other plant-microbial ¹⁵N partitioning experiments at elevated CO₂ suggest “the mechanisms controlling the effects of CO₂ on short- vs. long-term N uptake and turnover differ.” They state “short-term immobilization of added N by soil micro-organisms at elevated CO₂ does not appear to lead to long-term increases in N in soil microbial biomass,” noting the increased soil microbial C:N ratios they observed at elevated CO₂ “suggest that long-term exposure to CO₂ alters either the functioning or structure of these microbial communities.” Barnard *et al.* conclude “short-term immobilization of inorganic soil nitrogen or exploitation of nutrient pulses may be altered under conditions of elevated atmospheric CO₂ concentration,” and this alteration undermines the PNL hypothesis, likely allowing long-lived plants and ecosystems to maintain positive growth responses to atmospheric CO₂ enrichment.

Noting the photosynthetic down-regulation posited by the PNL hypothesis “may occur in ecosystems that have a low soil N availability, such as piedmont loblolly pine forests”—the setting in which the long-term Duke Forest FACE study was being conducted—Springer and Thomas (2007) tested the validity of the hypothesis on some of the site’s understory tree species. They “hypothesized that after seven years of exposure to elevated CO₂, significant photosynthetic down-regulation would be observed in these tree species,” which included red maple (*Acer rubrum* L.), hickory (*Carya glabra* Mill.), redbud

(*Cercis canadensis* L.), and sweetgum (*Liquidambar styraciflua* L.).

During the first year of the Duke Forest FACE experiment, DeLucia and Thomas (2000) examined the photosynthetic responses of these particular saplings to the 200 ppm increase in atmospheric CO₂ concentration employed in that study. Subsequently, Springer and Thomas “reexamined the photosynthetic responses of saplings of the same four understory species to determine whether the enhancement of photosynthesis observed during the first year of exposure to elevated CO₂ was sustained in the seventh year of the experiment.” They found “no evidence of photosynthetic down-regulation in any species in either early or late summer.” Not only did their measurements reveal no down-regulation of photosynthesis, they observed “a small increase in the photosynthetic capacity of all of the study species in response to elevated CO₂,” which they say “has been demonstrated in several studies (Campbell *et al.*, 1988; Ziska and Teramura, 1992; Idso *et al.*, 1991).”

Springer and Thomas note “the progressive N limitation hypothesis predicts a diminished response of plant productivity to elevated CO₂ as N availability decreases because of the increased nutrient demands of greater plant biomass production (Luo *et al.*, 2004).” They go on to reiterate their own finding: “after seven years of elevated CO₂ treatment in the Duke Forest FACE experiment, we see little evidence of progressive N limitation in the leaf level processes of these four species of understory trees.”

Working at the EUROFACE facility in central Italy near Viterbo, Liberloo *et al.* (2007) grew three species of poplar trees—robusta poplar (*Populus x euramericana*), white poplar (*P. alba*), and black poplar (*P. nigra*)—for two three-year periods, between which times the trees were coppiced and allowed to regrow, in either ambient air or air enriched with an extra 180 ppm of CO₂ (an approximate 49% enhancement). They applied no fertilization to any of the plots over the first growth cycle, then fertilized half of the trees over the second growth cycle. During the last year of the last cycle, they measured a number of plant processes and parameters and compared them with similar observations made throughout earlier years of the experiment.

The five researchers discovered, after six years of growth under elevated atmospheric CO₂, the poplar trees did not experience any down-regulation of leaf net photosynthesis, and the long-term stimulation was substantial. In response to the 49% increase in the

atmosphere's CO₂ concentration, the CO₂-induced stimulation of net photosynthesis, averaged over the three species, was 49%. In addition, they found no difference in CO₂-induced net photosynthetic stimulation between Sun and shade leaves, nor was there any difference in CO₂ effects between the fertilized and non-fertilized trees.

After thus finding "photosynthetic stimulation of poplar leaves was sustained in elevated CO₂ after six years of fumigation, even under non-fertilized conditions," Liberloo *et al.* state "these results give optimistic perspectives for the future, as the maintained enhancement of photosynthesis in poplar trees is likely to continue over several rotations, thereby providing more carbon for growth in a closed canopy forest."

Finzi *et al.* (2007) evaluated the PNL hypothesis based on data obtained from four well-known FACE experiments conducted on forests—the Rhinelander, Duke, and Oak Ridge National Laboratory (ORNL) studies in the United States and the POP-EUROFACE study in Europe—where previous research described by Norby *et al.* (2005) showed net primary production (NPP) increased by $23 \pm 2\%$ in response to a CO₂ concentration increase of 174 ppm (46%) above the mean ambient-air concentration. Finzi *et al.* found the CO₂-induced increase in forest productivity at the POP-EUROFACE site, which they note was "located on former agricultural land where soil nitrogen availability was high and not limiting," not to have been supported by greater nitrogen uptake from the soil but instead by an increase in nitrogen use efficiency (NUE). At the other three sites, however, the CO₂-induced increase in forest productivity was supported by greater N uptake from the soil, with no change in NUE. They state this result was "unexpected," especially for the Duke and ORNL sites, where they say "tree growth is demonstrably N-limited."

Focusing on the findings of the three U.S. studies, Finzi *et al.* state "the response of N uptake and NUE in these young temperate forests exposed to FACE is the opposite of that predicted by the current generation of biogeochemical models," meaning those based on the PNL hypothesis. After discussing how these forests might be obtaining the seemingly impossible-to-obtain nitrogen they needed to maintain their significantly CO₂-enhanced growth rates, the scientists conclude, "regardless of the specific mechanism, this analysis demonstrates that larger quantities of carbon entering the below-ground system under elevated CO₂ result in greater N uptake,

even in N-limited ecosystems."

Zak *et al.* (2007) initiated a year-long ecosystem-level ¹⁵N tracer experiment at the Rhinelander, Wisconsin (USA) FACE facility at the seven-year point of a long-term study of aspen (*Populus tremuloides*) and aspen-birch (*P. tremuloides*-*Betula papyrifera*) communities exposed to treatments of CO₂ (ambient and elevated to 200 ppm above ambient) and O₃ (ambient and elevated to 30–40 ppb above ambient). One year after adding tracer amounts of ¹⁵NH₄⁺ to the forest floor of the young tree stands, they found "both forest communities exposed to elevated CO₂ obtained greater amounts of ¹⁵N (29%) and N (40%) from soil, despite no change in soil N availability or plant N-use efficiency." They attribute this to greater belowground root growth and a more thorough exploration of the soil for nitrogen in the CO₂-enriched treatment. In contrast, they note the elevated O₃ treatment "decreased the amount of ¹⁵N (-15%) and N (-29%) in both communities." These decreases were significantly smaller than the corresponding CO₂-induced increases. Consequently, Zak *et al.* conclude "progressive nitrogen limitation is presently not a factor governing plant growth response to elevated CO₂ in these young, developing forest communities." In addition, they state their findings "are consistent with those in young sweet gum (*Liquidambar styraciflua*) and loblolly pine (*Pinus taeda*) forests exposed to elevated CO₂ (Finzi *et al.*, 2006; Norby and Iversen, 2006)."

Langley *et al.* (2009) "employed an acid-hydrolysis-incubation method and a net nitrogen-mineralization assay to assess stability of soil carbon pools and short-term nitrogen dynamics in a Florida scrub-oak ecosystem after six years of exposure to elevated CO₂" at the multiple open-top-chamber facility at NASA's Kennedy Space Center. Their research showed elevated atmospheric CO₂ (to 350 ppm above ambient concentrations) tended to increase net N mineralization in the top 10 cm of the soil, but it also decreased total soil organic carbon content there by 21%. That loss of carbon mass was equivalent only to "roughly one-third of the increase in plant biomass that occurred in the same experiment." They found the strongest increases in net N mineralization were in the 10–30 cm depth increment, and "release of N from this depth may have allowed the sustained CO₂ effect on productivity in this scrub-oak forest," which over the four years leading up to their study "increased litterfall by 19–59%."

Thus yet another experiment demonstrates

atmospheric CO₂ enrichment generally enables plants to find the extra nitrogen they need to take full advantage of the aerial fertilization effect of elevated atmospheric CO₂ concentrations, thus increasing total ecosystem carbon content. Although the PNL hypothesis sounds logical enough and many scientists initially embraced it as a fact, a vast array of observational data has subsequently proven it unfounded.

References

- Barnard, R., Barthes, L., and Leadley, P.W. 2006. Short-term uptake of ¹⁵N by a grass and soil micro-organisms after long-term exposure to elevated CO₂. *Plant and Soil* **280**: 91–99.
- Binkley, D., Son, Y., and Valentine, D.W. 2000. Do forests receive occult inputs of nitrogen? *Ecosystems* **3**: 321–331.
- Campbell, W.J., Allen, L.H., and Bowes, G. 1988. Effects of CO₂ concentration on rubisco activity, amount, and photosynthesis in soybean leaves. *Plant Physiology* **88**: 1310–1316.
- Crocker, R.L. and Major, J. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *Journal of Ecology* **43**: 427–448.
- DeLucia, E.H. and Thomas, R.B. 2000. Photosynthetic responses to CO₂ enrichment of four hardwood species in a forest understory. *Oecologia* **122**: 11–19.
- Finzi, A.C., Moore, D.J.P., DeLucia, E.H., Lichter, J., Hofmockel, K.S., Jackson, R.B., Kim, H.-S., Matamala, R., McCarthy, H.R., Oren, R., Pippen, J.S., and Schlesinger, W.H. 2006. Progressive nitrogen limitation of ecosystem processes under elevated CO₂ in a warm-temperate forest. *Ecology* **87**: 15–25.
- Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., and Ceulemans, R. 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂. *Proceedings of the National Academy of Sciences, USA* **104**: 14,014–14,019.
- Hungate, B.A. 1999. Ecosystem responses to rising atmospheric CO₂: Feedbacks through the nitrogen cycle. In: Luo, Y. and Mooney, H. (Eds.) *Carbon Dioxide and Environmental Stress*. Academic Press, San Diego, CA, USA., pp. 265–285.
- Hungate, B.A., Dukes, J.S., Shaw, M.R., Luo, Y., and Field, C.B. 2003. Nitrogen and climate change. *Science* **302**: 1512–1513.
- Hungate, B.A., Johnson, D.W., Dijkstra, P., Hymus, G., Stiling, P., Megonigal, J.P., Pagel, A.L., Moan, J.L., Day, F., Li, J., Hinkle, C.R., and Drake, B.G. 2006. Nitrogen cycling during seven years of atmospheric CO₂ enrichment in a scrub oak woodland. *Ecology* **87**: 26–40.
- Idso, S.B. and Kimball, B.A. 2001. CO₂ enrichment of sour orange trees: 13 years and counting. *Environmental and Experimental Botany* **46**: 147–153.
- Idso, S.B., Kimball, B.A., and Allen, S.G. 1991. CO₂ enrichment of sour orange trees: 2.5 years into a long-term experiment. *Plant, Cell and Environment* **14**: 351–353.
- Johnson, D.W., Hoyleman, A.M., Ball, J.T., and Walker, R.F. 2006. Ponderosa pine responses to elevated CO₂ and nitrogen fertilization. *Biogeochemistry* **77**: 157–175.
- Johnson, M.G., Phillips, D.L., Tingey, D.T., and Storm, M.J. 2000. Effects of elevated CO₂, N-fertilization, and season on survival of ponderosa pine fine roots. *Canadian Journal of Forest Research* **30**: 220–228.
- Kimball, B.A., Idso, S.B., Johnson, S., and Rillig, M.C. 2007. Seventeen years of carbon dioxide enrichment of sour orange trees: final results. *Global Change Biology* **13**: 2171–2183.
- Langley, J.A., McKinley, D.C., Wolf, A.A., Hungate, B.A., Drake, B.G., and Megonigal, J.P. 2009. Priming depletes soil carbon and releases nitrogen in a scrub-oak ecosystem exposed to elevated CO₂. *Soil Biology & Biochemistry* **41**: 54–60.
- Liberloo, M., Tulva, I., Raim, O., Kull, O., and Ceulemans, R. 2007. Photosynthetic stimulation under long-term CO₂ enrichment and fertilization is sustained across a closed *Populus* canopy profile (EUROFACE). *New Phytologist* **173**: 537–549.
- Luo, Y., Hui, D., and Zhang, D. 2006. Elevated CO₂ stimulates net accumulations of carbon and nitrogen in land ecosystems: A meta-analysis. *Ecology* **87**: 53–63.
- Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R.E., Oren, R., Parton, W.J., Pataki, D.E., Shaw, M.R., Zak, D.R., and Field, C.B. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* **54**: 731–739.
- Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, S.J., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., De Angelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarasci-Mugnozza, G.E., Schlesinger, W.H., and Oren, R. 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences* **102**: 10.1073/pnas.0509478102.

Norby, R.J. and Iversen, C.M. 2006. Nitrogen uptake, distribution, turnover, and efficiency of use in a CO₂-enriched sweetgum forest. *Ecology* **87**: 5–14.

Phillips, D.L., Johnson, M.G., Tingey, D.T., Storm, M.J., Ball, J.T., and Johnson, D.W. 2006. CO₂ and N-fertilization effects on fine-root length, production, and mortality: a 4-year ponderosa pine study. *Oecologia* **148**: 517–525.

Rastetter, E.B., McKane, R.B., Shaver, G.R., Melillo, J.M., Nadelhoffer, K.J., Bobbie, J.E., and Aber, J. D. 1992. Changes in C storage by terrestrial ecosystems: how C-N interactions restrict responses to CO₂ and temperature. *Water, Air and Soil Pollution* **64**: 327–344.

Springer, C.J. and Thomas, R.B. 2007. Photosynthetic responses of forest understory tree species to long-term exposure to elevated carbon dioxide concentration at the Duke Forest FACE experiment. *Tree Physiology* **27**: 25–32.

Tingey, D.T., Johnson, M.G., and Phillips, D.L. 2005. Independent and contrasting effects of elevated CO₂ and N-fertilization of root architecture in *Pinus ponderosa*. *Trees* **19**: 43–50.

Vitousek, P.M. 2004. *Nutrient Cycling and Limitation: Hawaii as a Model System*. Princeton University Press, Princeton, New Jersey, USA.

Zak, D.R., Holmes, W.E., and Pregitzer, K.S. 2007. Atmospheric CO₂ and O₃ alter the flow of ¹⁵N in developing forest ecosystems. *Ecology* **88**: 2630–2639.

Ziska, L.H. and Teramura, A.H. 1992. Intraspecific variation in the response of rice (*Oryza sativa*) to increased CO₂ concentration—photosynthetic, biomass, and reproductive characteristics. *Physiologia Plantarum* **84**: 269–274.

3.12 Salinity Stress

- The buildup of soil salinity from repeated irrigation can produce growth stresses in agricultural plants, but the rise in the air's CO₂ concentration can overcome these stresses.

In agricultural enterprises the buildup of soil salinity from repeated irrigations can reduce crop yields. Similarly, in unmanaged ecosystems where exposure to brackish or salty water is commonplace, saline soils can induce growth stresses in plants not adapted to these conditions. It is important to understand how rising atmospheric CO₂ concentrations may interact with soil salinity to affect plant growth. Experiments addressing this issue are discussed below.

Ball *et al.* (1997) grew two Australian mangrove species—*Rhizophora stylosa* and *Rhizophora apiculata*, the former of which has a slower relative growth rate than the latter but a greater salt tolerance—for 14 weeks in glasshouses with different combinations of atmospheric CO₂ (340 and 700 ppm), relative humidity (43 and 86%), and salinity (25 and 75‰ of seawater), to determine the effects of these variables on their development and growth. Averaged across the entire experiment, the elevated CO₂ treatment significantly increased the rates of net photosynthesis in both species, but only at the lower salinity level.

Mavrogianopoulos *et al.* (1999) grew parson melons (*Cucumis melo*) in greenhouses subjected to atmospheric CO₂ concentrations of 400, 800, and 1,200 ppm for the first five hours of each day, irrigating them with nutrient solutions containing 0, 25, and 50 mM NaCl to determine the interactive effects of elevated CO₂ and salinity on plant growth and yield. Exposure to CO₂ concentrations of 800 and 1,200 ppm increased net photosynthetic rates by averages of 75 and 120%, respectively—regardless of salinity—relative to rates measured at 400 ppm CO₂. The CO₂ enrichment partially reversed the negative effects of salinity on shoot growth, leaf growth, and leaf chlorophyll content, and although melon yields were significantly increased with atmospheric CO₂ enrichment at all salinity levels, the greatest CO₂-induced enhancement was observed at the lowest salinity level.

Also working in the agricultural sector, Maggio *et al.* (2002) grew tomato (*Lycopersicon esculentum* Mill.) plants in controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 400 or 900 ppm in combination with varying degrees of soil salinity for one month. They found plants grown in the elevated CO₂ treatment tolerated an average root-zone salinity threshold value about 60% greater than plants grown in the low CO₂ treatment, and the water-use of the CO₂-enriched plants was about half the low-CO₂ plants. In addition, the amount of chloride in the leaves of the CO₂-enriched plants was significantly lower than in the leaves of the low-CO₂ plants.

Poorter and Perez-Soba (2001) reported very similar findings in a review paper. They found the positive effects of elevated CO₂ on the growth responses of most plants over a wide range of soil salinities remained the same, which concurred with the earlier findings of Idso and Idso (1994) in their review. Hence, there is abundant evidence indicating

plants respond positively to increases in the air's CO₂ content, even where high soil salinity levels present mild to moderate stresses.

Syvertsen and Levy (2005) reviewed what was known about salinity stress in citrus trees and how atmospheric CO₂ enrichment might modify it. They note rapidly growing plants almost always use more water than slower-growing plants, and "in citrus, many vigorous rootstocks that produce fast-growing trees also tend to have poor salt tolerance (Castle *et al.*, 1993)," possibly because they accumulate more salt in their tissues because of their greater uptake of water. When growing plants in CO₂-enriched air, however, plant stomatal conductance and water use are often decreased at the same time net photosynthesis and growth are increased, so, in the words of the two scientists, "elevated CO₂ almost always leads to higher water use efficiency as it disconnects rapid tree growth from high water use." They explain, "if salt uptake is coupled with water uptake, then leaves grown at elevated CO₂ should have lower salt concentrations than leaves grown at ambient CO₂ (Ball and Munns, 1992)."

"As expected," Syvertsen and Levy continue, "all citrus rootstock species studied increased growth and water use efficiency in response to elevated CO₂ that was twice ambient," and generally, but not always, "the salinity-induced accumulation of sodium (Na⁺) in leaves was less when seedlings were grown at elevated CO₂ than at ambient CO₂." One exception—where Na⁺ accumulation was not affected by elevated CO₂—was Rangpur lime (*Citrus reticulata*), but they report this citrus variety was already relatively salt-tolerant, and another variety of the same species (Cleopatra mandarin) had lower leaf chloride concentrations in CO₂-enriched air than in ambient air.

Rasse *et al.* (2005) reported on the long-term effects of atmospheric CO₂ enrichment on the net CO₂ exchange, shoot density, and shoot biomass of the wetland sedge, *Scirpus olneyi*, as well as how those effects were influenced by salinity (one of the main environmental stressors of the wetlands), in one of the longest (17 years) *in situ* atmospheric CO₂ enrichment experiments ever conducted—in a natural wetland located at the Smithsonian Environmental Research Center on the Chesapeake Bay (USA). In every year of that period, the net CO₂ exchange rate and shoot biomass and density of the plants growing in the CO₂-enriched (ambient +340 ppm) air were greater than they were among the plants growing in ambient air. In the case of the net CO₂ exchange rate, for example,

the extra CO₂ boosted it by 80% in the first year of the study, but the enhancement declined to about 35% by the end of the third year and remained relatively constant at that value over the following 15 years. Shoot biomass and density also increased; while the CO₂-induced stimulation of the net CO₂ exchange rate remained essentially constant over the past 15 years, the CO₂-induced stimulations of shoot biomass and density increased over time. After five years of a nearly constant stimulation of 16%, for example, shoot density increased in near-linear fashion to a value 128% above the ambient-air value at the end of year 17. The response of shoot biomass to CO₂ enrichment was also nearly linear, reaching a value approximately 70% above ambient at year 17. The trends in shoot density and biomass did not appear to be leveling off.

Net CO₂ exchange, shoot density, and shoot biomass were also closely correlated with salinity—the higher the salinity, the more detrimental were its effects on these variables. But even at the highest levels of salinity reported, atmospheric CO₂ enrichment was able to produce a positive, albeit reduced, stimulation of net CO₂ exchange. For shoot biomass and density, the responses were better still. Not only did atmospheric CO₂ enrichment essentially eradicate the detrimental effects of salinity, there was, Rasse *et al.* write, "evidence suggesting that salinity stress increased the stimulation of shoot density by elevated atmospheric CO₂ concentration."

This experiment demonstrated several important facts. First, as the researchers state, their results "leave no doubt as to the sustained response of the salt marsh sedge to elevated atmospheric CO₂ concentration." Second, as the initial responses of the three growth variables declined or remained low during the first few years of the study, but leveled out or increased thereafter, it is clear long-term research must be carried out to ascertain the full and correct impacts of atmospheric CO₂ enrichment on plants. In the wetland sedge of this study, for example, it took about 10 growing seasons before an increasing trend in the shoot density could be recognized. Finally, there is what the researchers called their "most important finding": "a species response to elevated atmospheric CO₂ concentration can continually increase when [it] is under stress and declining in its natural environment."

Garcia-Sanchez and Syvertsen (2006) grew well-watered and -fertilized three-month-old rootstock seedlings of Cleopatra mandarin (*Citrus reticulata* Blanco) and Carrizo citrange (*Citrus sinensis* (L.)

Os. x *Poncirus trifoliata* L.), with or without salt stress (an additional 50 mM NaCl), for eight additional weeks, one plant each in 1.5-liter containers located in controlled-environment greenhouses maintained at either 360 or 700 ppm CO₂. During that time and at the end of the experiment, they measured a number of plant properties and physiological processes that allowed them to determine whether “salinity tolerance of citrus rootstock seedlings would be increased when grown in elevated CO₂.”

The two researchers found “elevated CO₂ increased plant growth, shoot/root ratio, leaf dry weight per area, net assimilation of CO₂, chlorophyll, and water-use efficiency.” The increase in the last parameter was caused by a decrease in transpiration and an increase in plant biomass. In Cleopatra mandarin, biomass received a 27% CO₂-induced boost in the salt-stress treatment and a 40% boost in the non-salt-stress treatment; in Carrizo citrange, biomass received a 49% boost in the salt-stress treatment and 43% in the non-salt-stress treatment. They note “elevated CO₂ increased salinity tolerance in the relatively salt-sensitive Carrizo more than in the salt-tolerant Cleopatra.”

Takagi *et al.* (2008) grew well-watered and well-fertilized *Solanum lycopersicum* (formerly *Lycopersicon esculentum*) tomato plant seedlings for two weeks at two levels of irrigation-water salinity (0 or 100 mM NaCl) in 3-L pots inside the greenhouse of Hiroshima University (Japan), at atmospheric CO₂ concentrations of either 370 or 1,000 ppm, measuring various plant properties and physiological responses. They report the “salt-stress treatment severely decreased whole-plant biomass” and “leaf photosynthesis and transport of carbon assimilates,” but “the impact of stress on these activities was alleviated under elevated CO₂ concentration.” This alleviation, they write, “was promoted when sink activity relative to source activity was higher,” which they say was “probably owing to improvement of oxidative stress,” due “at least partially to the higher constitutive antioxidant enzymes’ activities” as well as improved water status “through stomatal closure at high CO₂ concentration.” They conclude their study “corroborates earlier reports that the interaction between salinity stress and CO₂ concentration results in the alleviative effect of elevated CO₂ on the negative effects of salinity on plant growth.”

Geissler *et al.* (2009a) note, “desertification is often accompanied by soil salinization ... leading to growth conditions unacceptable for most conventional

crops.” They suggest “a promising solution” to the problem is “the desalinization and reclamation of degraded land by making sustainable use of naturally salt-tolerant halophytes under seawater irrigation (including drainage mechanisms which avoid salt accumulation in the soil).”

The three researchers grew well-fertilized two-month-old *Aster tripolium* plants in a hydroponic system maintained at seawater salinity (sws) levels of 0, 50, and 100% in open-top chambers at atmospheric CO₂ concentrations of either 380 ppm (ambient) or 520 ppm (elevated), during which time they measured several plant properties and processes. Growing the plants with water of 100% sws (as opposed to 0% sws) resulted in “a significant decrease in photosynthesis and water use efficiency and to an increase in oxidative stress.” When they raised the air’s CO₂ concentration by 37% (from 380 to 520 ppm), there was a subsequent increase of 84% in photosynthesis and 60% in water use efficiency. The researchers note “the improved water and energy supply was used to increase the investment in mechanisms reducing water loss and oxidative stress.” They conclude, because “elevated CO₂ concentration enhances the energy and water supply of *Aster tripolium*, ameliorates oxidative stress, and thus enhances the survival of this plant in saline habitats,” it “can help in desalinizing and reclaiming degraded land and sequestering CO₂, thus counteracting the greenhouse effect.”

Geissler *et al.* (2009b) write halophytes are “naturally salt tolerant plants which are able to complete their life cycle on a substrate rich in NaCl,” and cash-crop halophytes “can be used for various economical and ecological purposes, e.g. for food, fodder, for obtaining timber, fibers, reeds or chemicals, as ornamental plants, for coastal protection, land reclamation or greenification of deserts.” They note *Aster tripolium*, in particular, “can be used for food (the leaves have a high nutritional value and can be eaten as salad or vegetable), for fodder and as an ornamental plant.”

The three scientists state the 40% increase in the air’s CO₂ content in their experiment increased the light-saturated rate of net photosynthesis by 56%, 82%, and 71%, respectively, in the plants irrigated with water of 0, 50, and 100% sws, and it increased their water use efficiencies by 14, 26, and 61%, respectively. Other positive impacts of the CO₂-enriched air were “an enhanced synthesis of proline, carbohydrates and proteins,” and “these mechanisms led to a higher survival rate under saline conditions,

i.e. to an improved salt tolerance.” Thus, they conclude “*A. tripolium* is a promising cash crop halophyte which will probably benefit from rising atmospheric CO₂ concentrations in the future,” and “its sustainable use can help feeding the growing world population.”

Working with a more common crop, Perez-Lopez *et al.* (2009a) grew two barley (*Hordeum vulgare* L.) cultivars, Alpha and Iranis, in controlled-environment growth chambers at either ambient (350 ppm) or elevated (700 ppm) atmospheric CO₂ concentrations in a 3:1 perlite:vermiculite mixture watered with Hoagland’s solution every two days (until the first leaf was completely expanded at 14 days), after which they administered a salinity treatment by adding 0, 80, 160, or 240 mM NaCl to the Hoagland’s solution every two days for 14 more days. After a total of 28 days, the primary leaf of each barley plant was harvested and assessed for a number of biochemical properties.

In the various ambient-air salinity treatments, the deleterious effects of reactive oxygen species on barley leaves were made apparent through ion leakage and increases in thiobarbituric acid reactive substances (TBARS), which rose as salt concentrations rose. “On the other hand,” the seven scientists continue, “when [the] salinity treatment was imposed under elevated CO₂ conditions, lower solute leakage and TBARS levels were observed, suggesting that the oxidative stress caused by salinity was lower.” They conclude “elevated CO₂ protects barley cultivars from oxidative stress,” noting “the relief of oxidative stress damage observed in our barley leaves grown under a CO₂ enriched atmosphere has also been observed in alfalfa (Sgherri *et al.*, 1998), pine (Vu *et al.*, 1999) and oak (Schwanz and Polle, 2001).”

Working with the same plants in the same experiment, but focusing on different phenomena, Perez-Lopez *et al.* (2009b) measured relative water content, water potential and its components, transpiration rate, hydraulic conductance, and water use efficiency, computed as plant dry weight produced per unit of water transpired. They found “elevated CO₂ improves barley water relations under saline conditions because elevated CO₂ permits a greater osmotic adjustment, most likely due to a greater carbon supply from increased photosynthesis, and a lower passive dehydration due to reductions in stomatal conductance and hydraulic conductance.” Specifically, by the end of their study the water use efficiency of salt-stressed plants grown in the elevated CO₂ treatment was 61% greater in Alpha and 43%

greater in Iranis than that of plants grown in the ambient CO₂ treatment. The five researchers conclude, “elevated CO₂ will mitigate the negative impact of salinity on barley growth and will enable plants to remain turgid and functional for a longer period and for a higher salt concentration,” noting “these facts open the possibility of a future successful development of this species in saline areas in which nowadays growth is not possible.” This finding has enormous implications, as Frommer *et al.* (1999) have estimated approximately one-third of the world’s irrigated land is currently unsuitable for crop production because of its high salinity.

Also working with barley plants grown in the same experiment, Perez-Lopez *et al.* (2010) measured midday leaf water potential, osmotic potential, osmotic potential at full turgor, dehydration, and osmotic adjustment; they subsequently harvested the primary leaf of each plant and made assessments of its concentrations of various minerals and organic compounds. They write, “elevated CO₂ permitted plant metabolism to be maintained at a better status under salt stress than did ambient CO₂,” and “growth was reduced more at ambient than at elevated CO₂.” They also report, “elevated CO₂ widens the range of salt concentrations at which osmotic adjustment continues to be efficient by providing a greater supply of carbon and Adenosine-5’-triphosphate,” a multi-functional nucleotide that transports chemical energy in cells for metabolism and is “needed to perform the energetically expensive salt tolerance mechanisms.” Thus, they conclude—as they had in their earlier papers—“under future environmental conditions, barley species will be able to succeed in salinized areas in which growth is not currently possible.”

Azam *et al.* (2005) note “in agro-ecosystems, green manuring legumes occupy a key position in maintaining/improving soil fertility and productivity,” and the important role of these plants as a source of nitrogen has increased further due to economic and pollution concerns associated with nitrogen supplied by chemical fertilizers. They state, “species of sesbania have generally been considered as most important for green manuring, especially in wheat-rice rotation systems.”

In many situations, the growth of sesbania is suppressed by varying degrees of water stress and salinity, but the five Pakistani scientists state “elevated CO₂ favors different physiological processes of plants, thereby leading to increased biomass production and ecosystem functioning,” citing Drake and Leadley (1991), Idso and Idso

(1994), and Azam and Farooq (2001). They report this effect is more pronounced for plants facing stresses imposed through the soil or atmosphere, citing the collection of papers compiled and edited by Koch and Mooney (1996). They hypothesized rising atmospheric CO₂ concentrations might mitigate salinity stress in *Sesbania*, enabling the rotation cover-crop to more effectively “fix” atmospheric nitrogen and deposit the plant-usable form of it in the soil, where it could help promote the growth of such important agricultural staples as wheat and rice.

Conducting greenhouse experiments designed to assess the effects of elevated atmospheric CO₂ concentrations on growth and nitrogen fixation in *Sesbania aculeata* exposed to different salinity and water regimes, Azam *et al.* report “elevated CO₂ favored N₂ fixation leading to a greater contribution of fixed N to the total plant N.” In addition, “biological nitrogen fixation decreased with salinity” but “elevated CO₂ arrested the decrease to a significant extent.”

Perez-Lopez *et al.* (2012) write, “salt stress has a threefold effect on plant health” because it reduces water availability, causes ion imbalance, and causes toxicity, all of which phenomena, they write, “curtail growth, photosynthesis, protein synthesis, energy storage, and lipid metabolism,” as described in detail by Munns (2005) and Parida and Das (2005). In a study designed to explore the negative consequences of potentially greater salt stress in a CO₂-enriched environment, they grew barley (*Hordeum vulgare*) plants in pots containing a 3:1 mix of perlite:vermiculite in controlled-environment chambers maintained at either ambient or elevated atmospheric CO₂ concentrations (350 or 700 ppm) for the last 14 days of a 28-day post-planting period. They also instituted four salt-stress treatments on the 15th day by supplying the plants then and thereafter with water of one of four degrees of saltiness (0, 80, 160, or 240 mM NaCl). At the end of the 28-day period they measured a number of plant physiological properties and processes related to the maximal rate of net photosynthesis (Amax) exhibited by the first fully expanded attached leaf of each plant.

The five Spanish scientists report, “in the zero-saline treatment, elevated CO₂ increased the Amax by 49% compared with the Amax measured at ambient CO₂,” whereas “under ambient CO₂ conditions, saline treatments (80-, 160- and 240-mM NaCl) reduced the Amax by 18, 32 and 39%, respectively.” They add, “these reductions were lower at elevated CO₂: 8, 22 and 28% for 80-, 160-, and 240-mM NaCl.” Based on

the graphical representations of their results, the CO₂-induced enhancements of Amax in the four saline treatments (0-, 80-, 160-, and 240-mM NaCl) appear to have been, respectively, 49%, 68%, 71%, and 76%, revealing the greater the salinity-induced percentage reduction in barley Amax becomes, the greater the CO₂-induced percentage increase in barley Amax becomes.

Also investigating salt stress in barley, Perez-Lopez *et al.* (2013) write, “soil salinization is an important growth limiting factor for most plants,” citing the United Nations’ Food and Agriculture Organization (FAO, 2007) and noting “around 20% of the irrigated land and one third of the world’s arable soil are affected by a progressive salinization.” They note “barley is one of the most extensively cultivated crops worldwide” but “salt stress reduces its productivity.”

Perez-Lopez *et al.* analyzed “the effect of salinity on nitrogen acquisition, distribution and assimilation, the consequences of these effects on growth in barley (*Hordeum vulgare* L., cv. Iranis), and the possible effects on these processes provoked by elevated CO₂ levels.” They sowed six barley seeds in each of several 2.5-liter pots containing a 3:1 mix of perlite:vermiculite in controlled-environment chambers maintained at either ambient (350 ppm) or elevated (700 ppm) CO₂ concentrations and watered the plants with 250 ml of Hoagland’s solution containing 0, 80, 160, or 240 mM concentrations of NaCl every two days until the end of the 28-day study.

The six Spanish scientists report, “under ambient CO₂ conditions, 80, 160, and 240 mM NaCl reduced the total plant biomass by 12%, 30%, and 44%, respectively.” By contrast, “growth at elevated CO₂ levels led to 24%, 20%, and 33% higher total biomass than under ambient CO₂ levels for 80, 160, and 240 mM NaCl, respectively.” And because “the relative stimulation of total plant biomass in response to elevated CO₂ levels was higher in salt-stressed plants than in non-stressed ones,” they conclude, “barley plants subjected to elevated CO₂ levels will likely overcome mild saline conditions.”

References

- Azam, F., Aziz, F., Sial, M.H., Ashraf, M., and Farooq, S. 2005. Mitigation of salinity effects on *Sesbania aculeata* L., through enhanced availability of carbon dioxide. *Pakistan Journal of Botany* 37: 959–967.
- Azam, F. and Farooq, S. 2001. Impact of elevated

Climate Change Reconsidered II: Biological Impacts

- atmospheric CO₂ on crop plants—an overview. *Pakistan Journal of Biological Sciences* **4**: 220–22.
- Ball, M.C., Cochrane, M.J., and Rawson, H.M. 1997. Growth and water use of the mangroves *Rhizophora apiculata* and *R. stylosa* in response to salinity and humidity under ambient and elevated concentrations of atmospheric CO₂. *Plant, Cell and Environment* **20**: 1158–1166.
- Ball, M.C. and Munns, R. 1992. Plant responses to salinity under elevated atmospheric concentrations of CO₂. *Australian Journal of Botany* **40**: 515–525.
- Castle, W.S., Tucker, D.P.H., Krezdorn, A.H., and Youtsey, C.O. 1993. *Rootstocks for Florida Citrus: Rootstock Selection, the First Step to Success*. University of Florida, Institute of Food and Agricultural Science, Gainesville, Florida, USA.
- Drake, B.G. and Leadley, P.W. 1991. Canopy photosynthesis of crops and native plant communities exposed to long-term elevated CO₂. *Plant, Cell & Environment* **14**: 853–860.
- FAO, 2007. Global Network on Integrated Soil Management for Sustainable Use of Salt-affected Soils. <http://www.fao.org/nr/land/soils/>.
- Frommer, W.B., Ludewig, U., and Rentsch, D. 1999. Taking transgenic plants with a pinch of salt. *Science* **285**: 1222–1223.
- Garcia-Sanchez, F. and Syvertsen, J.P. 2006. Salinity tolerance of Cleopatra mandarin and Carrizo citrange citrus rootstock seedlings is affected by CO₂ enrichment during growth. *Journal of the American Society of Horticultural Science* **131**: 24–31.
- Geissler, N., Hussin, S., and Koyro, H.-W. 2009a. Elevated atmospheric CO₂ concentration ameliorates effects of NaCl salinity on photosynthesis and leaf structure of *Aster tripolium* L. *Journal of Experimental Botany* **60**: 137–151.
- Geissler, N., Hussin, S., and Koyro, H.-W. 2009b. Interactive effects of NaCl salinity and elevated atmospheric CO₂ concentration on growth, photosynthesis, water relations and chemical composition of the potential cash crop halophyte *Aster tripolium* L. *Environmental and Experimental Botany* **65**: 220–231.
- Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: A review of the past 10 years' research. *Agricultural and Forest Meteorology* **69**: 153–203.
- Koch, G.W. and Mooney, H.A. (Eds.) 1996. *Carbon Dioxide and Terrestrial Ecosystems*. Academic Press, San Diego, California, USA.
- Maggio, A., Dalton, F.N., and Piccinni, G. 2002. The effects of elevated carbon dioxide on static and dynamic indices for tomato salt tolerance. *European Journal of Agronomy* **16**: 197–206.
- Mavrogianopoulos, G.N., Spanakis, J., and Tsikalas, P. 1999. Effect of carbon dioxide enrichment and salinity on photosynthesis and yield in melon. *Scientia Horticulturae* **79**: 51–63.
- Munns, R. 2005. Genes and salt tolerance: bringing them together. *New Phytologist* **167**: 645–663.
- Parida, A.K. and Das, A.B. 2005. Salt tolerance and salinity effects on plants: a review. *Ecotoxicology and Environmental Safety* **60**: 324–349.
- Perez-Lopez, U., Robredo, A., Lacuesta, M., Mena-Petite, A., and Munoz-Rueda, A. 2009b. The impact of salt stress on the water status of barley plants is partially mitigated by elevated CO₂. *Environmental and Experimental Botany* **66**: 463–470.
- Perez-Lopez, U., Robredo, A., Lacuesta, M., Mena-Petite, A., and Munoz-Rueda, A. 2012. Elevated CO₂ reduces stomatal and metabolic limitations on photosynthesis caused by salinity in *Hordeum vulgare*. *Photosynthesis Research* **111**: 269–283.
- Perez-Lopez, U., Robredo, A., Lacuesta, M., Munoz-Rueda, A., and Mena-Petite, A. 2010. Atmospheric CO₂ concentration influences the contributions of osmolyte accumulation and cell wall elasticity to salt tolerance in barley cultivars. *Journal of Plant Physiology* **167**: 15–22.
- Perez-Lopez, U., Robredo, A., Lacuesta, M., Sgherri, C., Munoz-Rueda, A., Navari-Izzo, F., and Mena-Petite, A. 2009a. The oxidative stress caused by salinity in two barley cultivars is mitigated by elevated CO₂. *Physiologia Plantarum* **135**: 29–42.
- Perez-Lopez, U., Robredo, A., Miranda-Apodaca, J., Lacuesta, M., Munoz-Rueda, A., and Mena-Petite, A. 2013. Carbon dioxide enrichment moderates salinity-induced effects on nitrogen acquisition and assimilation and their impact on growth in barley plants. *Environmental and Experimental Botany* **87**: 148–158.
- Poorter, H. and Perez-Soba, M. 2001. The growth response of plants to elevated CO₂ under non-optimal environmental conditions. *Oecologia* **129**: 1–20.
- Rasse, D.P., Peresta, G., and Drake, B.G. 2005. Seventeen years of elevated CO₂ exposure in a Chesapeake Bay Wetland: sustained but contrasting responses of plant growth and CO₂ uptake. *Global Change Biology* **11**: 369–377.
- Schwanz, P. and Polle, A. 2001. Differential stress responses of antioxidative systems to drought in pedunculate oak (*Quercus robur*) and maritime pine (*Pinus*

pinaster) grown under high CO₂ concentrations. *Journal of Experimental Botany* **52**: 133–143.

Sgherri, C., Quartacci, M., Menconi, M., Raschi, A., and Navari-Izzo, F. 1998. Interactions between drought and elevated CO₂ on alfalfa plants. *Journal of Plant Physiology* **152**: 118–124.

Syvetsen, J. and Levy, Y. 2005. Salinity interactions with other abiotic and biotic stresses in citrus. *HortTechnology* **15**: 100–103.

Takagi, M., El-Shemy, H.A., Sasaki, S., Toyama, S., Kanai, S., Saneoka, H., and Fujita, K. 2008. Elevated CO₂ concentration alleviates salinity stress in tomato plant. *Acta Agriculturae Scandinavica Section B—Soil and Plant Science*: 10.1080/09064710801932425.

Vu, J.C., Gesch, R., Allen, L.H., Boote, K., and Bowes, G. 1999. CO₂ enrichment delays a rapid, drought induced decrease in Rubisco small subunit transcript abundance. *Journal of Plant Physiology* **155**: 139–142.

3.13 Temperature Stress

As the atmosphere's CO₂ content rises, nearly all agricultural crops, grassland plants, and trees will exhibit enhanced rates of photosynthesis and biomass production that will not be diminished by any global warming that might accompany it. If ambient air temperatures rise concurrently, the growth-promoting effects of atmospheric CO₂ enrichment likely will rise even more, as the Earth gets "greener."

3.13.1 Agricultural Crops

- As the air's CO₂ concentration rises, nearly all agricultural crops will exhibit enhanced rates of photosynthesis and biomass production that will not be diminished by any concomitant global warming. If air temperatures rise concurrently, the growth-promoting effects of atmospheric CO₂ enrichment likely will rise even more.

As the air's CO₂ content rises, most plants exhibit increased rates of photosynthesis and biomass production (see Chapter 1), which should increase the amount of food, fiber, and timber production that can be utilized to feed, clothe, and shelter the expanding human population. However, some researchers argue the growth-promoting effects of atmospheric CO₂ enrichment may be largely negated by the global warming predicted to occur in the near future by a number of state-of-the-art climate models. Such an

outcome could compromise the planet's ability to sustain a greater human population without increasing use of land for agriculture. This section examines the scientific literature to see whether plants will continue to exhibit CO₂-induced growth increases under conditions of predicted future warming, reviewing what has been learned about the photosynthetic and growth responses of CO₂-enriched agricultural crops grown at both current and projected future growing-season temperatures.

The optimum growth temperatures of several plants have been shown to rise substantially with increasing levels of atmospheric CO₂ (Berry and Bjorkman, 1980; Stuhlfauth and Fock, 1990; McMurtrie *et al.*, 1992; McMurtrie and Wang, 1993). This phenomenon was explained by Long (1991), who calculated from well-established plant physiological principles that most C₃ plants should increase their optimum growth temperatures by approximately 5°C for a 300 ppm increase in the air's CO₂ concentration. Thus plant photosynthetic rates should rise in response to concomitant increases in both the air's CO₂ concentration and temperature, as Idso and Idso (1994) and Cowling (1999) have shown to be typically the case. These positive CO₂ x temperature interactions have been observed in subsequent scientific studies, as indicated below.

Zhu *et al.* (1999) report pineapples grown at 700 ppm CO₂ assimilated 15, 97, and 84% more total carbon than pineapples grown at the current ambient CO₂ concentration in day/night air temperature regimes of 30/20 (which is optimal for pineapple growth at ambient CO₂), 30/25, and 35/25 °C, respectively. Similarly, Taub *et al.* (2000) demonstrated net photosynthetic rates of cucumbers grown at twice-ambient levels of atmospheric CO₂ and air temperatures of 40°C were 3.2 times greater than those of control plants grown at ambient CO₂ and this same elevated air temperature. Thus, at air temperatures normally considered to be deleterious to plant growth, rates of photosynthesis are typically considerably greater for CO₂-enriched vs. ambient-grown plants.

Reddy *et al.* (1999) reported similar results when they grew cotton plants at air temperatures ranging from 2°C below to 7°C above ambient air temperature, finding the plants simultaneously exposed to 720 ppm CO₂ had photosynthetic rates 137 to 190% greater than those of plants exposed to ambient CO₂ concentrations across this temperature range. Cowling and Sage (1998) found a 200 ppm increase in the air's CO₂ concentration boosted

photosynthetic rates of young bean plants by 58 and 73% at growth temperatures of 25 and 36°C, respectively. Bunce (1998) grew wheat and barley at 350 and 700 ppm CO₂ across a wide range of temperatures and found elevated CO₂ stimulated photosynthesis in these species by 63 (wheat) and 74% (barley) at an air temperature of 10°C and by 115 (wheat) and 125% (barley) at 30°C. These studies show the percentage increase in photosynthetic rate resulting from atmospheric CO₂ enrichment often increases substantially with increasing air temperature.

Elevated CO₂ also helps plants recover from high-temperature- and drought-induced reductions in photosynthetic capacity, as Ferris *et al.* (1998) demonstrated. They grew soybeans for 52 days under normal air temperatures and soil water conditions at atmospheric CO₂ concentrations of 360 and 700 ppm, then subjected the plants to an eight-day period of high temperature and water stress. When the researchers restored normal air temperatures and soil water conditions, the CO₂-enriched plants attained photosynthetic rates 72% of their unstressed controls, and the plants grown at ambient CO₂ attained photosynthetic rates only 52% of their controls. At the end of the growing season, Ferris *et al.* (1999) report, plants growing in the elevated CO₂ treatment exhibited an average biomass 24% greater than plants grown in ambient CO₂, and a seed yield 32% greater.

CO₂-induced increases in plant growth under high air temperatures also have been observed in other agricultural plants. In the previously mentioned study of Cowling and Sage (1998), for example, the 200 ppm increase in the air's CO₂ content boosted total plant biomass for wheat and barley by a combined average of 59 and 200% at air temperatures of 25 and 36°C. Similarly, Ziska (1998) found a doubling of the atmospheric CO₂ concentration increased the total dry weight of soybeans by 36 and 42% at root zone temperatures of 25 and 30°C, respectively, and Hakala (1998) noted spring wheat grown at 700 ppm CO₂ attained total biomass values 17 and 23% greater than those attained by ambient-grown plants exposed to ambient and elevated (ambient plus 3°C) air temperatures. After inputting various observed CO₂-induced growth responses of winter wheat into plant growth models, Alexandrov and Hoogenboom (2000) predicted 12 to 49% increases in wheat yield in Bulgaria, even if air temperatures were to ultimately rise by as much as 4°C. And Reddy *et al.* (1998) found elevated CO₂ (700 ppm) increased total cotton biomass by 31 to

78% across an air temperature range of 20 to 40°C.

These studies make it clear elevated air temperatures often significantly enhance the beneficial effects of elevated atmospheric CO₂ on agricultural crop yields. In some cases, however, rising air temperatures do not interact with rising atmospheric CO₂ concentrations to further increase the growth-promoting effects of atmospheric CO₂ enrichment. Instead, they simply do not interfere with the status quo.

Demmers-Derks *et al.* (1998) found sugar beets grown at 700 ppm CO₂ produced 25% more biomass than ambient-grown plants, regardless of air temperature, which was increased by 3°C. Similarly, Frittschi *et al.* (1999) found significant warming (4.5°C above ambient) had no impact on the growth of rhizoma peanut, whereas a 300 ppm increase in the air's CO₂ content increased the plant's total biomass by 52% regardless of air temperature. In the unlikely event the air's CO₂ content were to cease rising or have no effect on the productivity of certain plants, it is possible the temperature increase itself may promote plant growth and development, as was found in the experiment conducted by Wurr *et al.* (2000), where elevated CO₂ had essentially no effect on the yield of French beans but a 4°C increase in air temperature increased their yield by approximately 50%.

Aloni *et al.* (2001) grew bell pepper (*Capsicum annuum* L. cv. Mazurka) plants under optimal conditions until eight days prior to anthesis, then placed the plants in greenhouses maintained at atmospheric CO₂ concentrations of either 350 or 800 ppm and normal (28/22°C) or elevated (32/26°C) day/night air temperatures to determine the effects of these two environmental changes on reproductive parameters associated with pollen, which is extremely sensitive to high temperatures. The high temperature stress reduced pollen germination by 75% at ambient CO₂, but atmospheric CO₂ enrichment completely ameliorated this negative effect. The high temperature treatment also reduced the number of seeds produced per fruit by 68%, but the elevated CO₂ treatment nearly compensated for this deleterious effect, reducing the warming-induced seed-per-fruit reduction to only 9%.

Tako *et al.* (2001) grew rice (*Oryza sativa* L. cv. Mutsu-homare) plants hydroponically in controlled-environment chambers having atmospheric CO₂ concentrations of 350 and 700 ppm and day/night air temperatures of 24/17 (ambient) and 26/19°C (elevated), to study the interactive effects of elevated

CO₂ and temperature on the growth of this important crop. After 18 weeks, elevated CO₂ had no effect on whole-plant biomass at ambient growth temperatures, but with the additional 2°C of warming, atmospheric CO₂ enrichment produced a whole-plant biomass enhancement of 22%.

Bunce (2001) grew strawberry (*Fragaria x ananassa* Duchesne cv. Honeoye) plants in the field in open-top chambers maintained at atmospheric CO₂ concentrations of 350, 650, and 950 ppm for two years to study the effects of elevated CO₂ on photosynthesis in this important fruit crop. They took measurements weekly to evaluate the temperature dependence of the photosynthetic stimulation resulting from the two levels of atmospheric CO₂ enrichment. Plants grown at 650 and 950 ppm CO₂ exhibited mean photosynthetic rates 77 and 106% greater, respectively, than those of control plants exposed to ambient air.

Prasad *et al.* (2003) grew peanuts (*Arachis hypogaea* L. cv. Georgia Green, of the Virginia Runner type) from seed to maturity in sunlit controlled-environment growth chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm and daytime-maximum/nighttime-minimum air temperatures of 32/22, 36/26, 40/30, and 44/34°C. During this study, leaf photosynthetic rates were unaffected by air temperatures over the range studied, but they rose by approximately 27% in response to the experimental doubling of the air's CO₂ content. Vegetative biomass increased by 51% and 54% in ambient air and CO₂-enriched air, respectively, as temperatures rose from 32/22 to 40/30°C. A further temperature increase to 44/34°C caused moderate to slight declines in vegetative biomass in ambient and CO₂-enriched air, respectively, so the final biomass increase over the entire temperature range investigated was 27% in the ambient air and 53% in the CO₂-enriched air. Going from the lowest-temperature, ambient CO₂ treatment to the highest-temperature, elevated CO₂ treatment led to a 106% increase in vegetative biomass.

In contrast, seed yields in both the ambient and CO₂-enriched air dropped dramatically with each of the three temperature increases studied, declining at the highest temperature regime to but a small percentage of what they were at the lowest temperature regime. Nevertheless, Prasad *et al.* report, "seed yields at 36.4/26.4°C under elevated CO₂ were similar to those obtained at 32/22°C under ambient CO₂," describing the latter pair of temperatures as "present-day seasonal temperatures."

Even an unrealistically large warming of 4.4°C above present-day growing temperatures for peanut production would have essentially no effect on peanut seed yields, as long as the atmosphere's CO₂ concentration rose concurrently by something on the order of 350 ppm. And more realistic values of CO₂-induced global warming—temperature increases on the order of 0.4°C or less for a doubling of the air's CO₂ content (Idso, 1998)—likely would lead to a significant increase in peanut production.

Vu (2005) grew peanut plants of the cultivar Florunner from seed to maturity in greenhouses maintained at atmospheric CO₂ concentrations of 360 and 720 ppm and at air temperatures 1.5 and 6.0°C above outdoor air temperatures, measuring a number of parameters related to the plants' photosynthetic performance. They report rubisco photosynthetic efficiency—the ratio of midday light-saturated carbon exchange rate to rubisco initial or total activity—of the elevated-CO₂ plants was 1.3- to 1.9-fold greater than rubisco efficiency of the ambient-CO₂ plants at both growth temperatures. In addition, leaf soluble sugars and starch of plants grown at elevated CO₂ were 1.3- and 2-fold higher, respectively, than those of plants grown at ambient CO₂. Leaf transpiration of the elevated-CO₂ plants relative to the ambient-CO₂ plants was 12% less at near-ambient temperatures and 17% less in the higher temperature regime, and the water use efficiency of the elevated-CO₂ plants relative to the ambient-CO₂ plants was 56% greater at near-ambient temperatures and 41% greater in the higher temperature environment. Because less rubisco protein was required by the elevated-CO₂ plants, the subsequent redistribution of excess leaf nitrogen "would increase the efficiency of nitrogen use for peanut under elevated CO₂," just as the optimization of inorganic carbon acquisition and greater accumulation of the primary photosynthetic products in the CO₂-enriched plants "would be beneficial for peanut growth at elevated CO₂," Vu writes. Consequently, in the absence of other stresses, "peanut photosynthesis would perform well under rising atmospheric CO₂ and temperature predicted for this century," Vu concludes.

Crafts-Brandner and Salvucci (2004) explored the concurrent effects of elevated atmospheric CO₂ concentration and temperature on photosynthetic CO₂ fixation in cotton (*Gossypium hirsutum* L. cv. Coker 100A-glandless), using "intact plants and biochemical measurements to directly determine how environmental change impacts specific physiological mechanisms important to plant productivity." They report

“net photosynthesis of cotton leaves at ambient levels of CO₂ was inhibited at leaf temperatures above about 32°C.” At a leaf internal CO₂ concentration 4.3 times greater than ambient, however, net photosynthesis did not begin to decline until leaf temperatures rose above 40°C. Viewed another way, the net photosynthetic rate of cotton leaves exposed to ambient air declined by approximately 77% as leaf temperature rose from 32 to 40°C, whereas in leaves exposed to the CO₂-enriched air it rose by about 9%, indicating the increase in atmospheric CO₂ concentration more than compensated for the dramatic decrease in photosynthetic rate that would ordinarily result from the 8°C increase in temperature.

Aranjuelo *et al.* (2005) grew the forage crop alfalfa (*Medicago sativa* L.) in 13-L pots for three consecutive June–July periods (2001–2003) out-of-doors in polyethylene-covered temperature gradient tunnels maintained at atmospheric CO₂ concentrations that averaged 405 and 730 ppm at ambient (AT) and elevated (ET) temperatures (ET = AT + 4°C) and at high (HW) and low (LW) soil water contents (LW = 0.5HW). They fed all of the plants adequate nutrients except for nitrogen, to ensure the only source of nitrogen for the plants was that which was fixed by their nodules in response to inoculation with *Sinorhizobium meliloti* strain 102F78. The researchers report “the effect of elevated CO₂ on plant growth interacted positively with temperature,” and “higher dry mass production of plants grown under elevated CO₂ and temperature was a consequence of enhanced photosynthetic rates.” Mean CO₂-induced increases in leaf net photosynthesis over the entire experiment were found to be: +5% (HW, AT), +50% (HW, ET), +17% (LW, AT), and +42% (LW, ET), as best as can be determined from the bar graphs in the paper describing their study. Mean CO₂-induced increases in leaf biomass were +4% (HW, AT), +54% (HW, ET), +23% (LW, AT), and +58% (LW, ET), with the same caveat.

For both leaf net photosynthesis and biomass production, Aranjuelo *et al.* found the stimulatory effect of the elevated CO₂ was about 2.5 times greater in the warmer of the two temperature treatments in the low soil water regime and 10 times greater in the high soil water regime. In addition, the extra CO₂ benefited plant water loss via transpiration, which declined by 25% (HW, AT), 41% (HW, ET), 31% (LW, AT), and 31% (LW, ET). Under both well-watered and droughty conditions in this study, atmospheric CO₂ enrichment enhanced photosynthesis and biomass production in alfalfa, and

simultaneously decreased transpirational water losses.

Bencze *et al.* (2005) grew specimens of three varieties (Emma, Martina, and Mezofold) of winter wheat (*Triticum aestivum*) in controlled-environment chambers under ambient (375 ppm) and elevated (750 ppm) CO₂ at minimum, maximum, and mean temperature regimes of 10, 12, and 10.7°C, respectively. Twelve days after the average date of heading, they subjected several plants of each variety to 15 more days of elevated temperatures (min/max/mean of 20, 35, and 25.2°C) to assess the independent effects of both elevated CO₂ and temperature on wheat growth and yield.

They found the temperature treatment accelerated the aging process in the three wheat varieties, and concurrent atmospheric CO₂ enrichment generally helped them maintain a higher and longer level of photosynthetic activity during grain-filling and maturation. Bencze *et al.* report the CO₂-enriched plants “suffered less damage from heat stress and produced a higher yield than at the ambient level.” In addition, the extra CO₂ supplied to the Emma cultivar plants meant the difference between life and premature death, since by the end of the 15-day high-temperature treatment the plants growing in ambient air were dead, whereas those growing in elevated CO₂ survived for a few more days. In a future world of higher atmospheric CO₂ concentrations, wheat crops should be better able to withstand the stress of potentially higher temperatures, suffering less damage and producing greater yields.

Cen and Sage (2005) grew well-watered and well-fertilized sweet potato (*Ipomoea batatas* L.) plants in 20-L pots of soil in a greenhouse, periodically measuring light-saturated rates of net photosynthesis in new but fully expanded leaves in response to short-term changes in air temperature and atmospheric CO₂ concentration. In response to an approximate 370 ppm increase in the air’s CO₂ concentration, the optimum leaf temperature for net photosynthesis—the leaf temperature at which net photosynthesis proceeds at its maximum rate—rose by approximately 4.5°C, and its maximal rate of net photosynthesis rose by about 75%. The doubling of the air’s CO₂ concentration had no impact on net photosynthesis at a leaf temperature of 15°C but boosted it by 28% at 21°C, by 43% at 27°C, by 56% at 33°C, and by 70% at 39°C. In order for the net photosynthetic rate of sweet potatoes growing in air of 740 ppm CO₂ to drop below the maximum rate exhibited by plants growing in air of 370 ppm CO₂ (which occurred at a leaf temperature of 30°C), leaf

temperature would have to rise by 12°C to a value of 42°C.

De Costa *et al.* (2006) write, “doubts have been expressed whether the expected yield increases [of rice] in response to increased CO₂ could be sustained under high temperature regimes.” The investigators set out to learn whether this might happen in sub-humid Sri Lanka, where weekly maximum temperatures during both the maha (January to March) and yala (May to August) growing seasons typically range from 30 to 33°C. They grew two crops of rice (one in the maha season and one in the yala season) in open-top chambers maintained at atmospheric CO₂ concentrations of either 363 or 567 ppm under normal field conditions at the Rice Research and Development Institute of Sri Lanka, measuring a number of meteorological and plant physiological parameters throughout both seasons, as well as total biomass production and grain yield at the times of final harvest. They found the CO₂-induced increase in total plant biomass at the time of final harvest was 23% in the maha season and 37% in the yala season, and final grain yields were enhanced by 24% and 39% in the maha and yala seasons, respectively. These increases occurred even though air temperatures in the CO₂-enriched chambers were on average 1.6°C higher than air temperatures in the ambient-air chambers.

Borjigidai *et al.* (2006) grew rice (cv Akitakomachi) plants from seed in greenhouses maintained at atmospheric CO₂ concentrations of 370 and 570 ppm and then transplanted them to the field and grew them in a well-fertilized paddy culture in a FACE study at the same CO₂ concentrations under which the seeds were sprouted in both 2003 and 2004. At various times throughout the two growing seasons during the field portion of the experiments, the researchers made photosynthetic measurements of the most recently fully expanded leaves in full sunlight at a variety of different leaf temperatures. They report “the optimal temperature of photosynthesis (T_{opt} , the value where the photosynthetic rate was maximum) was significantly higher at elevated CO₂: it ranged from 22 to 34.5°C with an average value of 28.9°C at ambient CO₂, and from 29.5 to 37°C with an average value of 33.5°C at elevated CO₂.”

Bernacchi *et al.* (2006) grew soybeans (*Glycine max* (L.) Merr.) for three years at the SoyFACE facility of the University of Illinois at Urbana-Champaign, Illinois (USA) at atmospheric CO₂ concentrations of either 375 or 550 ppm under natural field conditions, measuring a number of weather and

plant physiological parameters from pre-dawn to post-dusk on several days during the three growing seasons. They found the mean daily integral of leaf-level net photosynthesis (A) was enhanced by nearly 25% in the CO₂-enriched air. In addition, the 11 scientists write, “there was a strong positive correlation between daytime maximum temperatures and mean daily integrated A at elevated CO₂.” Their graphical representation of this relationship indicates at a daily maximum temperature of approximately 26.5°C, the CO₂-enriched air stimulated leaf-level net photosynthesis by about 14%, and at a daily maximum temperature of approximately 34.5°C, CO₂ enrichment stimulated photosynthesis by about 35%.

Koti *et al.* (2007) used Soil-Plant-Atmosphere-Research (SPAR) chambers at Mississippi State University (USA) to investigate the effects of doubled atmospheric CO₂ concentration (720 vs. 360 ppm) on the growth and development of six well-watered and well-fertilized soybean genotypes they grew from seed in pots filled with fine sand and exposed to the dual stresses of high day/night temperatures (38/30°C vs. 30/22°C) and high UV-B radiation levels (10 vs. 0 kJ/m²/day). They found the elevated CO₂ partially compensated for the damaging effects on vegetative growth and physiology caused by high temperatures and enhanced UV-B radiation levels, and elevated CO₂ had a positive influence on plant height, leaf area, total biomass, net photosynthesis, total chlorophyll content, phenolic content, and wax content, as well as relative plant injury.

Mishra *et al.* (2008) documented the positive impact of atmospheric CO₂ enrichment on the photosynthetic rates of field-grown soybean plants subjected to the simultaneous negative effects of acute heat stress and elevated atmospheric ozone (O₃) concentrations at the SoyFACE facility of the University of Illinois. The seven scientists discovered elevated ozone exacerbated heat-related decreases in photosynthetic electron transport, but “elevated CO₂ minimized or prevented light-dependent O₃-related decreases in electron transport (and thus photoinhibition) during heat stress.”

Alonso *et al.* (2009) sequentially grew well-watered and well-fertilized plants of the wheat cultivar Alcala in 16-liter pots of perlite (sown at a rate of 35 seeds per pot) in a controlled-environment growth chamber—first at an atmospheric CO₂ concentration of 370 ppm and then at 700 ppm—from sowing through anthesis. They measured gas exchange in flag leaves at ear emergence to obtain the values of various plant physiological parameters

required for the biochemical photosynthesis model developed by Farquhar *et al.* (1980), along with the responses of those parameters to changes in temperature. They found “photosynthesis response to temperature was negative at low air CO₂ concentrations and became progressively positive as CO₂ increased,” which might have been expected “from the increase in photorespiration with temperature and the gradual inhibition of this process as CO₂ increases (Long, 1991).” In addition, “at high chloroplastic CO₂, photosynthesis in elevated growth CO₂ was lower at 15–25°C and higher at 30–35°C, than in ambient growth CO₂, implying an enhanced photosynthesis response to temperature in plants grown in elevated CO₂.”

In 2004 and 2005, Gutierrez *et al.* (2009) grew well-watered and well-fertilized spring wheat (*Triticum aestivum* L. cv. Gazul) plants from seed to maturity out-of-doors in Salamanca, Spain in temperature-gradient chambers maintained at ambient (370 ppm) and elevated (700 ppm) atmospheric CO₂ concentrations and ambient air temperature (TA) and elevated air temperature (TE = TA plus 4°C). They titled their paper, “Acclimation to future atmospheric CO₂ levels increases photochemical efficiency and mitigates photochemistry inhibition by warm temperatures in wheat.” They report net photosynthesis was increased by 62–72% in both years in the CO₂-enriched chambers; at the conclusions of the two growing seasons, total plant biomass production in the CO₂-enriched chambers was increased by 12–18%. They conclude, “future increases in atmospheric CO₂ and temperature may have a positive effect on photochemical efficiency,” noting their work “provides evidence that with air CO₂ enrichment a reallocation of resources favoring light capture may occur.”

Xiao *et al.* (2010) note “the impact of future climate change on crop production has been widely predicted by modeling the interaction between crops and climate change,” adding it is currently thought “overall crop yields will decrease by 5–10% in China by 2030 as a result of climatic changes, and that the yields of wheat, rice and maize will be greatly reduced.” They further note “the direct fertilization effect of rising CO₂ will offset these losses,” citing Ewert *et al.* (2002) and Long *et al.* (2006). In addition, they remark, few real-world observations of the impacts of climate change on crop production have been reported.

The seven scientists conducted two sets of field experiments to evaluate the effects of warming on the

productivity of winter wheat from 2006 to 2008 in the semiarid northwestern part of China: one set of experiments at the Tongwei County station located at the foot of Lulu Mountain (35°13'N, 105°14'E) at an altitude of 1,798 meters above sea level, and another set at the mountain's summit at an altitude of 2,351 meters. At each of these locations, they established four air temperature treatments (ambient and ambient plus 0.6, 1.4, and 2.2°C), which they created by placing electric heating wires on the surface of the soil between the rows of wheat, which induced the 0.6–2.2°C air temperature increases they measured at a height of 20 cm above the tops of the wheat canopies. They found this increase in temperature “will lead to a significant change in the growth stages and water use of winter wheat,” and “crop yields at both high and low altitudes will likely increase,” by 2.6% at low altitudes and 6.0% at high altitudes. Even without the benefits of the aerial fertilization and anti-transpiration effects of the rise in the air's CO₂ content, the increase in temperature predicted by climate models for the year 2050 likely will lead to increases in winter wheat production in the northwestern part of China, not the decreases some modeling studies have predicted.

Yoon *et al.* (2009) grew well-watered and well-fertilized cotton plants from seed to maturity—one plant to each container of washed sand, with spacing between plants similar to the plant spacing found in typical cotton fields—in the Georgia Envirotron at the University of Georgia Griffin Campus. They placed the containers with their plants in chambers maintained at all combinations of two day/night air temperatures regimes (25/15°C and 35/25°C) and three atmospheric CO₂ concentrations (400, 600, and 800 ppm). At the lower of the two air temperature regimes, the authors found “final boll weight at harvest was 1.59 times (at 600 ppm) and 6.3 times (at 800 ppm) higher compared to ambient CO₂.” Further increasing the temperature tremendously increased this difference, as “the final boll weight was 34.1 times (at 600 ppm) and 23.3 times (at 800 ppm) higher compared to ambient CO₂.” In addition, “the response of final lint yield to CO₂ was more or less similar to the response of boll weight.”

Thus a significant body of scientific literature suggests a continuation of the rise in the air's CO₂ content likely will lead to enhanced rates of photosynthesis and biomass production by agricultural crops, which will not be diminished by any global warming that might occur concurrently. If the ambient air temperature rises, the growth-promoting

effects of atmospheric CO₂ enrichment likely will rise right along with it, in agreement with the experimental observations reviewed by Idso and Idso (1994). The biosphere will continue producing the food and fiber needed for an increasing population.

Beyond this natural phenomenon, Meerburg *et al.* (2009) describe how crop yields will continue to increase in the future because of “the development and adoption of new technologies and improved farm management,” citing Ewert *et al.* (2005), who demonstrated continuing advances in agricultural technology historically have been the most important drivers of productivity change. Between 1961 and 2007, Meerburg *et al.* report, “average US corn yields increased by 240%, from 3.9 tons per hectare per year to 9.4 tons per hectare per year,” citing the FAO (2009) and noting some researchers have predicted “advances in agronomics, breeding, and biotechnology will lead to an average corn yield in the US of just over 20 tons per hectare per year in 2030,” citing Duvick (2005).

Meerburg *et al.* also note farmers in Brazil successfully increased the productivity of soybeans, maize, and cotton during the past decade even though the cumulative number of days of exposure to temperatures above the three crops’ optimum values “is far greater than in the US.” In the Brazilian state of Mato Grosso, for example, “maximum average day temperature exceeds 35°C for 118 days per year, of which 75 days are in the average soybean-growing season.” Nevertheless, they report the average production of soybeans in 2008 was about 3.1 tons per hectare per year in Mexico, and the average yield in the United States was 2.8 tons per hectare per year. Similarly, they note the mean cotton yield in Brazil in 2006/2007 was 1.4 tons per hectare per year, while in the United States it was 0.9 tons per hectare per year.

The seven scientists thus conclude “temperatures higher than currently experienced in the US do not necessarily need to coincide with lower crop yields and ... already existing technology and future advances (new varieties, optimized farm management, biotechnology, etc.) can overrule the negative effect of increasing temperatures on yield.”

References

- Alexandrov, V.A. and Hoogenboom, G. 2000. The impact of climate variability and change on crop yield in Bulgaria. *Agricultural and Forest Meteorology* **104**: 315–327.
- Aloni, B., Peet, M., Pharr, M., and Karni, L. 2001. The

effect of high temperature and high atmospheric CO₂ on carbohydrate changes in bell pepper (*Capsicum annuum*) pollen in relation to its germination. *Physiologia Plantarum* **112**: 505–512.

Alonso, A., Perez, P., and Martinez-Carrasco, R. 2009. Growth in elevated CO₂ enhances temperature response of photosynthesis in wheat. *Physiologia Plantarum* **135**: 109–120.

Aranjuelo, I., Irigoyen, J.J., Perez, P., Martinez-Carrasco, R., and Sanchez-Diaz, M. 2005. The use of temperature gradient tunnels for studying the combined effect of CO₂, temperature and water availability in N₂ fixing alfalfa plants. *Annals of Applied Biology* **146**: 51–60.

Bencze, S., Veisz, O., and Bedo, Z. 2005. Effect of elevated CO₂ and high temperature on the photosynthesis and yield of wheat. *Cereal Research Communications* **33**: 385–388.

Bernacchi, C.J., Leakey, A.D.B., Heady, L.E., Morgan, P.B., Dohleman, F.G., McGrath, J.M., Gillespie, K.M., Wittig, V.E., Rogers, A., Long, S.P., and Ort, D.R. 2006. Hourly and seasonal variation in photosynthesis and stomatal conductance of soybean grown at future CO₂ and ozone concentrations for 3 years under fully open-air field conditions. *Plant, Cell and Environment* 10.1111/j.1365-3040.2006.01581.x

Berry, J. and Bjorkman, O. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* **31**: 491–543.

Borjigidai, A., Hikosaka, K., Hirose, T., Hasegawa, T., Okada, M., and Kobayashi, K. 2006. Seasonal changes in temperature dependence of photosynthetic rate in rice under a free-air CO₂ enrichment. *Annals of Botany* **97**: 549–557.

Bunce, J.A. 1998. The temperature dependence of the stimulation of photosynthesis by elevated carbon dioxide in wheat and barley. *Journal of Experimental Botany* **49**: 1555–1561.

Bunce, J.A. 2001. Seasonal patterns of photosynthetic response and acclimation to elevated carbon dioxide in field-grown strawberry. *Photosynthesis Research* **68**: 237–245.

Cen, Y.-P. and Sage, R.E. 2005. The regulation of Rubisco activity in response to variation in temperature and atmospheric CO₂ partial pressure in sweet potato. *Plant Physiology* **139**: 979–990.

Cowling, S.A. 1999. Plants and temperature—CO₂ uncoupling. *Science* **285**: 1500–1501.

Cowling, S.A. and Sage, R.F. 1998. Interactive effects of low atmospheric CO₂ and elevated temperature on growth,

Climate Change Reconsidered II: Biological Impacts

photosynthesis and respiration in *Phaseolus vulgaris*. *Plant, Cell and Environment* **21**: 427–435.

Crafts-Brandner, S.J. and Salvucci, M.E. 2004. Analyzing the impact of high temperature and CO₂ on net photosynthesis: biochemical mechanisms, models and genomics. *Field Crops Research* **90**: 75–85.

De Costa, W.A.J.M., Weerakoon, W.M.W., Herath, H.M.L.K., Amaratunga, K.S.P., and Abeywardena, R.M.I. 2006. Physiology of yield determination of rice under elevated carbon dioxide at high temperatures in a subhumid tropical climate. *Field Crops Research* **96**: 336–347.

Demmers-Derks, H., Mitchell, R.A.G., Mitchell, V.J., and Lawlor, D.W. 1998. Response of sugar beet (*Beta vulgaris* L.) yield and biochemical composition to elevated CO₂ and temperature at two nitrogen applications. *Plant, Cell and Environment* **21**: 829–836.

Duvick, D.N. 2005. The contribution of breeding to yield advances in maize (*Zea mays* L.). *Advances in Agronomy* **86**: 83–145.

Ewert, F., Rodriguez, D., Jamieson, P., Semenov, M.A., Mitchell, R.A.C., Goudriaan, J., Porter, J.R., Kimball, B.A., Pinter Jr., P.J., Manderscheid, R., Weigel, H.J., Fangmeier, A., Fereres, E., and Villalobos, F. 2002. Effects of elevated CO₂ and drought on wheat: testing crop simulation models for different experimental and climatic conditions. *Agriculture, Ecosystems and Environment* **93**: 249–266.

Ewert, F., Rounsevell, M.D.A., Reginster, I., Metzger, M.J., and Leemans, R. 2005. Future scenarios of European agricultural land use: I. Estimating changes in crop productivity. *Agriculture, Ecosystems and Environment* **107**: 101–116.

FAO. 2009. FAOSTAT Database. United Nations Food and Agriculture Organization. Available at www.fao.org. Accessed 8 September 2009.

Farquhar, G.D., von Caemmerer, S., and Berry, J.A. 1980. A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* **149**: 78–90.

Ferris, R., Wheeler, T.R., Ellis, R.H., and Hadley, P. 1999. Seed yield after environmental stress in soybean grown under elevated CO₂. *Crop Science* **39**: 710–718.

Ferris, R., Wheeler, T.R., Hadley, P., and Ellis, R.H. 1998. Recovery of photosynthesis after environmental stress in soybean grown under elevated CO₂. *Crop Science* **38**: 948–955.

Fritschi, F.B., Boote, K.J., Sollenberger, L.E., Allen Jr., L.H., and Sinclair, T.R. 1999. Carbon dioxide and temperature effects on forage establishment: photosynthesis and biomass production. *Global Change Biology* **5**: 441–453.

Gutierrez, D., Gutierrez, E., Perez, P., Morcuende, R., Verdejo, A.L., and Martinez-Carrasco, R. 2009. Acclimation to future atmospheric CO₂ levels increases photochemical efficiency and mitigates photochemistry inhibition by warm temperatures in wheat under field chambers. *Physiologia Plantarum* **137**: 86–100.

Hakala, K. 1998. Growth and yield potential of spring wheat in a simulated changed climate with increased CO₂ and higher temperature. *European Journal of Agronomy* **9**: 41–52.

Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: A review of the past 10 years' research. *Agricultural and Forest Meteorology* **69**: 153–203.

Idso, S.B. 1998. CO₂-induced global warming: a skeptic's view of potential climate change. *Climate Research* **10**: 69–82.

Koti, S., Reddy, K.R., Kakani, V.G., Zhao, D., and Gao, W. 2007. Effects of carbon dioxide, temperature and ultraviolet-B radiation and their interactions on soybean (*Glycine max* L.) growth and development. *Environmental and Experimental Botany* **60**: 1–10.

Long, S.P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: Has its importance been underestimated? *Plant, Cell and Environment* **14**: 729–739.

Long, S.P., Ainsworth, E.A., Leakey, A.D.B., Nosberger, J., and Ort, D.R. 2006. Food for thought: lower-than-expected crop yield simulation with rising CO₂ concentrations. *Science* **312**: 1918–1921.

McMurtrie, R.E., Comins, H.N., Kirschbaum, M.U.F., and Wang, Y.-P. 1992. Modifying existing forest growth models to take account of effects of elevated CO₂. *Australian Journal of Botany* **40**: 657–677.

McMurtrie, R.E. and Wang, Y.-P. 1993. Mathematical models of the photosynthetic response of tree stands to rising CO₂ concentrations and temperatures. *Plant, Cell and Environment* **16**: 1–13.

Meerburg, B.G., Verhagen, A., Jongschaap, R.E.E., Franke, A.C., Schaap, B.F., Dueck, T.A., and van der Werf, A. 2009. Do nonlinear temperature effects indicate severe damages to US crop yields under climate change? *Proceedings of the National Academy of Sciences USA* **106**: 10.1073.pnas.0910618106.

Mishra, S., Heckathorn, S.A., Barua, D., Wang, D., Joshi, P., Hamilton III, E.W., and Frantz, J. 2008. Interactive effects of elevated CO₂ and ozone on leaf thermotolerance in field-grown *Glycine max*. *Journal of Integrative Plant Biology* **50**: 1396–1405.

Prasad, P.V.V., Boote, K.J., Allen Jr., L.H., and Thomas, J.M.G. 2003. Super-optimal temperatures are detrimental to peanut (*Arachis hypogaea* L.) reproductive processes and yield at both ambient and elevated carbon dioxide. *Global Change Biology* **9**: 1775–1787.

Reddy, K.K., Davidonis, G.H., Johnson, A.S., and Vinyard, B.T. 1999. Temperature regime and carbon dioxide enrichment alter cotton boll development and fiber properties. *Agronomy Journal* **91**: 851–858.

Reddy, K.R., Robana, R.R., Hodges, H.F., Liu, X.J., and McKinion, J.M. 1998. Interactions of CO₂ enrichment and temperature on cotton growth and leaf characteristics. *Environmental and Experimental Botany* **39**: 117–129.

Stuhlfauth, T. and Fock, H.P. 1990. Effect of whole season CO₂ enrichment on the cultivation of a medicinal plant, *Digitalis lanata*. *Journal of Agronomy and Crop Science* **164**: 168–173.

Tako, Y., Arai, R., Otsubo, K., and Nitta, K. 2001. Application of crop gas exchange and transpiration data obtained with CEEF to global change problem. *Advances in Space Research* **27**: 1541–1545.

Taub, D.R., Seeman, J.R., and Coleman, J.S. 2000. Growth in elevated CO₂ protects photosynthesis against high-temperature damage. *Plant, Cell and Environment* **23**: 649–656.

Vu, J.C.V. 2005. Acclimation of peanut (*Arachis hypogaea* L.) leaf photosynthesis to elevated growth CO₂ and temperature. *Environmental and Experimental Botany* **53**: 85–95.

Wurr, D.C.E., Edmondson, R.N., and Fellows, J.R. 2000. Climate change: a response surface study of the effects of CO₂ and temperature on the growth of French beans. *Journal of Agricultural Science* **135**: 379–387.

Xiao, G., Zhang, Q., Li, Y., Wang, R., Yao, Y., Zhao, H., and Bai, H. 2010. Impact of temperature increase on the yield of winter wheat at low and high altitudes in semiarid northwestern China. *Agricultural Water Management* **97**: 1360–1364.

Yoon, S.T., Hoogenboom, G., Flitcroft, I., and Bannayan, M. 2009. Growth and development of cotton (*Gossypium hirsutum* L.) in response to CO₂ enrichment under two different temperature regimes. *Environmental and Experimental Botany* **67**: 178–187.

Zhu, J., Goldstein, G., and Bartholomew, D.P. 1999. Gas exchange and carbon isotope composition of *Ananas comosus* in response to elevated CO₂ and temperature. *Plant, Cell and Environment* **22**: 999–1007.

Ziska, L.H. 1998. The influence of root zone temperature on photosynthetic acclimation to elevated carbon dioxide concentrations. *Annals of Botany* **81**: 717–721.

3.13.2 Grasslands

- As the air's CO₂ content rises, grassland plants likely will exhibit enhanced rates of photosynthesis and biomass production that will not be diminished by any global warming that might occur. If the ambient air temperature does rise, the growth-promoting effects of atmospheric CO₂ enrichment likely will rise also. Grasslands are likely to produce increasingly greater amounts of forage and perhaps reclaim areas of barren ground in certain environments.

As the atmosphere's CO₂ content rises, most plants, including those of various grassland ecosystems, will exhibit increased rates of photosynthesis and biomass production. This increase in productivity should increase the amount of forage available for grazing animals and possibly reduce the land area occupied by bare soil in certain environments. However, some researchers claim global warming will negate the growth-promoting effects of atmospheric CO₂ enrichment and cause the opposite to occur. This section reviews the results of experimental studies of the photosynthetic and growth responses of grassland plants to atmospheric CO₂ enrichment when exposed to higher-than-normal-temperatures.

The optimum growth temperatures of many plants have been demonstrated to rise substantially with increasing concentrations of atmospheric CO₂ (Berry and Bjorkman, 1980; Stuhlfauth and Fock, 1990; McMurtrie *et al.*, 1992; McMurtrie and Wang, 1993), as has been described in more detail by Long (1991), Idso and Idso (1994), and Cowling and Sykes (1999). These previously observed positive CO₂ x temperature interactions have continued to appear in more recent studies of the subject for grassland species.

Lilley *et al.* (2001) grew swards of subterranean clover (*Trifolium subterraneum*) at 380 and 690 ppm CO₂ in combination with simultaneous exposure to ambient and elevated (ambient plus 3.4°C) air temperatures. After one year of these treatments, they found elevated CO₂ increased foliage growth by 19% at ambient air temperatures. At elevated air temperatures, the CO₂-enriched plants displayed a growth enhancement of only 8%, but the plants grown at ambient CO₂ exhibited a 28% reduction in foliage growth. Similarly, Morgan *et al.* (2001) determined twice-ambient levels of atmospheric CO₂ increased aboveground biomass in native shortgrass steppe ecosystems by an average of 38%, despite an average

air temperature increase of 2.6°C. And when bahiagrass was grown across a temperature gradient of 4.5°C, Fritschi *et al.* (1999) found a 275 ppm increase in the air's CO₂ content boosted photosynthesis and aboveground biomass by 22 and 17%, respectively, independent of air temperature.

Greer *et al.* (2000) grew five pasture species at 18 and 28°C and found plants concomitantly exposed to 700 ppm CO₂ displayed average photosynthetic rates 36 and 70% greater, respectively, than average rates of control plants grown in air of ambient CO₂ concentration. The average CO₂-induced biomass increase for the five species rose dramatically with increasing air temperature, from only 8% at 18°C to 95% at 28°C.

Stirling *et al.* (1998) had found much the same thing. They nurtured five fast-growing native annual species in glasshouses maintained at two combinations of CO₂ (ambient and ambient plus 340 ppm) and temperature (ambient and ambient plus 3°C) for eight weeks, to assess their growth responses to elevated CO₂ and temperature. Elevated CO₂ significantly increased photosynthetic rates, by 18–36% for all species, independent of growth temperature, for the entire eight weeks of the experiment. The persistence of this photosynthetic enhancement led to total plant biomass increases for CO₂-enriched plants, on average, 25% greater than those of control plants grown in ambient-CO₂ air. And although elevated CO₂ and elevated temperature together had few significant interactive effects on the various metrics of growth, the overall CO₂ growth response was generally slightly larger at elevated than at ambient temperatures.

In a similar study with similar findings, Newman *et al.* (2001) grew two perennial grassland species (rhizoma peanut-*Arachis glabrata* and bahiagrass-*Paspalum notatum*) native to South America and common to Florida (USA) in greenhouses fumigated with air of either 360 or 700 ppm CO₂ for three full growing seasons. The C₃ and C₄ grasses were simultaneously exposed to air temperatures ranging from ambient to 4.5°C above ambient. Averaged across the three growing seasons, elevated CO₂ increased dry matter production in rhizoma peanut and bahiagrass by 25 and 15%, respectively. Here too, the researchers found no significant interactive effects of elevated CO₂ and temperature on dry mass production in these species, and on their own, air temperatures 4.5°C above ambient increased dry matter production in both species by an average of 13% across all three years.

Niklaus *et al.* (2001) established experimental plots in a nutrient-poor calcareous grassland in northwestern Switzerland that contained either 31, 12, or five species, removing selected species from some of the plots so the proportion of plant functional types in each of the plots remained unchanged (55% graminoids, 15% legumes, and 30% non-legume forbs). They fumigated the plots with air of either 360 or 600 ppm CO₂ for four years, to determine the ecological effects of elevated CO₂ across a biodiversity gradient in this grassland community. As plant community diversity decreased at ambient CO₂, soil nitrate concentrations increased, the scientists report. Elevated CO₂, however, reduced soil nitrate concentrations at all the studied levels of plant diversity. In addition, nitrification—a biological process that yields nitrate—increased with decreasing species diversity at ambient CO₂, and at elevated CO₂, rates of nitrification were 25% lower than those observed at ambient CO₂ at all levels of community diversity, suggesting a CO₂-enriched environment would reduce the risk of nitrate pollution of groundwater.

Hakala and Mela (1996) grew field-sown meadow fescue (*Festuca pratensis* cv. Kalevi) in open-top chambers and glasshouses maintained at atmospheric CO₂ concentrations of 350 and 700 ppm in combination with ambient and elevated (ambient plus 3°C) air temperatures for four consecutive years to determine the effects on aboveground biomass production in this important forage crop. They found elevated CO₂ significantly increased aboveground biomass by an average of 18% in each of the four study years, but the effect occurred only when plants were concomitantly exposed to elevated air temperatures.

Sinclair *et al.* (2007) note it has long been assumed global warming would be bad for plants that appear to be adapted to cool temperatures and typically exhibit reduced growth rates in warmer environments. Using climate-controlled mini-greenhouses, the five researchers tested this assumption by examining the interacting effects of air temperature and vapor pressure deficit (VPD) on the growth of tall fescue (*Festuca arundinacea* Schreb), a cool-season grass that from past studies was expected to show declining growth with warmer temperatures over the range of 18.5 to 27°C. They grew well-watered and -fertilized plants in two sets of six-week-long experiments, one in which air VPD was held constant at 1.2 kPa while air temperature was maintained at either 18.5, 21, 24, or 27°C, and one in

which air temperature was held constant at 22°C while air VPD was maintained at either 0.9, 1.2, 1.4, or 1.7 kPa.

In the experiment where the air VPD was held constant, they write, “in direct contrast to the anticipated results, the weekly growth of the tall fescue was substantially increased with increased temperature,” as “growth at 24 and 27°C was about 2.3 times that at 18.5°C and 1.4 times that at 21°C.” In the experiment where air temperature was held constant, “there was a strong, negative influence of increasing VPD on plant growth.” In addition, “transpiration rates were similar across treatments,” indicating “water movement through the plants did not increase in response to increasing VPD.” This led them to conclude limitation of water movement through the plant “is likely a result of stomatal closure in response to elevated VPD (Bunce, 2006).” This phenomenon also would restrict the CO₂ diffusion pathway into the plants and result in a decrease in photosynthesis, which is likely what caused the decreased growth at increased VPD. Nonetheless, their results indicate as long as the air VPD does not rise concurrently, increasing temperatures do not lead to growth reductions in this cool-season plant. In fact, they observe just the opposite to be true—warming dramatically increased tall fescue growth.

Sinclair *et al.* note, “during the past 50 years, VPD has remained virtually constant (Szilagyi *et al.*, 2001) due to an increase in atmospheric dew point temperature (Gaffen and Ross, 1999),” even in the face of what IPCC describes as unprecedented global warming. In a future warmer world, they conclude, “tall fescue, and perhaps other cool season species, could experience a substantial benefit with temperature increases expected in temperate zones if VPD were to remain unchanged.”

Wolfe-Bellin *et al.* (2006) write, “nocturnal temperatures are predicted to increase more than diurnal temperatures,” as has been observed in the real world over much of the twentieth century, and it might be expected “increased nocturnal temperature would increase dark respiration rate” and thereby “diminish the positive effects of elevated CO₂ on whole-plant growth, as measured by total biomass.” In an experiment designed to explore this hypothesis, they grew the C₃ forb *Phytolacca americana* L. from the four-leaf stage to maturity under well-watered and well-fertilized conditions in 6.2-L containers filled with a general purpose growing medium in controlled-environment glass chambers maintained at either 370 or 740 ppm CO₂ at diurnal/nocturnal

temperatures of either 26°/20°C or 26°/24°C. They periodically measured the plants’ light-saturated photosynthetic rates and whole-plant biomass. They found “plant photosynthetic rate was greater under elevated CO₂ [+69% during the first part of the growing season], and dark respiration rate, predicted to increase under higher nocturnal temperatures, exhibited no response to the nocturnal temperature treatment.” In contrast to their prediction, the forb they studied “exhibited no diminishment of total plant size in response to elevated nocturnal temperature,” and “time to flowering decreased and biomass allocation to reproduction increased under conditions of elevated nocturnal temperatures.” They conclude, “elevated CO₂ and high nocturnal temperatures of the future could have a neutral or even positive effect on the growth of northern *P. americana* populations,” even to the extent of “increasing population sizes, at least for plants growing at the northern edge of the species’ range.”

Niu *et al.* (2010) note, “most modeling studies predict ecosystem carbon storage will decrease as respiration is stimulated more than photosynthesis by rising temperature, with a consequent positive feedback to climate warming.” Working in a tallgrass prairie in McClain County, Oklahoma (USA) dominated by C₄ grasses and C₃ forbs that had not been grazed for the prior 40 years, they conducted a warming experiment in which they used infrared heaters to elevate soil temperature at a depth of 2.5 cm by an average of 1.96°C from 2000 to 2008, and “yearly biomass clipping mimicked hay or biofuel feedstock harvest.”

They found the experimental warming “significantly stimulated carbon storage in aboveground plant, root, and litter pools by 17%, 38%, and 29%, respectively, averaged over the nine years,” but it “did not change soil carbon content or nitrogen content in any pool.” They conclude increased plant nitrogen use efficiency played a more important role than soil nitrogen availability in regulating carbon cycling in this ecosystem, as the tallgrass prairie experienced a significant increase in productivity caused solely by the warming of its soil and not promoted by any addition of nitrogen to it. They explain this result by stating, “increased inputs of more recalcitrant [higher carbon:nitrogen ratio] material into soil counterbalanced any direct warming stimulation of carbon release, leading to little change in soil carbon stock and no apparent feedback to climate warming.”

Morgan *et al.* (2011) write, “global warming is

predicted to induce desiccation in many world regions through increases in evaporative demand,” but “rising CO₂ may counter that trend by improving plant water-use efficiency.” However, they note, “it is not clear how important this CO₂-enhanced water use efficiency might be in offsetting warming-induced desiccation because higher CO₂ also leads to higher plant biomass, and therefore greater transpirational surface.”

Morgan *et al.* conducted a prairie heating and CO₂ enrichment (PHACE) experiment in which they evaluated the productivity of native mixed-grass prairie west of Cheyenne, Wyoming (USA) to two levels of atmospheric CO₂ concentration (385 and 600 ppm, supplied via standard FACE technology) and two temperature regimes—ambient and elevated (ambient plus 1.5/3.0°C warmer day/night temperatures) for three full growing seasons (2007–2009) by means of T-FACE technology (Kimball *et al.*, 2008)—after first having measured grassland productivity under unmodified conditions for one growing season (2005) and with CO₂ enrichment alone for a second season (2006).

The 10 researchers report their warming treatment reduced annual soil water content by 13.1%, but their elevated CO₂ treatment increased annual soil water content by 17.3%, demonstrating “the water conservation effects of elevated CO₂ can completely cancel the desiccating effects of moderately warmer temperatures.” In addition, they write, “exposure of the prairie to 600 ppm CO₂ increased peak total above-ground biomass by an average 33% in the first 3 years of the experiment when annual precipitation amounts were in 7% of the site’s 132-year average of 388 mm,” but “CO₂ enrichment had no effect on above-ground biomass in 2009,” when “annual precipitation was 17% higher than the long-term mean.” They speculate the “higher soil water content in 2009 minimized the potential water-relations benefit of CO₂ enrichment on plant productivity.”

Morgan *et al.* write, “many believe that CO₂-induced reductions in transpiration at the leaf level will be largely offset at the canopy level by increases in leaf area,” citing McNaughton and Jarvis (1991), Piao *et al.* (2007), Frelich and Reich (2010), and Seager and Vecchi (2010). They say their results “clearly illustrate the importance of compensating CO₂ and warming effects in semi-arid ecosystems” and “indicate that in a warmer, CO₂-enriched world, both soil water content and productivity in semi-arid grasslands may be higher than previously expected.” In an accompanying commentary on their paper,

Baldocchi (2011) writes, “Morgan and colleagues provide one of the first and best views of how a mixed-grass ecosystem growing in a semi-arid climate will respond to future CO₂ and climatic conditions.” Morgan *et al.*’s findings help explain the great CO₂-induced greening of the Earth phenomenon (see section 4.2, this volume), especially as manifested in semi-arid regions of the planet.

Even if the air’s CO₂ content were to cease rising or have no effect on plants, it is still possible temperature increases alone would promote plant growth and development in some situations. Norton *et al.* (1999) found this to be the case. Elevated CO₂ had essentially no effect on the growth of the perennial grass *Agrostis curtisii* after two years of fumigation, whereas a 3°C increase in air temperature increased the growth of the species considerably.

The recent scientific literature indicates grassland plants likely will exhibit enhanced rates of photosynthesis and biomass production as the air’s CO₂ content rises, and those benefits will not be diminished by any global warming that might occur. If the ambient air temperature does rise, the growth-promoting effects of atmospheric CO₂ enrichment likely will rise right along with it, becoming increasingly robust in agreement with the experimental observations reviewed by Idso and Idso (1994). As long as the air’s CO₂ content continues to rise, grasslands will likely produce increasingly great amounts of forage, and perhaps reclaim areas of barren ground in certain environments.

References

- Baldocchi, D. 2011. The grass response. *Nature* **476**: 160–161.
- Berry, J. and Bjorkman, O. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* **31**: 491–543.
- Bunce, J.A. 2006. How do leaf hydraulics limit stomatal conductance at high water vapor pressure deficits? *Plant, Cell and Environment* **29**: 1644–1650.
- Cowling, S.A. and Sykes, M.T. 1999. Physiological significance of low atmospheric CO₂ for plant-climate interactions. *Quaternary Research* **52**: 237–242.
- Frelich, L.E. and Reich, P.B. 2010. Will environmental changes reinforce the impact of global warming on the prairie-forest border of central north America? *Frontiers in Ecology and the Environment* **8**: 371–378.
- Fritschi, F.B., Boote, K.J., Sollenberger, L.E., Allen Jr.,

Plants Under Stress

- L.H., and Sinclair, T.R. 1999. Carbon dioxide and temperature effects on forage establishment: photosynthesis and biomass production. *Global Change Biology* 5: 441–453.
- Gaffen, D.J. and Ross, R.J. 1999. Climatology and trends of U.S. surface humidity and temperature. *Journal of Climate* 12: 811–828.
- Greer, D.H., Laing, W.A., Campbell, B.D., and Halligan, E.A. 2000. The effect of perturbations in temperature and photon flux density on the growth and photosynthetic responses of five pasture species. *Australian Journal of Plant Physiology* 27: 301–310.
- Hakala, K. and Mela, T. 1996. The effects of prolonged exposure to elevated temperatures and elevated CO₂ levels on the growth, yield and dry matter partitioning of field-sown meadow fescue. *Agriculture and Food Science in Finland* 5: 285–298.
- Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: A review of the past 10 years' research. *Agricultural and Forest Meteorology* 69: 153–203.
- Kimball, B.A., Conley, M., Wang, S., Xingwu, L., Morgan, J., and Smith, D. 2008. Infrared heater arrays for warming ecosystem field plots. *Global Change Biology* 14: 309–320.
- Lilley, J.M., Bolger, T.P., and Gifford, R.M. 2001. Productivity of *Trifolium subterraneum* and *Phalaris aquatica* under warmer, higher CO₂ conditions. *New Phytologist* 150: 371–383.
- Long, S.P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: Has its importance been underestimated? *Plant, Cell and Environment* 14: 729–739.
- McMurtrie, R.E., Comins, H.N., Kirschbaum, M.U.F., and Wang, Y.-P. 1992. Modifying existing forest growth models to take account of effects of elevated CO₂. *Australian Journal of Botany* 40: 657–677.
- McMurtrie, R.E. and Wang, Y.-P. 1993. Mathematical models of the photosynthetic response of tree stands to rising CO₂ concentrations and temperatures. *Plant, Cell and Environment* 16: 1–13.
- McNaughton, K.G. and Jarvis, P.G. 1991. Effects of spatial scale on stomatal control of transpiration. *Agricultural and Forest Meteorology* 54: 279–301.
- Morgan, J.A., LeCain, D.R., Mosier, A.R., and Milchunas, D.G. 2001. Elevated CO₂ enhances water relations and productivity and affects gas exchange in C₃ and C₄ grasses of the Colorado shortgrass steppe. *Global Change Biology* 7: 451–466.
- Morgan, J.A., LeCain, D.R., Pendall, E., Blumenthal, D.M., Kimball, B.A., Carrillo, Y., Williams, D.G., Heisler-White, J., Dijkstra, F.A., and West, M. 2011. C₄ grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature* 476: 202–205.
- Newman, Y.C., Sollenberger, L.E., Boote, K.J., Allen Jr., L.H., and Littell, R.C. 2001. Carbon dioxide and temperature effects on forage dry matter production. *Crop Science* 41: 399–406.
- Niklaus, P.A., Kandeler, E., Leadley, P.W., Schmid, B., Tscherko, D., and Körner, C. 2001. A link between plant diversity, elevated CO₂ and soil nitrate. *Oecologia* 127: 540–548.
- Niu, S., Sherry, R.A., Zhou, X., Wan, S., and Luo, Y. 2010. Nitrogen regulation of the climate-carbon feedback: evidence from a long-term global change experiment. *Ecology* 91: 3261–3273.
- Norton, L.R., Firbank, L.G., Gray, A.J., and Watkinson, A.R. 1999. Responses to elevated temperature and CO₂ in the perennial grass *Agrostis curtisii* in relation to population origin. *Functional Ecology* 13: 29–37.
- Piao, S., Friedlingstein, P., Ciais, P., de Noblet-Ducoudre, N., Labat, D., and Zaehle, S. 2007. Changes in climate and land use have a larger direct impact than rising CO₂ on global river runoff trends. *Proceedings of the National Academy of Sciences USA* 104: 15,242–15,247.
- Seager, R. and Vecchi, G.A. 2010. Greenhouse warming and the 21st century hydroclimate of southwestern North America. *Proceedings of the National Academy of Sciences USA* 107: 21,277–21,282.
- Sinclair, T., Fiscus, E., Wherley, B., Durham, M., and Rufty, T. 2007. Atmospheric vapor pressure deficit is critical in predicting growth response of “cool-season” grass *Festuca arundinacea* to temperature change. *Planta* 227: 273–276.
- Stirling, C.M., Heddell-Cowie, M., Jones, M.L., Ashenden, T.W., and Sparks, T.H. 1998. Effects of elevated CO₂ and temperature on growth and allometry of five native fast-growing annual species. *New Phytologist* 140: 343–354.
- Stuhlfauth, T. and Fock, H.P. 1990. Effect of whole season CO₂ enrichment on the cultivation of a medicinal plant, *Digitalis lanata*. *Journal of Agronomy and Crop Science* 164: 168–173.
- Szilagyi, J., Katul, G.G., and Parlange, M.B. 2001. Evapotranspiration intensifies over the conterminous United States. *Journal of Water Resources Planning and Management* 127: 354–362.
- Wolfe-Bellin, K.S., He, J.-S., and Bazzaz, F.A. 2006. Leaf-level physiology, biomass, and reproduction of *Phytolacca*

americana under conditions of elevated carbon dioxide and increased nocturnal temperature. *International Journal of Plant Science* **167**:1011–1020.

3.13.3 Woody Plants

- As the air's CO₂ content rises, trees likely will exhibit enhanced rates of photosynthesis and biomass production that will not be counteracted by any global warming that might occur. If the ambient air temperature rises, the growth-promoting effects of atmospheric CO₂ enrichment likely will rise also. Trees are likely to produce greater amounts of biomass and, therefore, more timber products to meet the increasing needs of Earth's growing human population in the future.

As the air's CO₂ content rises, most trees likely will exhibit increased rates of photosynthesis and biomass production, which can help meet human demands for wood products. However, some researchers claim global warming will negate the growth-promoting effects of atmospheric CO₂ enrichment and actually reduce tree growth. To determine whether this claim has any validity, this section examines the results of several studies designed to reveal the net effect of both elevated CO₂ and air temperature on the growth of trees and other woody plants.

The optimum growth temperature for several plants already has been shown to rise substantially with increasing levels of atmospheric CO₂ (Berry and Bjorkman, 1980; Stuhlfauth and Fock, 1990; McMurtrie *et al.*, 1992; McMurtrie and Wang, 1993). Long (1991) described this phenomenon at length, having calculated from well-established plant physiological principles that most C₃ plants should increase their optimum growth temperature by approximately 5°C in response to a 300 ppm increase in the atmosphere's CO₂ concentration. In a subsequent review of the pertinent scientific literature, Cowling and Sykes (1999) demonstrated this was true for a number of plants. The photosynthetic rates of woody plants also are likely to rise in tandem with increases in the air's CO₂ concentration and temperature, as previously documented by Idso and Idso (1994) and by more recent studies for various trees and shrubs.

Kellomaki and Wang (2001) grew birch seedlings at atmospheric CO₂ concentrations of 350 and 700 ppm in combination with ambient and elevated (ambient plus 3°C) air temperatures. After five

months, the photosynthetic rates of the CO₂-enriched seedlings were 21 and 28% greater than their ambient-grown counterparts at ambient and elevated air temperatures, respectively. Carter *et al.* (2000) report a 300 ppm increase in the air's CO₂ content allowed leaves of sugar maple seedlings to remain green and non-chlorotic when exposed to air temperatures 3°C above ambient air temperature, and seedlings fumigated with ambient air exhibited severe foliar chlorosis when exposed to the same elevated air temperatures. At elevated air temperatures, rates of photosynthesis are greater and foliar health is typically better in CO₂-enriched as opposed to ambient air.

Many other studies report similar results. Sheu *et al.* (1999), for example, grew a subtropical tree at day/night temperatures of 25/20 (ambient) and 30/25°C (elevated) for six months, reporting seedlings exposed to 720 ppm CO₂ displayed photosynthetic rates 20 and 40% higher, respectively, than those of their ambient-grown controls. The CO₂-induced increases in total dry weight for this species were 14 and 49%, respectively, at the ambient and elevated air temperatures. Similarly, Maherali *et al.* (2000) report a 5°C increase in ambient air temperature increased the CO₂-induced biomass enhancement resulting from a 750 ppm CO₂ enrichment of ponderosa pine seedlings from 42 to 62%. In addition, Wayne *et al.* (1998) observed that a 5°C increase in the optimal growth temperature of yellow birch seedlings fumigated with an extra 400 ppm of CO₂ increased the CO₂-induced increase in biomass from 60% to 227%. The beneficial effects of elevated CO₂ on tree photosynthesis and growth are often further enhanced by elevated air temperatures, a fact also observed during natural seasonal temperature changes, as documented by Hymus *et al.* (1999) for loblolly pine and Roden *et al.* (1999) for snow gum seedlings.

In some cases, however, there appear to be few interactive effects between elevated CO₂ and temperature on photosynthesis and growth in trees. For example, when Tjoelker *et al.* (1998a) grew seedlings of quaking aspen, paper birch, tamarack, black spruce, and jack pine at atmospheric CO₂ concentrations of 580 ppm, they reported an average increase in photosynthetic rates of 28%, irrespective of air temperature, which varied from 18 to 30°C. And after analyzing the CO₂-induced increases in dry mass for these seedlings, Tjoelker *et al.* (1998b) further reported dry mass values were about 50 and 20% greater for the deciduous and coniferous species, respectively, again irrespective of air temperature.

The list of recent studies of woody plants that experience a CO₂-induced enhancement of growth in response to environmental warming is extensive, starting with Hamerlynck *et al.* (2000), who grew seedlings of the evergreen perennial shrub *Larrea tridentata* in glasshouses maintained at atmospheric CO₂ concentrations of 360, 550, and 700 ppm for one year. The researchers withheld water from half of the seedlings for three months prior to a nine-day high-temperature treatment. Elevated CO₂ largely offset the detrimental effects of drought and high temperature on water relations and photosynthesis in this species. Averaged across the entire experiment, the photosynthetic rates of seedlings grown at 550 and 700 ppm CO₂ were 31 and 90% greater, respectively, than the rates of the ambient-grown control plants.

Usami *et al.* (2001) grew two-year-old saplings of *Quercus myrsinaefolia*, an evergreen broad-leaved oak species, in controlled-environment chambers having various atmospheric CO₂ concentrations and air temperatures for approximately one year, to study the interactive effects of elevated CO₂ and temperature on the development and growth of this important tree, which is widely distributed throughout Laos, Vietnam, China, Taiwan, South Korea, and southwestern Japan. In ambient air, 3 and 5°C increases in air temperature boosted final sapling biomass by 53 and 47%, respectively. At elevated CO₂ concentrations 1.5 or 2 times greater than the ambient CO₂ concentration, the same 3 and 5°C increases in air temperature enhanced final biomass by 110 and 140%, respectively.

Turbull *et al.* (2002) manipulated day/night air temperatures around 4-m-tall cottonwood (*Populus deltoides* Bartr. Ex Marsh) trees growing in large experimental enclosures, to study the effects of temperature on carbon relations. A 6°C increase in daytime temperature, coupled with a 10°C increase in nighttime temperature, enhanced rates of net photosynthesis by 64% and rates of dark respiration by 77%. On an absolute scale, the photosynthetic carbon gains due to the daytime temperature increase were nearly an order of magnitude greater than the nocturnal carbon losses caused by the greater increase in nighttime temperature. Consequently, if Earth were to begin to warm again, carbon uptake by cottonwood trees should increase significantly.

Peltola *et al.* (2003) constructed closed chambers around 20-year-old Scots pine (*Pinus sylvestris* L.) trees growing on a low-nitrogen-containing soil, and for three years thereafter they fumigated the trees in the chambers with air containing either 350 or

700 ppm CO₂ at either ambient or elevated air temperatures (about 4°C above ambient temperatures), to study the effects of elevated CO₂ and air temperature on stem development in this coniferous species when growing on a soil low in nitrogen. After three years, they found cumulative stem diameter growth in the CO₂-enriched trees grown at ambient air temperature was 57% greater than that of control trees grown at ambient CO₂ and ambient air temperature. The trees subjected to elevated CO₂ and elevated air temperature exhibited cumulative stem-diameter growth 67% greater than trees grown in ambient air at ambient air temperatures.

Sallas *et al.* (2003) grew seedlings of Scots pine and Norway spruce (*Picea abies* (L.) Karst.) for 50 days in computer-controlled environmental growth chambers in air of ambient or twice-ambient CO₂ concentration (normal or elevated (EC) treatments) at day/night temperature combinations of 19/12°C or 23/16°C (normal or elevated (ET) treatments), making a host of measurements. Seedlings of both species were shown to accumulate the most biomass in the combined EC + ET treatment.

Hymus *et al.* (2003) studied net ecosystem exchange (NEE) of CO₂ in a scrub-oak ecosystem—85–90% of the aboveground biomass of which was comprised of three oak species (*Quercus myrtifolia*, *Quercus geminate*, and *Quercus chapmani*)—on Merritt Island in NASA's Kennedy Space Center on the coast of central Florida (USA). This ecosystem was completely burned in January 1996, after which 16 open-top chambers (OTCs) were placed on it in the spring of that year, half of which were maintained at the ambient atmospheric CO₂ concentration while the other half were maintained at ambient plus 350 ppm, with routine measurements being started in June 1999 and continuing for 25 months through July 2001. The scientists found the extra CO₂ supplied to the CO₂-enriched OTCs “increased maximum NEE and the apparent quantum yield of the NEE during the photoperiod,” and the magnitude of the stimulation of maximum NEE, expressed per unit ground area, “was seasonal, rising from 50% in the winter to 180% in the summer,” in accord with what is known about the interactive effects of atmospheric CO₂ enrichment and daily, seasonal, and multiyear warming.

Turnbull *et al.* (2004) studied four- to five-meter-tall cottonwood trees (*Populus deltoides* Bartr.) grown for three years in air of different CO₂ concentrations (420, 800, and 1,200 ppm) in the three bays of the Biosphere 2 facility near Tucson, Arizona (USA). They maintained the trees at three nocturnal

temperatures (15, 20, or 25°C) and a single constant daytime temperature ($31 \pm 1^\circ\text{C}$) in a short-term experiment in which they routinely measured maximum photosynthesis (A_{max}) rates at growth CO_2 concentrations. As nocturnal air temperature rose from 15 to 25°C, the researchers observed subsequent daytime A_{max} increased by 16% in air of 420 ppm CO_2 , 12% in air of 800 ppm CO_2 , and 4% in air of 1,200 ppm CO_2 , leading them to conclude “at future elevated night temperatures suggested by global climate monitoring and modeling, net photosynthesis at elevated CO_2 may be increased.” It appears the response could saturate at a CO_2 partial pressure of somewhat more than 1,200 ppm CO_2 , but that value is far greater than anyone is suggesting will ever be reached as a consequence of mankind’s burning of fossil fuels.

But what if air temperatures get *really* hot, for some as-yet-unknown reason? Idso *et al.* (1995) grew well-watered and -fertilized sour orange (*Citrus aurantium* L.) trees from the seedling stage out-of-doors at Phoenix, Arizona (USA) in clear-plastic-wall open-top chambers continuously maintained at mean atmospheric CO_2 concentrations of either approximately 400 or 700 ppm for 5.5 years. During the warmest parts of some of the hottest days of summer, the scientists measured the temperatures and rates of net photosynthesis of fully expanded outer-canopy sunlit leaves.

Figure 3.13.3.1 portrays the results of plotting their net photosynthesis measurements against leaf temperature. Based on the linear regression lines fit to the data, it can be determined the 75% increase in the air’s CO_2 content led to a 75% enhancement of leaf net photosynthesis at a leaf temperature of 31°C, a 100% enhancement at a leaf temperature of 35°C, and a 200% enhancement at 42°C. At higher leaf temperatures, the net photosynthetic rate of the foliage growing in ambient air dropped to zero at

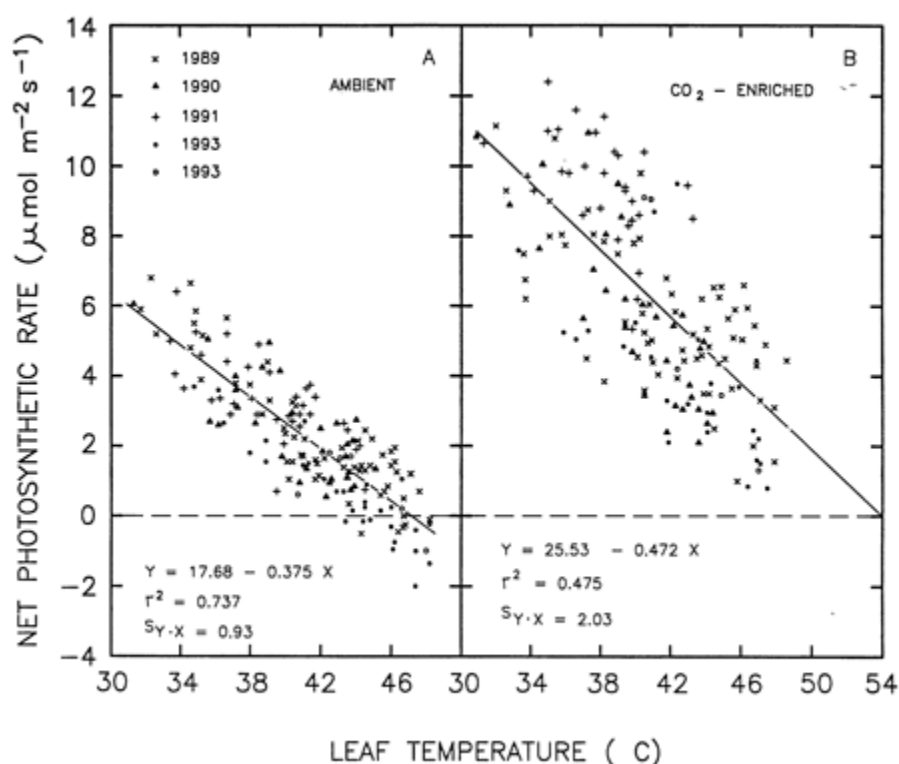


Figure 3.13.3.1. Leaf net photosynthetic rate vs. leaf temperature for the foliage of sour orange trees growing in air of either 400 or 700 ppm CO_2 . Adapted from Idso *et al.* (1995).

47°C (making the CO_2 -induced enhancement of photosynthesis at that point essentially infinite), and it became negative thereafter (which condition, if prolonged, would ultimately lead to plant death).

In the CO_2 -enriched trees, by contrast, the net photosynthetic rate of the foliage was still substantial at 47°C, and the regression line for those trees suggests their mean rate of foliage net photosynthesis likely would not have declined to zero until leaf temperature reached 54°C, approximately 7°C above the upper-limiting temperature for positive net photosynthesis in the trees grown in ambient air.

These findings show if Earth’s air temperature continues to rise significantly in the future, a concomitant rise in the air’s CO_2 content would serve as a powerful antidote for the ill—and sometimes deadly—effects of temperature stress.

Lewis *et al.* (2001) reached somewhat similar conclusions when they grew Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings in sunlit chambers programmed to track either ambient atmospheric CO_2 concentration or ambient + 200 ppm CO_2 , as well as either ambient air temperature or ambient + 4°C, over a 21-month period, measuring

light-saturated rates of net photosynthesis at approximately monthly intervals. The extra CO₂ they supplied to the seedlings “increased net photosynthetic rates by an average of 21% across temperature treatments during both the 1996 hydrologic year, the third year of exposure, and the 1997 hydrologic year,” and “elevated mean annual temperature increased net photosynthetic rates by an average of 33% across CO₂ treatments during both years.” In addition, “between February and August 1996, the short-term temperature optima for photosynthesis shifted by approximately 10°C higher in both CO₂ treatments,” and the elevated CO₂ treatment “increased the short-term (minutes to hours) temperature optima for photosynthesis, as has been observed in other tree species (Idso and Idso, 1994; Eamus *et al.*, 1995).” The four researchers conclude “an increase of 200 ppm above current atmospheric CO₂ concentrations may shift temperature optima upward 3–4°C, paralleling the increase in mean annual temperatures predicted to occur during the next century,” and “by shifting temperature optima upward, elevated CO₂ may ‘acclimate’ photosynthetic processes to future temperature regimes.”

Huang *et al.* (2007) compared, synthesized, and evaluated the scientific literature to that point in time, describing atmospheric CO₂ enrichment experiments conducted on trees and empirical tree-ring studies designed to ascertain whether the growth-promoting effects of rising atmospheric CO₂ concentrations occur in natural forests. They found numerous CO₂-enrichment experiments have “demonstrated significantly positive physiological and growth responses of trees to CO₂, providing strong evidence to support the direct CO₂ fertilization effect (increased photosynthesis, water use efficiency, above- and below-ground growth) and thus allowing prediction of which ecosystems might be most responsive to CO₂.” They suggest the latter will be “warm, moderately drought-stressed ecosystems with an ample nitrogen supply,” because “drought-stressed trees could benefit from increased water use efficiency to enhance growth.” They note tree-ring studies on the cold and arid Tibetan Plateau also “showed significant growth enhancements as well as increased water use efficiency (24.7% and 33.6% for each species, respectively) in Qilian juniper and Qinghai spruce since the 1850s,” citing Zhang *et al.* (2003), Shao *et al.* (2005), Liang *et al.* (2006), Huang and Zhang (2007), and Zhang and Qiu (2007).

Hickler *et al.* (2008) evaluated the process-based LPJ-GUESS model of vegetation dynamics and

biogeochemistry (Smith *et al.*, 2001; Hickler *et al.*, 2004) via a site-by-site comparison with the results of four temperate forest FACE experiments (Norby *et al.*, 2005). After demonstrating the model simulations adequately reproduced the magnitude of the FACE site measurements—a mean model-derived net primary productivity (NPP) increase of 25.9% for CO₂ raised to a value of 550 ppm vs. a mean measured NPP increase of 27.8% for the same CO₂ increase—they conducted what they called a “global forest FACE experiment” to see what the reality-tested model suggested about CO₂ enrichment effects on the NPP of boreal and tropical forests, as well as its temperate forests.

For the world as a whole, the model suggests raising the air’s CO₂ concentration to 550 ppm would increase the NPP of temperate forests by an average of 25.7%. The NPP of boreal forests would be raised by 15.1%, and tropical forests would experience an NPP increase of 35.1%. Hickler *et al.* note warming “is likely to increase NPP more in cold northern regions than close to the equator because of a greater proportional growing season extension in temperature-limited environments.”

Martinez-Vilalta *et al.* (2008) describe their use of tree-ring data from the Catalan Ecological and Forest Inventory “to study the temporal variability of Scots pine stem radial growth (period 1901–1997) across a relatively large region (Catalonia, NE Spain) situated close to the southern limit of the distribution of the species.” This inventory, they write, “included a total of 10,664 plots randomly distributed throughout the forested area of Catalonia,” where Scots pine was present in 30.2% of the plots and dominant in 18.4% of them. They found “an overall increase of 84% in Scots pine BAI [basal area increment] during the 20th century, consistent with most previous studies for temperate forests.” They state, “this trend was associated with increased atmospheric CO₂ concentration,” which they interpret to be “a fertilization effect.” Over the same period, the five researchers note, “there was also a marked increase in temperature across the study region (0.19°C per decade on average),” and “this warming had a negative impact on radial growth, particularly at the drier sites.” They add “its magnitude was not enough to counteract the fertilization effect.”

Darbah *et al.* (2010) measured the effects of a natural and prolonged heat wave on the photosynthetic rates of quaking aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera*) trees grown from the seedling stage for an additional nine

years in the free-air CO₂-enrichment (FACE) facility near Rhinelander, Wisconsin (USA), where from 0700 to 1900 hours each day throughout the growing season half of the trees were exposed to an extra ~190 ppm of CO₂. For the aspen trees, the heat wave produced “no visible symptoms of stress,” but the birch trees exhibited “leaf curling and then yellowing of leaves and finally leaf shedding,” with trees in the control treatment dropping 33% of their leaves and those in the CO₂-enriched treatment dropping 20%. Aspen clone 42E exhibited a 30% CO₂-induced increase in the rate of photosynthesis at saturating light intensities in the 32–35°C temperature range, and 218% in the 36–39°C range. Similarly, aspen clone 271 exhibited a 38% CO₂-induced increase in the 32–35°C range and a 199% increase in the 36–39°C range. The birch trees exhibited a 95% CO₂-induced increase in photosynthetic rates in the 32–35°C range and a 297% increase in the 36–39°C range.

The four researchers say their findings agree with those of Idso and Kimball (1992), who reported elevated CO₂ (ambient + 300 ppm) increased net photosynthetic rates in sour orange tree (*Citrus aurantium* L.) leaves exposed to full sunlight by 75, 100, and 200% compared to leaves in ambient CO₂ air at temperatures of 31, 35, and 42°C, respectively, suggesting “elevated CO₂ ameliorates heat stress in tree leaves.” They also note their observations “agree with Veteli *et al.* (2007), who reported that elevated CO₂ ameliorated the negative effects of high temperature in three deciduous tree species,” and “Wayne *et al.* (1998) reported that elevated CO₂ ameliorated high temperature stress in yellow birch trees (*Betula alleghaniensis*).” They conclude, “in the face of rising atmospheric CO₂ and temperature (global warming), trees will benefit from elevated CO₂ through increased thermotolerance.”

Ghannoum, *et al.* (2010b) grew individual well-watered and -fertilized plants of two species of Australian eucalypts—faster-growing *Eucalyptus saligna* and slower-growing *E. sideroxylon*—from seed in 10-L pots filled with 9 kg of loamy sand in naturally lit glasshouse compartments maintained at either ambient or ambient + 4°C air temperature and three different CO₂ concentrations (280, 400, or 650 ppm) for 140 days, measuring various plant responses throughout the course of the experiment. They found light-saturated net photosynthesis (Asat) increased by ~50% with each step-increase in the air’s CO₂ concentration—going from 280 to 400 ppm, and going from 400 to 650 ppm—and in the higher of the

two temperature treatments the optimal temperature for Asat increased by 2–7°C across the three CO₂ treatments. They note these results “partly explain the strong growth responses to elevated CO₂ and temperature observed in a previous study with the same eucalypt seedlings,” citing Ghannoum *et al.* (2010a).

Keenan *et al.* (2011) note climate models consistently project significant increases in temperature and decreases in precipitation in the Mediterranean basin, and they state these changes may have a large impact on current Mediterranean forests and the related ecosystem services they provide. They say niche-based models—also known as bioclimatic envelope models or habitat models—are the most commonly used method for predicting potential species distribution responses to future climatic changes, and they note these models typically predict significant negative consequences for terrestrial plants and animals in the face of increasing atmospheric CO₂ concentrations.

Keenan *et al.* say they prefer process-based models, which describe eco-physiological processes ranging from purely empirical relationships to mechanistic descriptions based on physical laws. These models, supported by experiments and growth and yield surveys, “suggest that global warming will have a positive impact on forest productivity (van der Meer *et al.*, 2002; Nigh *et al.*, 2004; Norby and Luo, 2004; Briceño-Elizondo *et al.*, 2006; Gaucharel *et al.*, 2008), due to the direct fertilization effect of increased CO₂ and indirect effects such as lengthening of the growing period.” To elucidate the difference in results obtained by employing these two approaches, the five researchers assessed and compared the projections when applied to stands of three forest species (*Quercus ilex*, *Pinus halepensis*, and *Pinus sylvestris*) that have widely contrasting distributions in continental Spain.

Keenan *et al.* found CO₂ fertilization tends to show an increase in forest productivity in mechanistic process-based models (despite increased drought and presumed temperature stress) by up to three times the non-CO₂ fertilization scenario by the period 2050–2080, in stark contrast to projections of reduced habitat suitability based on niche-based models for the same period. Their results show “previous reports of species decline in continental Spain (e.g. Benito-Garzon *et al.*, 2008) may be overestimated due to two reasons.” One of these is the use of only one predictive niche-based model, and the other is the failure to account for positive effects of CO₂

fertilization in a warming world. They note similar studies in other regions that do not consider these two aspects are also potentially overestimating species decline due to climate change, because “niche-based model results also likely overestimate the decline in [habitat] suitability.” They conclude, “an organism’s niche must be modeled mechanistically if we are to fully explain distribution limits,” citing Kearney (2006).

Osorio *et al.* (2011) investigated the impacts of drought and high-temperature stresses on photosynthesis, energy partitioning, and membrane lipids—as well as the potential ability of Carob or St. John’s (*Ceratonia siliqua*) trees to attenuate oxidative damage. They studied seedlings growing in controlled-environment chambers and rooted in 3-dm³ pots filled with a 2:1 mixture of a fertilized substrate and natural soil, maintained under two thermal regimes—low and high temperature (LT: 25/18°C; HT: 32/21°C)—and three soil water conditions (control, water stress, and rewetting), monitoring numerous physiological and biochemical plant properties and processes. The decrease in net photosynthesis (P_N) caused by drought was 33% in the LT chamber and 84% in the HT chamber. They note, “the negative effects of soil drying on P_N and stomatal conductance of HT plants were no longer detected 36 hours following rewatering.” Also, “although *C. siliqua* seedlings exhibit clear signs of oxidative stress under drought and high temperature, they retain a remarkable ability to quickly restore normal physiological activity on rehydration.” This ability was so strong the five Portuguese scientists say they “can state that although *C. siliqua* seedlings exhibit clear signs of oxidative stress under drought and high temperature, they retain a remarkable ability to quickly restore normal physiological activity on rehydration, which let us believe that they can satisfactorily deal with predicted climate warming and increased soil drying in the Mediterranean area.”

Wertin *et al.* (2012) examined the influence of elevated temperature (ambient + 2°C) and atmospheric CO₂ concentration (700 ppm), applied singly and in combination, on biomass accumulation and the temperature response of net photosynthesis (A_{net}) and leaf respiration (R_d) of loblolly pine (*Pinus taeda* L.) seedlings grown simultaneously at a northern and a southern site in the species’ range, where the long-term mean growing season temperature (from February through October) at the cool site was 15.2°C and at the warm site was 21.5°C. They grew the well-watered and -fertilized seedlings over two con-

secutive years in half-cylindrical polyfilm-enclosed chambers located in open fields.

Wertin *et al.* determined “biomass accumulation was substantially greater at the warmer site compared with the cooler site regardless of treatment,” and “at each site, biomass accumulation was greater in the elevated temperature treatment compared with the ambient treatment.” They also found “elevated CO₂ increased biomass accumulation and A_{net} at both sites and in both temperature treatments.” The five University of Georgia (USA) researchers conclude their study “provides an indication that future projected increases in CO₂ and air temperature of 700 ppm and +2°C, respectively, are likely to increase loblolly pine growth in most, if not all, of its current range.” And they state, “the large number of studies that have reported an increase in tree growth in elevated growth temperatures compared with current ambient temperature (Way and Oren, 2010) suggest that other species may respond similarly.”

Ameye *et al.* (2012) note that in studies where the air’s CO₂ content was doubled, “increases in net photosynthesis were reported ranging from 43% to 192% in *Pinus taeda* (Teskey, 1997; Tissue *et al.*, 1997; Ellsworth, 1999; Wertin *et al.*, 2010; Frenck *et al.*, 2011) and from 30% to 256% in *Quercus rubra* (Kubiske and Pregitzer, 1996; Anderson and Tomlinson, 1998; Cavender-Bares *et al.*, 2000).” Moreover, “generally, an increase in air temperature also has a positive effect on net photosynthesis and growth,” citing Sage and Kubien (2007) and Way and Oren (2010).

Investigating how loblolly pine and northern red oak trees might respond to the extreme heat waves often predicted to occur in a future CO₂-enriched world, the scientists examined the most recent fully developed leaves of well-watered and -fertilized seedlings of *Pinus taeda* and *Quercus rubra* grown in 7.6-L pots out-of-doors at Athens, Georgia (USA) in polyethylene chambers maintained at ambient and elevated air temperatures (T_{amb} and $T_{amb} + 3^\circ\text{C}$), as well as seven-day heat waves consisting of a biweekly +6°C heat wave or a monthly +12°C heat wave. These treatments were maintained throughout the growing season, and Ameye *et al.* measured rates of net photosynthesis before, during, and after the many midsummer heat waves they created. They report “an immediate and significant decline in net photosynthesis was observed in seedlings subjected to a +12°C heat wave, but not in seedlings subjected to a +6°C heat wave.” They also state, “after the third day of the +12°C heat wave, net photosynthesis values

stabilized at positive values and did not show signs of further reduction, indicating that the photosynthetic apparatus did not accrue additional stress or damage as the heat wave continued.” Therefore, they conclude, “if soil moisture is adequate, trees will experience negative effects in photosynthetic performance only with the occurrence of extreme heat waves.” Also, as “elevated CO₂ diminished these negative effects,” they conclude “the future climate may not be as detrimental to plant communities as previously assumed.”

In concluding this literature review, it is instructive to consider the Paleocene-Eocene Thermal Maximum (PETM) of some 56 million years ago. According to Jaramillo *et al.* (2010), it “was one of the most abrupt global warming events of the past 65 million years (Kennett and Stott, 1991; Zachos *et al.*, 2003; Westerhold *et al.*, 2009).” It was presumed to have been driven, they write, by “a massive release of ¹³C-depleted carbon (Pagani *et al.*, 2006; Zeebe *et al.*, 2009)” that led to “an approximate 5°C increase in mean global temperature in about 10,000 to 20,000 years (Zachos *et al.*, 2003).” Earth’s tropical ecosystems “suffered extensively because mean temperatures are surmised to have exceeded the ecosystems’ heat tolerance (Huber, 2008),” according to many scientists, Jaramillo *et al.* write.

To ascertain whether the ancient warming of the world truly constituted a major problem for the planet’s rainforests, the 29 researchers from eight countries analyzed pollen and spore contents and the stable carbon isotopic composition of organic materials obtained from three tropical terrestrial PETM sites in eastern Colombia and western Venezuela. Contrary to the prevailing wisdom of the recent past, they found the onset of the PETM was “concomitant with an increase in diversity produced by the addition of many taxa (with some representing new families) to the stock of preexisting Paleocene taxa.” They determined this increase in biodiversity “was permanent and not transient.”

Jaramillo *et al.* write, “today, most tropical rainforests are found at mean annual temperatures below 27.5°C,” and several scientists have argued “higher temperatures could be deleterious to the health of tropical ecosystems,” citing Stoskopf (1981), Bassow *et al.* (1994), Lewis *et al.* (2004), Huber (2008, 2009), and Tewksbury *et al.* (2008). They report tropical warming during the PETM is actually thought to have produced intolerable conditions for tropical ecosystems, citing Huber (2008, 2009). Nevertheless, Jaramillo *et al.* reiterate

that at the sites that they studied, “tropical forests were maintained during the warmth of the PETM (~31° to 34°C).” Thus they conclude, “it is possible that higher Paleocene CO₂ levels (Royer, 2010) contributed to their success.”

Their conclusion is supported by what is now the well-established fact that most woody plants tend to exhibit their greatest photosynthetic rates at increasingly warmer temperatures as the air’s CO₂ content rises. It is becoming increasingly clear that greater warmth and atmospheric CO₂ concentrations are not as detrimental as IPCC and others typically make them out to be. Quite to the contrary, they are likely to make ecosystems both more stable and more productive.

The scientific literature of the past few decades indicates a continuing rise in the air’s CO₂ content likely will lead to enhanced rates of photosynthesis and biomass production that will not be negated by any global warming that might occur. If the ambient air temperature rises, the growth-promoting effects of atmospheric CO₂ enrichment likely will rise right along with it. Trees are likely to produce greater amounts of biomass and, therefore, more timber products to meet the increasing needs of Earth’s expanding human population.

References

- Ameye, M., Wertin, T.M., Bauweraerts, I., McGuire, M.A., Teskey, R.O., and Steppe, K. 2012. The effect of induced heat waves on *Pinus taeda* and *Quercus rubra* seedlings in ambient and elevated CO₂ atmospheres. *New Phytologist* **196**: 448–461.
- Anderson, P.D. and Tomlinson, P.T. 1998. Ontogeny affects response of northern red oak seedlings to elevated CO₂ and water stress. I. Carbon assimilation and biomass production. *New Phytologist* **140**: 477–491.
- Bassow, S.L., McConnaughay, K.D., and Bazzaz, F.A. 1994. The Response of temperate tree seedlings grown in elevated CO₂ to extreme temperature events. *Ecological Applications* **4**: 593–603.
- Benito-Garzon, M., Sanchez de Dios, R., and Sainz Ollero, H. 2008. Effects of climate change on the distribution of Iberian tree species. *Applied Vegetation Science* **11**: 169–178.
- Berry, J. and Bjorkman, O. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* **31**: 491–543.
- Briceño-Elizondo, R., Garcia-Gonzalo, J., Peltola, H.,

- Matala, J., and Kellomaki, S. 2006. Sensitivity of growth of Scots pine, Norway spruce and silver birch to climate change and forest management in boreal conditions. *Forest Ecology and Management* **232**: 152–167.
- Carter, G.A., Bahadur, R., and Norby, R.J. 2000. Effects of elevated atmospheric CO₂ and temperature on leaf optical properties in *Acer saccharum*. *Environmental and Experimental Botany* **43**: 267–273.
- Cavender-Bares, J., Potts, M., Zacharias, E., and Bazzaz, F.A. 2000. Consequences of CO₂ and light interactions for leaf phenology, growth, and senescence in *Quercus rubra*. *Global Change Biology* **6**: 877–887.
- Cowling, S.A. and Sykes, M.T. 1999. Physiological significance of low atmospheric CO₂ for plant-climate interactions. *Quaternary Research* **52**: 237–242.
- Darbah, J.N.T., Sharkey, T.D., Calfapietra, C., and Karnosky, D.F. 2010. Differential response of aspen and birch trees to heat stress under elevated carbon dioxide. *Environmental Pollution* **158**: 1008–1014.
- Eamus, D., Duff, G.A., and Berryman, C.A. 1995. Photosynthetic responses to temperature, light flux-density, CO₂ concentration and vapor pressure deficit in *Eucalyptus tetrodonia* grown under CO₂ enrichment. *Environmental Pollution* **90**: 41–49.
- Ellsworth, D.S. 1999. CO₂ enrichment in a maturing pine forest: are CO₂ exchange and water status in the canopy affected? *Plant, Cell and Environment* **22**: 461–472.
- Frenck, G., van der Linden, L., Mikkelsen, T.N., Brix, H., and Jorgensen, R.B. 2011. Increased CO₂ does not compensate for negative effects on yield caused by higher temperature and O₃ in *Brassica napus* L. *European Journal of Agronomy* **35**: 127–134.
- Gaucharel, C., Guiot, J., and Misson, L. 2008. Changes of the potential distribution area of French Mediterranean forests under global warming. *Biogeosciences* **5**: 1493–1503.
- Ghannoum, O., Phillips, N.G., Conroy, J.P., Smith, R.A., Attard, R.D., Woodfield, R., Logan, B.A., Lewis, J.D., and Tissue, D.T. 2010a. Exposure to preindustrial, current and future atmospheric CO₂ and temperature differentially affects growth and photosynthesis in *Eucalyptus*. *Global Change Biology* **16**: 303–319.
- Ghannoum, O., Phillips, N.G., Sears, M.A., Logan, B.A., Lewis, J.D., Conroy, J.P., and Tissue, D.T. 2010b. Photosynthetic responses of two eucalypts to industrial-age changes in atmospheric [CO₂] and temperature. *Plant, Cell and Environment* **33**: 1671–1681.
- Hamerlynck, E.P., Huxman, T.E., Loik, M.E., and Smith, S.D. 2000. Effects of extreme high temperature, drought and elevated CO₂ on photosynthesis of the Mojave Desert evergreen shrub, *Larrea tridentata*. *Plant Ecology* **148**: 183–193.
- Hickler, T., Smith, B., Prentice, I.C., Mjofors, K., Miller, P., Arneth, A., and Sykes, M.T. 2008. CO₂ fertilization in temperate FACE experiments not representative of boreal and tropical forests. *Global Change Biology* **14**: 1531–1542.
- Hickler, T., Smith, B., Sykes, M.T., Davis, M., Sugita, S., and Walker, K. 2004. Using a generalized vegetation model to simulate vegetation dynamics in northeastern USA. *Ecology* **85**: 519–530.
- Huang, J.-G., Bergeron, Y., Denneker, B., Berninger, F., and Tardif, J. 2007. Response of forest trees to increased atmospheric CO₂. *Critical Reviews in Plant Sciences* **26**: 265–283.
- Huang, J.G. and Zhang, Q.B. 2007. Tree-rings and climate for the last 680 years in Wulan area of northeastern Qinghai-Tibetan Plateau. *Climatic Change* **80**: 369–377.
- Huber, M. 2008. A hotter greenhouse? *Science* **321**: 353–354.
- Huber, M. 2009. Snakes tell a torrid tale. *Nature* **457**: 669–670.
- Hymus, G.J., Ellsworth, D.S., Baker, N.R., and Long, S.P. 1999. Does free-air carbon dioxide enrichment affect photochemical energy use by evergreen trees in different seasons? A chlorophyll fluorescence study of mature loblolly pine. *Plant Physiology* **120**: 1183–1191.
- Hymus, G.J., Johnson, D.P., Dore, S., Anderson, H.P., Hinkle, C.R., and Drake, B.G. 2003. Effects of elevated atmospheric CO₂ on net ecosystem CO₂ exchange of a scrub-oak ecosystem. *Global Change Biology* **9**: 1802–1812.
- Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: A review of the past 10 years' research. *Agricultural and Forest Meteorology* **69**: 53–203.
- Idso, S.B., Idso, K.E., Garcia, R.L., Kimball, B.A., and Hooper, J.K. 1995. Effects of atmospheric CO₂ enrichment and foliar methanol application on net photosynthesis of sour orange tree (*Citrus aurantium*; Rutaceae) leaves. *American Journal of Botany* **82**: 26–30.
- Idso, S.B. and Kimball, B.A. 1992. Effects of atmospheric CO₂ enrichment on photosynthesis, respiration and growth of sour orange trees. *Plant Physiology* **99**: 341–343.
- Jaramillo, C., Ochoa, D., Conteras, L., Pagani, M., Carvajal-Ortiz, H., Pratt, L.M., Krishnan, S., Cardona, A., Romero, M., Quiroz, L., Rodriguez, G., Rueda, M.J., de la

Climate Change Reconsidered II: Biological Impacts

- Parra, F., Moron, S., Green, W., Bayona, G., Montes, C., Quintero, O., Ramirez, R., Mora, G., Schouten, S., Bermudez, H., Navarrete, R., Parra, F., Alvaran, M., Osorno, J., Crowley, J.L., Valencia, V., and Vervoort, J. 2010. Effects of rapid global warming at the Paleocene-Eocene boundary on neotropical vegetation. *Science* **330**: 957–961.
- Kearney, M. 2006. Habitat, environment and niche: what are we modeling? *Oikos* **115**: 186–191.
- Keenan, T., Serra, J.M., Lloret, F., Ninyerola, M., and Sabate, S. 2011. Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO₂ matters! *Global Change Biology* **17**: 565–579.
- Kellomaki, S. and Wang, K.-Y. 2001. Growth and resource use of birch seedlings under elevated carbon dioxide and temperature. *Annals of Botany* **87**: 669–682.
- Kennett, J.P. and Stott, L.D. 1991. Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene. *Nature* **353**: 225–229.
- Kubiske, M.E. and Pregitzer, K.S. 1996. Effects of elevated CO₂ and light availability on the photosynthetic response of trees of contrasting shade tolerance. *Tree Physiology* **16**: 351–358.
- Lewis, J.D., Lucash, M., Olszyk, D., and Tingey, D.T. 2001. Seasonal patterns of photosynthesis in Douglas fir seedlings during the third and fourth year of exposure to elevated CO₂ and temperature. *Plant, Cell and Environment* **24**: 539–548.
- Lewis, S.L., Malhi, Y., and Phillips, O.L. 2004. Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society B* **359**: 437–462.
- Liang, E.Y., Shao, X.M., Eckstein, D., Huang, L., and Liu, X.H. 2006. Topography- and species-dependent growth response of *Sabina przewalskii* and *Picea crassifolia* to climate on the northeast Tibetan Plateau. *Forest Ecology and Management* **236**: 268–277.
- Long, S.P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: Has its importance been underestimated? *Plant, Cell and Environment* **14**: 729–739.
- Maherali, H. and DeLucia, E.H. 2000. Interactive effects of elevated CO₂ and temperature on water transport in ponderosa pine. *American Journal of Botany* **87**: 243–249.
- Martinez-Vilalta, J., Lopez, B.C., Adell, N., Badiella, L., and Ninyerola, M. 2008. Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. *Global Change Biology* **14**: 2868–2881.
- McMurtrie, R.E., Comins, H.N., Kirschbaum, M.U.F., and Wang, Y.-P. 1992. Modifying existing forest growth models to take account of effects of elevated CO₂. *Australian Journal of Botany* **40**: 657–677.
- McMurtrie, R.E. and Wang, Y.-P. 1993. Mathematical models of the photosynthetic response of tree stands to rising CO₂ concentrations and temperatures. *Plant, Cell and Environment* **16**: 1–13.
- Nigh, G.D., Ying, C.C., and Qian, H. 2004. Climate and productivity of major conifer species in the interior of British Columbia, Canada. *Forest Science* **50**: 659–671.
- Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, S.J., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., De Angelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarasci-Mugnozza, G.E., Schlesinger, W.H., and Oren, R. 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences* **102**: 18,052–18,056.
- Norby, R.J. and Luo, Y. 2004. Evaluating ecosystem responses to rising atmospheric CO₂ and global warming in a multi-factor world. *New Phytologist* **162**: 281–293.
- Osorio, M.L., Osorio, J., Vieira, A.C., Goncalves, S., and Romano, A. 2011. Influence of enhanced temperature on photosynthesis, photooxidative damage, and antioxidant strategies in *Ceratonia siliqua* L. seedlings subjected to water deficit and rewatering. *Photosynthetica* **49**: 3–12.
- Pagani, M., Caldeira, K., Archer, D., and Zachos, J.C. 2006. An ancient carbon mystery. *Science* **314**: 1556–1557.
- Peltola, H., Kilpelainen, A., and Kellomaki, S. 2002. Diameter growth of Scots pine (*Pinus sylvestris*) trees grown at elevated temperature and carbon dioxide concentration under boreal conditions. *Tree Physiology* **22**: 963–972.
- Roden, J.S., Egerton, J.J.G., and Ball, M.C. 1999. Effect of elevated [CO₂] on photosynthesis and growth of snow gum (*Eucalyptus pauciflora*) seedlings during winter and spring. *Australian Journal of Plant Physiology* **26**: 37–46.
- Royer, D.L. 2010. Fossil soils constrain ancient climate sensitivity. *Proceedings of the National Academy of Sciences, USA* **107**: 517–518.
- Sage, R.F. and Kubien, D.S. 2007. The temperature response of C₃ and C₄ photosynthesis. *Plant, Cell and Environment* **30**: 1086–1106.
- Sallas, L., Luomala, E.-M., Utriainen, J., Kainulainen, P., and Holopainen, J.K. 2003. Contrasting effects of elevated carbon dioxide concentration and temperature on Rubisco activity, chlorophyll fluorescence, needle ultrastructure and secondary metabolites in conifer seedlings. *Tree Physiology* **23**: 97–108.

- Shao, X.M., Huang, L., Liu, H.B., Liang, E.Y., Fang, X.Q., and Wang, L.L. 2005. Reconstructions of precipitation variation from tree-rings in recent 1000 years in Delingha, Qinghai. *Science in China (Series D)* **48**: 939–949.
- Sheu, B.-H. and Lin, C.-K. 1999. Photosynthetic response of seedlings of the sub-tropical tree *Schima superba* with exposure to elevated carbon dioxide and temperature. *Environmental and Experimental Botany* **41**: 57–65.
- Smith, B., Prentice, I.C., and Sykes, M.T. 2001. Representation of vegetation dynamics in the modeling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Global Ecology & Biogeography* **10**: 621–637.
- Stoskopf, N. 1981. *Understanding Crop Production*. Prentice-Hall, Upper Saddle River, New Jersey, USA.
- Stuhlfauth, T. and Fock, H.P. 1990. Effect of whole season CO₂ enrichment on the cultivation of a medicinal plant, *Digitalis lanata*. *Journal of Agronomy and Crop Science* **164**: 168–173.
- Teskey, R.O. 1997. Combined effects of elevated CO₂ and air temperature on carbon assimilation of *Pinus taeda* trees. *Plant, Cell and Environment* **20**: 373–380.
- Tewksbury, J.J., Huey, R.B., and Deutsch, C.A. 2008. Putting the heat on tropical animals. *Science* **320**: 1296–1297.
- Tissue, D.T., Thomas, R.B., and Strain, B.R. 1997. Atmospheric CO₂ enrichment increases growth and photosynthesis of *Pinus taeda*: a 4-year experiment in the field. *Plant, Cell and Environment* **20**: 1123–1134.
- Tjoelker, M.G., Oleksyn, J., and Reich, P.B. 1998a. Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO₂ and temperature. *Tree Physiology* **18**: 715–726.
- Tjoelker, M.G., Oleksyn, J., and Reich, P.B. 1998b. Temperature and ontogeny mediate growth response to elevated CO₂ in seedlings of five boreal tree species. *New Phytologist* **140**: 197–210.
- Turnbull, M.H., Murthy, R., and Griffin, K.L. 2002. The relative impacts of daytime and night-time warming on photosynthetic capacity in *Populus deltoides*. *Plant, Cell and Environment* **25**: 1729–1737.
- Turnbull, M.H., Tissue, D.T., Murthy, R., Wang, X., Sparrow, A.D., and Griffin, K.L. 2004. Nocturnal warming increases photosynthesis at elevated CO₂ partial pressure in *Populus deltoides*. *New Phytologist* **161**: 819–826.
- Usami, T., Lee, J., and Oikawa, T. 2001. Interactive effects of increased temperature and CO₂ on the growth of *Quercus myrsinaefolia* saplings. *Plant, Cell and Environment* **24**: 1007–1019.
- van der Meer, P.J., Jorritsma, I.T.M., and Kramer, J.K. 2002. Assessing climate change effects on long-term forest development: adjusting growth, phenology and seed production in a gap model. *Forest Ecology and Management* **162**: 39–52.
- Veteli, T.O., Mattson, W.J., Niemela, P., Julkunen-Tiitto, R., Kellomaki, S., Kuokkanen, K., and Lavola, A. 2007. Do elevated temperature and CO₂ generally have counteracting effects on phenolic phytochemistry of boreal trees? *Journal of Chemical Ecology* **33**: 287–296.
- Way, D.A. and Oren, R. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology* **30**: 669–688.
- Wayne, P.M., Reekie, E.G., and Bazzaz, F.A. 1998. Elevated CO₂ ameliorates birch response to high temperature and frost stress: implications for modeling climate-induced geographic range shifts. *Oecologia* **114**: 335–342.
- Wertin, T.M., McGuire, M.A., and Teskey, R.O. 2010. The influence of elevated temperature, elevated atmospheric CO₂ concentration and water stress on net photosynthesis of loblolly pine (*Pinus taeda* L.) at northern, central and southern sites in its native range. *Global Change Biology* **16**: 2089–2103.
- Wertin, T.M., McGuire, M.A., van Iersel, M., Ruter, J.M., and Teskey, R.O. 2012. Effects of elevated temperature and [CO₂] on photosynthesis, leaf respiration, and biomass accumulation of *Pinus taeda* seedlings at a cool and a warm site within the species' current range. *Canadian Journal of Forest Research* **42**: 943–957.
- Westerhold, T., Rohl, U., McCarren, H.K., and Zachos, J.C. 2009. Latest on the absolute age of the Paleocene-Eocene Thermal Maximum (PETM): New insights from exact stratigraphic position of key ash layers + 19 and - 17. *Earth and Planetary Science Letters* **287**: 412–419.
- Zachos, J.C., Wara, M.W., Bohaty, S., Delaney, M.L., Petrizzo, M.R., Brill, A., Bralower, T.J., and Premoli-Silva, I. 2003. A transient rise in tropical sea surface temperature during the Paleocene-Eocene Thermal Maximum. *Science* **302**: 1551–1554.
- Zeebe, R.E., Zachos, J.C., and Dickens, G.R. 2009. Carbon dioxide forcing alone insufficient to explain Palaeocene-Eocene Thermal Maximum warming. *Nature Geoscience* **2**: 576–580.
- Zhang, Q.B., Cheng, G.D., Yao, T.D., Kang, X.C., and Huang, J.G. 2003. A 2,326-year tree-ring record of climate variability on the northeastern Qinghai-Tibetan Plateau. *Geophysical Research Letters* **30**: 10.1029/2003GL017425.
- Zhang, Q.B. and Qiu, H.Y. 2007. A millennium-long tree-

ring chronology of *Sabina przewalskii* on northeastern Qinghai-Tibetan Plateau. *Dendrochronologia* **24**: 91–95.

3.14 UV-B Radiation Stress

- The rise in the air's CO₂ content is a powerful antidote to the deleterious biological impacts that might be caused by an increase in the flux of UV-B radiation at the surface of Earth due to depletion of the planet's stratospheric ozone layer.

Zhao *et al.* (2004) state “as a result of stratospheric ozone depletion, UV-B radiation (280–320 nm) levels are still high at the Earth's surface and are projected to increase in the near future (Madronich *et al.*, 1998; McKenzie *et al.*, 2003),” noting, “increased levels of UV-B radiation are known to affect plant growth, development and physiological processes (Dai *et al.*, 1992; Nogues *et al.*, 1999).” High UV-B levels often result in “inhibition of photosynthesis, degradation of protein and DNA, and increased oxidative stress (Jordan *et al.*, 1992; Stapleton, 1992).” In light of these observations, it is only natural to wonder how the rise in the air's CO₂ content might affect the deleterious effects of UV-B radiation on vegetation.

Zhao *et al.* grew well-watered and -fertilized cotton plants in sunlit controlled-environment chambers maintained at atmospheric CO₂ concentrations of 360 or 720 ppm from emergence until three weeks past first-flower stage under three levels of UV-B radiation (0, 8, and 16 kJ m⁻² d⁻¹). On five dates between 21 and 62 days after emergence, they measured a number of plant physiological processes and parameters. Over the course of the experiment, the mean net photosynthetic rate of the upper-canopy leaves in the CO₂-enriched chambers was increased relative to that in the ambient-air chambers by 38.3% in the low UV-B treatment (from 30.3 to 41.9 m m⁻² s⁻¹), 41.1% in the medium UV-B treatment (from 28.7 to 40.5 m m⁻² s⁻¹), and 51.5% in the high UV-B treatment (from 17.1 to 25.9 m m⁻² s⁻¹).

In the medium UV-B treatment, the growth stimulation from the elevated CO₂ was sufficient to raise net photosynthesis rates 33.7% above the rates experienced in the ambient air and no UV-B treatment (from 30.3 to 40.5 m m⁻² s⁻¹). In the high UV-B treatment, however, the radiation damage was so great the 51.5% increase in net photosynthesis provided by the doubled-CO₂ air could not prevent the destruction, and the mean net photosynthesis rate of the cotton leaves was 14.5% less than in the

ambient air and no UV-B treatment (dropping from 30.3 to 25.9 m m⁻² s⁻¹).

The medium UV-B treatment of this study was chosen to represent the intensity of UV-B radiation presently received on a clear summer day in the major cotton production region of Mississippi (USA) under current stratospheric ozone conditions, and the high UV-B treatment was chosen to represent what might be expected there following a 30% depletion of the ozone layer, which has been predicted to double the region's reception of UV-B radiation from 8 to 16 kJ m⁻² d⁻¹. Thus doubling the current CO₂ concentration and current UV-B radiation level would reduce the net photosynthetic rate of cotton leaves by just under 10% (from 28.7 to 25.9 m m⁻² s⁻¹), whereas in the absence of a doubling of the air's CO₂ content, a doubling of the UV-B radiation level would reduce cotton net photosynthesis by just over 40% (from 28.7 to 17.1 m m⁻² s⁻¹). Doubling the current atmospheric CO₂ concentration thus would compensate for more than three-fourths of the loss of cotton photosynthetic capacity caused by a doubling of the current UV-B radiation intensity. And it might do even better than that: Zhao *et al.* (2003) reported both Adamse and Britz (1992) and Rozema *et al.* (1997) found a doubling of CO₂ fully compensated for the negative effects of equally high UV-B radiation.

Deckmyn *et al.* (2001) grew white clover plants for four months in four small greenhouses, in two of which they allowed 88% of the incoming UV-B radiation to pass through the roofs and walls and two of which allowed 82% to pass through. They maintained one of the two greenhouses in each of the UV-B treatments at ambient CO₂ (371 ppm) and the other at elevated CO₂ (521 ppm). At the midseason point of their study, the 40% increase in atmospheric CO₂ concentration stimulated the production of flowers in the low UV-B treatment by 22% and in the slightly higher UV-B treatment by 43%. At the end of the season, the extra CO₂ provided no stimulation of biomass production in the low UV-B treatment but stimulated biomass production by 16% in the high UV-B treatment.

The results of this study indicate the positive effects of atmospheric CO₂ enrichment on flower and biomass production in white clover are greater at more realistic or natural values of UV-B radiation than those found in many greenhouses. Deckmyn *et al.* state their results “clearly indicate the importance of using UV-B transmittant greenhouses or open-top chambers when conducting CO₂ studies,” lest the results obtained significantly underestimate the

magnitude of the benefits provided by the rise in the air's CO₂ content.

Qaderi and Reid (2005) grew well-watered and well-fertilized canola plants (*Brassica napus*) from seed to maturity in pots in controlled-environment chambers maintained at either 370 or 740 ppm CO₂ with and without a daily dose of UV-B radiation in the amount of 4.2 kJ m⁻², measuring a number of plant parameters at various times throughout the growing season. The final seed yield was 0.98 g/plant in the control treatment (ambient CO₂, with UV-B). Doubling the CO₂ concentration increased yield by 25.5% to 1.23 g/plant, and removing the UV-B radiation flux increased yield by 91.8% to 1.88 g/plant. Doing both (doubling the CO₂ concentration while simultaneously removing the UV-B flux) increased final seed yield by 175.5% to 2.7 g/plant. Hence, doubling the air's CO₂ concentration in the presence of the UV-B radiation flux enhanced final seed yield by 25.5%, and doubling CO₂ in the absence of the UV-B radiation flux increased seed yield by 43.6%. Qaderi and Reid conclude, "elevated CO₂ may have a positive effect on plants by mitigating the detrimental effects caused by UV-B radiation."

In a follow-up paper, Qaderi *et al.* (2007) examined the effects of elevated CO₂ and UVB radiation on the photosynthetic rates and water use efficiency of the maturing husks (siliques) that surround the canola plant's seeds. For the plants exposed to 4.2 kJ m⁻² d⁻¹ of UVB radiation, the experimental doubling of the air's CO₂ concentration led to a 29% increase in silique net photosynthesis, an 18% decrease in silique transpiration, and a 58% increase in silique water use efficiency. For the plants exposed to no UVB radiation, silique net photosynthesis was increased by 38%, transpiration was decreased by 22%, and water use efficiency was increased by 87% in the CO₂-enriched air.

Tohidimoghadam *et al.* (2011) grew two varieties (Okapi and Talaye) of canola out-of-doors over the 2008 and 2009 growing seasons beneath rigid frames covered with polyethylene plastic film in air maintained at ambient and elevated atmospheric CO₂ concentrations of 400 and 900 ppm, at ambient and elevated levels of UV radiation, and under well-watered and deficit-watered conditions, measuring numerous plant properties during and after the growing period. They found "water stress significantly decreased yield and yield components, oil yield, protein percentage, height, specific leaf area and the number of branches." Elevated CO₂

"increased the final yield, 1000-seed weight, oil percentage, oil yield, height, specific leaf area and number of branches." UV radiation "decreased the yield, yield components, oil and protein percentages and growth parameters." They also note "the highest seed weight was obtained from the 'Talaye' cultivar treated with compete irrigation and elevated CO₂ and grown under sunlight radiation," whereas "the seed weights of both cultivars visibly decreased due to UV-B, UV-C and water stress under an ambient CO₂ concentration." The three Iranian researchers who conducted the study state, "an increase in UV exposure decreases plant growth and development," but "elevated CO₂ ameliorate(s) the adverse effects of UV radiation in the final yield, seed weight, oil percentage, oil yield, plant height, specific leaf area and number of branches per plant." They conclude an increase in the atmosphere's CO₂ concentration "could improve yield, yield components and growth parameters for plants subjected to elevated levels of UV radiation."

In a study of UV-B and CO₂ effects on a natural ecosystem, conducted at the Abisko Scientific Research Station in Swedish Lapland, Johnson *et al.* (2002) studied plots of subarctic heath composed of open canopies of downy birch and dense dwarf-shrub layers containing herbs and grasses. For five years, they exposed the plots to factorial combinations of UV-B radiation (ambient and that expected to result from a 15% stratospheric ozone depletion) and atmospheric CO₂ concentration (ambient, around 365 ppm, and enriched, around 600 ppm), after which they determined the amounts of microbial carbon (C_{mic}) and nitrogen (N_{mic}) in the soils of the plots.

When the plots were exposed to the enhanced UV-B radiation, the amount of C_{mic} in the soil was reduced to only 37% of what it was at the ambient UV-B level when the air's CO₂ content was maintained at the ambient concentration. When the UV-B increase was accompanied by the CO₂ increase, however, there was no decrease in C_{mic} but an increase of 37%. When the plots were exposed to the enhanced level of UV-B radiation, the amount of N_{mic} in the soil showed a 69% increase when the air's CO₂ content was maintained at the ambient concentration, and when the UV-B increase was accompanied by the CO₂ increase, N_{mic} rose by 138%.

These findings, Johnson *et al.* write, "may have far-reaching implications ... because the productivity of many semi-natural ecosystems is limited by N (Ellenberg, 1988)." Thus, the 138% increase in soil microbial N observed in this study to accompany a

15% reduction in stratospheric ozone and a 64% increase in atmospheric CO₂ concentration should significantly enhance the input of plant litter to the soils of these ecosystems, which represents the first half of the carbon sequestration process—the carbon input stage.

As to the second stage—keeping as much of that carbon as possible in the soil—Johnson *et al.* note “the capacity for subarctic semi-natural heaths to act as major sinks for fossil fuel-derived carbon dioxide is [also] likely to be critically dependent on the supply of N,” as indicated in the literature review of Berg and Matzner (1997). The latter report the presence of additional nitrogen in the soil significantly enhances the long-term storage of carbon, as more litter is chemically transformed into humic substances when nitrogen is more readily available, and these more recalcitrant carbon compounds can be successfully stored in the soil for many millennia.

Koti *et al.* (2007) investigated the interactive effects of elevated atmospheric CO₂ (720 vs. 360 ppm), UV-B radiation levels (0 vs. 10 kJ/m²/day), and temperature (38/30°C vs. 30/22°C day/night) on the growth and development of six well-watered and well-fertilized soybean (*Glycine max* L.) genotypes. They found “elevated CO₂ partially compensated [for] the damaging effects on vegetative growth and physiology caused by negative stressors such as high temperatures and enhanced UV-B radiation levels in soybean.” The authors note CO₂’s positive influence on plant height, leaf area, total biomass, net photosynthesis, total chlorophyll content, phenolic content, and wax content, as well as relative plant injury. Thus, with respect to almost all of the ways high air temperatures and high UV-B radiation levels retard the growth and development of soybeans, elevated atmospheric CO₂ concentrations appear to provide significant ameliorative relief.

Estiarte *et al.* (1999) grew spring wheat in FACE plots in Arizona (USA) at atmospheric CO₂ concentrations of 370 and 550 ppm and two levels of soil moisture (50 and 100% of potential evapotranspiration). Under those conditions, leaves of plants growing in elevated CO₂ had 14% higher total flavonoid concentrations than those of plants grown in ambient air, and soil water content did not affect the relationship. One of the functions of flavonoids in plant leaves is to protect them against UV-B radiation. Hence, more studies of this nature should be conducted to see how general this beneficial response may be throughout the plant world.

These findings indicate the rise in the air’s CO₂

content is a powerful counterbalance against the deleterious biological impacts that could be caused by an increase in the flux of UV-B radiation at the surface of Earth due to depletion of the planet’s stratospheric ozone layer.

References

- Adamse, P. and Britz, S.J. 1992. Amelioration of UV-B damage under high irradiance. I. Role of photosynthesis. *Photochemistry and Photobiology* **56**: 645–650.
- Berg, B. and Matzner, E. 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest ecosystems. *Environmental Reviews* **5**: 1–25.
- Dai, Q., Coronal, V.P., Vergara, B.S., Barnes, P.W., and Quintos, A.T. 1992. Ultraviolet-B radiation effects on growth and physiology of four rice cultivars. *Crop Science* **32**: 1269–1274.
- Deckmyn, G., Caeyenberghs, E., and Ceulemans, R. 2001. Reduced UV-B in greenhouses decreases white clover response to enhanced CO₂. *Environmental and Experimental Botany* **46**: 109–117.
- Ellenberg, H. 1988. *Vegetation Ecology of Central Europe*. Cambridge University Press, Cambridge, UK.
- Estiarte, M., Peñuelas, J., Kimball, B.A., Hendrix, D.L., Pinter Jr., P.J., Wall, G.W., LaMorte, R.L., and Hunsaker, D.J. 1999. Free-air CO₂ enrichment of wheat: leaf flavonoid concentration throughout the growth cycle. *Physiologia Plantarum* **105**: 423–433.
- Johnson, D., Campbell, C.D., Lee, J.A., Callaghan, T.V., and Gwynn-Jones, D. 2002. Arctic microorganisms respond more to elevated UV-B radiation than CO₂. *Nature* **416**: 82–83.
- Jordan, B.R., Chow, W.S., and Anderson, J.M. 1992. Changes in mRNA levels and polypeptide subunits of ribulose 1,5-bisphosphate carboxylase in response to supplementary ultraviolet-B radiation. *Plant, Cell and Environment* **15**: 91–98.
- Koti, S., Reddy, K.R., Kakani, V.G., Zhao, D., and Gao, W. 2007. Effects of carbon dioxide, temperature and ultraviolet-B radiation and their interactions on soybean (*Glycine max* L.) growth and development. *Environmental and Experimental Botany* **60**: 1–10.
- Madronich, S., McKenzie, R.L., Bjorn, L.O., and Caldwell, M.M. 1998. Changes in biologically active ultraviolet radiation reaching the Earth’s surface. *Journal of Photochemistry and Photobiology B: Biology* **46**: 5–19.
- McKenzie, R.L., Bjorn, L.O., Bais, A., and Ilyasd, M. 2003. Changes in biologically active ultraviolet radiation

reaching the Earth's surface. *Photochemical and Photobiological Sciences* **2**: 5–15.

Nogues, S., Allen, D.J., Morison, J.I.L., and Baker, N.R. 1999. Characterization of stomatal closure caused by ultraviolet-B radiation. *Plant Physiology* **121**: 489–496.

Qaderi, M.M. and Reid, D.M. 2005. Growth and physiological responses of canola (*Brassica napus*) to UV-B and CO₂ under controlled environment conditions. *Physiologia Plantarum* **125**: 247–259.

Qaderi, M.M., Reid, D.M., and Yeung, E.C. 2007. Morphological and physiological responses of canola (*Brassica napus*) siliques and seeds to UVB and CO₂ under controlled environment conditions. *Environmental and Experimental Botany* **60**: 428–437.

Rozema, J., Lenssen, G.M., Staaij, J.W.M., Tosserams, M., Visser, A.J., and Brockman, R.A. 1997. Effects of UV-B radiation on terrestrial plants and ecosystems: interaction with CO₂ enrichment. *Plant Ecology* **128**: 182–191.

Stapleton, A.E. 1992. Ultraviolet radiation and plants: Burning questions. *The Plant Cell* **105**: 881–889.

Tohidimoghadam, H.R., Ghooshchi, F., and Zahedi, H. 2011. Effect of UV radiation and elevated CO₂ on morphological traits, yield and yield components of canola (*Brassica napus* L.) grown under water deficit. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* **39**: 213–219.

Zhao, D., Reddy, K.R., Kakani, V.G., Mohammed, A.R., Read, J.J., and Gao, W. 2004. Leaf and canopy photosynthetic characteristics of cotton (*Gossypium hirsutum*) under elevated CO₂ concentration and UV-B radiation. *Journal of Plant Physiology* **161**: 581–590.

Zhao, D., Reddy, K.R., Kakani, V.G., Read, J.J., and Sullivan, J.H. 2003. Growth and physiological responses of cotton (*Gossypium hirsutum* L.) to elevated carbon dioxide and ultraviolet-B radiation under controlled environmental conditions. *Plant, Cell and Environment* **26**: 771–782.

3.15 Water Stress

As the CO₂ content of the air rises, nearly all plants will exhibit increases in photosynthesis and biomass production, but some researchers claim water stress will negate these benefits. This section examines the results of several CO₂-enrichment studies designed to show the net effect of elevated CO₂ and water stress on the growth of Earth's vegetation.

3.15.1 Agricultural Crops

- The rise in the atmosphere's CO₂ content likely will lead to substantial increases in the photosynthetic rates and biomass production of the world's chief agricultural crops, even in stressful situations imposed by less-than-optimum soil moisture.

As the air's CO₂ content rises, nearly all plants will exhibit increases in photosynthesis and biomass production, but some researchers claim elevated concentrations of atmospheric CO₂ will lead to more droughty conditions in many parts of the world and thereby significantly reduce or totally negate these CO₂-induced benefits. This section reviews the results of numerous studies that show atmospheric CO₂ enrichment may help important food crops cope with periods of less-than-optimal water availability.

One way atmospheric CO₂ enrichment helps plants in this regard is by stimulating them to develop larger-than-usual and more robust root systems that enable them to probe greater volumes of soil for moisture. Wechsung *et al.* (1999), for example, observed a 70% increase in lateral root dry weights of water-stressed wheat grown at 550 ppm CO₂, and De Luis *et al.* (1999) reported a 269% increase in root-to-shoot ratio of water-stressed alfalfa growing at 700 ppm CO₂. Thus, elevated CO₂ may often elicit stronger-than-usual positive root responses in agricultural species under conditions of water stress.

Elevated levels of atmospheric CO₂ also tend to reduce the openness of stomatal pores on leaves, thus decreasing plant stomatal conductance. This phenomenon, in turn, reduces the amount of water lost to the atmosphere by transpiration and, consequently, lowers overall plant water use. Serraj *et al.* (1999), for example, reported water-stressed soybeans grown at 700 ppm CO₂ reduced their total seasonal water loss by 10% relative to water-stressed control plants grown at 360 ppm CO₂. And Conley *et al.* (2001) found a 200 ppm increase in the air's CO₂ concentration reduced cumulative evapotranspiration in water-stressed sorghum by about 4%.

Atmospheric CO₂ enrichment thus increases plant water acquisition by stimulating root growth, and it reduces plant water loss by constricting stomatal apertures. These two phenomena typically enhance plant water-use efficiency, even under conditions of less-than-optimal soil water content. They have other implications as well.

CO₂-induced increases in root development

together with CO₂-induced reductions in stomatal conductance often improve plant water status during times of drought. Sgherri *et al.* (1998), for example, found leaf water potential, which is a good indicator of overall plant water status, was 30% higher (less negative and therefore more favorable) in water-stressed alfalfa grown at an atmospheric CO₂ concentration of 600 ppm versus 340 ppm. Wall (2001) found leaf water potentials were similar in CO₂-enriched water-stressed plants and ambient-grown well-watered control plants, which implies a complete CO₂-induced amelioration of water stress in the CO₂-enriched plants. Lin and Wang (2002) demonstrated elevated CO₂ caused a several-day delay in the onset of the water stress-induced production of the highly reactive oxygenated compound H₂O₂ in spring wheat. Also, they found plants grown in elevated CO₂ maintained higher enzymatic activities of superoxide dismutase and catalase—two important antioxidants—relative to those observed in ambient-grown plants, following the induction of water stress.

If atmospheric CO₂ enrichment allows plants to maintain a better water status during times of water stress, it is only logical to surmise they would exhibit greater rates of photosynthesis than plants growing in similarly water-deficient soil in non-CO₂-enriched air. With the onset of experimentally induced water stress in India Mustard (*Brassica juncea*), Rabha and Upreti (1998) observed photosynthetic rates dropped by 40% in plants growing in ambient air, while plants growing in air containing 600 ppm CO₂ experienced only a 30% reduction in net photosynthesis. Ferris *et al.* (1998) imposed water-stress conditions on soybeans and allowed them to recover following complete rewetting of the soil, finding plants grown in air containing 700 ppm CO₂ reached pre-stressed rates of photosynthesis after six days, whereas plants grown in ambient air never recovered to pre-stressed photosynthetic rates.

Analogously, it is also to be expected that elevated CO₂ concentrations would enhance plant biomass production under drought conditions. Ferris *et al.* (1999) report water-stressed soybeans grown at 700 ppm CO₂ attained seed yields 24% greater than those of similarly water-stressed plants grown at ambient CO₂ concentrations, and Hudak *et al.* (1999) determined water stress had no detrimental effect on yield in CO₂-enriched spring wheat. Many studies have found the CO₂-induced biomass increase to be greater for water-stressed plants than for well-watered plants, as demonstrated in the review of the subject by

Idso and Idso (1994).

Li *et al.* (2000), reported a 180 ppm increase in the air's CO₂ content increased final grain weights in the upper and lower sections of the main stems of the spring wheat they studied by 10 and 24%, respectively, under water-stressed conditions, but under well-watered conditions elevated CO₂ increased final grain weights only in the lower sections of the main stems and by only 14%. Thus elevated CO₂ had a greater positive impact on final grain weights of spring wheat under water-stressed field conditions than in non-water-stressed field conditions, once again demonstrating atmospheric CO₂ enrichment is often more important to stressed plants than to non-stressed plants.

Similarly, spring wheat grown in air containing an additional 280 ppm CO₂ exhibited 57 and 40% increases in grain yield under water-stressed and well-watered conditions, respectively (Schutz and Fangmeier, 2001). Ottman *et al.* (2001) found elevated CO₂ increased plant biomass in water-stressed sorghum by 15%, but no biomass increase occurred in well-watered sorghum. In predicting maize and winter wheat yields in Bulgaria under future scenarios of increased air temperature and decreased precipitation, Alexandrov and Hoogenboom (2000) note yield losses were likely to occur if the air's CO₂ content remained unchanged, but if the atmospheric CO₂ concentration doubled, maize and winter wheat yields likely would increase, even under the combined stresses of elevated temperature and reduced rainfall.

Widodo *et al.* (2003) grew rice (*Oryza sativa* [L.] cv. IR-72) in eight outdoor, sunlit, controlled-environment chambers at daytime atmospheric CO₂ concentrations of 350 and 700 ppm for an entire season. In one pair of chambers the plants were continuously flooded, in a second pair drought stress was imposed during panicle initiation, in a third pair it was imposed during anthesis, and in a fourth pair it was imposed at both stages. In the elevated CO₂ treatment, midday leaf photosynthetic CO₂ exchange rates (CER) and chlorophyll concentrations were higher at most sampling dates. In addition, the CO₂-enriched plants exhibited enhanced midday leaf sucrose and starch accumulation during early reproductive phases.

Near the end of the imposed drought periods, water deficits caused substantial decreases in midday leaf CER and chlorophyll concentrations, along with concomitant reductions in the primary products of photosynthesis. These drought-induced effects,

Widodo *et al.* note, “were more severe for plants grown at ambient than at elevated CO₂.” They report, for example, “plants grown under elevated CO₂ were able to maintain midday leaf photosynthesis, and to some extent other photosynthetic-related parameters, longer into the drought period than plants grown at ambient CO₂,” as also has been observed for a number of other plants (Rogers *et al.*, 1984; Jones *et al.*, 1985; Idso, 1988; Bhattacharya *et al.*, 1990; Chaves and Pereira, 1992; Clifford *et al.*, 1993; Baker *et al.*, 1997; Vu *et al.*, 1998).

Recovery from drought-induced water stress was more rapid in the elevated CO₂ treatment. At panicle initiation, for example, Widodo *et al.* write, “as water was added back following a drought induction, it took more than 24 days for the ambient CO₂-[water] stressed plants to recuperate in midday leaf CER, compared with only 6–8 days for the elevated CO₂-[water] stressed plants.” Similarly, they note, “for the drought imposed during anthesis, midday leaf CER of the elevated CO₂-[water] stressed plants was fully recovered after 16 days of re-watering, whereas those of the ambient CO₂-[water] stressed plants were still 21% lagging behind their unstressed controls at that date.” The five researchers conclude, “rice grown under future rising atmospheric CO₂ should be better able to tolerate drought situations.”

Triggs *et al.* (2004) grew sorghum (*Sorghum bicolor* (L.) Moench, a C₄ grain crop) for two full seasons in control CO₂ plots (about 370 ppm) and FACE plots (Control + 200 ppm) under both well-watered (Wet) and water-stressed (Dry, less than half the total water received by the Wet treatment via rainfall and irrigation) conditions near Maricopa, Arizona (USA). They assessed evapotranspiration (ET) on a continuous basis by means of micro-meteorological measurements designed to allow the calculation of all the other elements (net radiation, sensible heat flux, and soil surface heat flux) of the energy balance of the crop-soil interface with the atmosphere. Sorghum water use efficiency (WUE) was calculated using final grain yield data obtained by Ottman *et al.* (2001).

Triggs *et al.* write, “in the Wet treatments, a reduction in ET of about 19%, combined with only a slight increase in total biomass (+4%), resulted in a 28% increase in WUE in elevated CO₂ conditions,” whereas “in the Dry treatments, the relatively large increase in total biomass (+16% for both years) more than compensated for the approximate 5% increase in total ET, giving the FACE-Dry treatments an increase in WUE of 16% over both seasons.” They conclude,

“even if future climate change results in less water available for agriculture, higher atmospheric CO₂ concentrations will still benefit C₄ crops,” although “in regions with ample precipitation or irrigation, C₃ crops with higher growth responses may be preferable.”

Kaddour and Fuller (2004) grew three commercial cultivars of durum wheat (*Triticum durum* Desf.) registered in Syria (Cham 1, Cham 3, and Cham 5) from seed in 10-liter pots in different compartments of a phytotron. Half of the compartments were maintained at an atmospheric CO₂ concentration of approximately 400 ppm and half were maintained at a concentration of approximately 1,000 ppm. Half of each of these treatments were further subdivided into two soil water treatments: well-watered, where available water content (AWC) was replenished to 90% of full capacity when it dropped to 60%, and water-stressed, where AWC was replenished to 70% of full capacity when it dropped to 45%. Averaged over the three cultivars, the extra 600 ppm of CO₂ supplied to the CO₂-enriched compartments led to total plant biomass increases of 62% in the well-watered treatment and 60% in the water-stressed treatment. The extra CO₂ also led to increases in the nitrogen concentrations of stems and ears. Nitrogen concentration of the ears was increased by 22% in the well-watered plants and by 16% in the water-stressed plants.

Kaddour and Fuller write their results “have important implications for the production of durum wheat in the future.” They state “yields can be expected to rise as atmospheric CO₂ levels rise,” and “this increase in yield can be expected under both water restricted and well irrigated conditions.” Therefore, “where water availability is a prime limiting economic resource, it can be distributed more effectively under higher CO₂ conditions,” and “for countries such as Syria where average national production is well below the physiological maximum due largely to drought stress, the predicted rise in atmospheric CO₂ could have a positive effect on production.”

Richter and Semenov (2005) note, “with global warming, evapotranspiration is likely to increase and, with more variable rainfall, droughts could occur more often.” They evaluated the impact of potential climate change on drought indicators and yields of winter wheat in England and Wales using a crop simulation model (*Sirius*) that also incorporates the effects of elevated atmospheric CO₂ concentration and temperature on crop growth and development,

where the CO₂ scenario driving the model was of medium to high anthropogenic emissions that raise the air's CO₂ concentration from 334 ppm (the 1961–1990 baseline) to 554 ppm in the 2050s. Probability distributions derived from multiple simulations using representative weather, soil types, and sowing dates indicate maximum soil moisture deficit “is likely to increase in the future, especially on shallow soils, and the probability of potential yield reductions exceeding 25% will increase by 10% until the 2050s.” Nevertheless, they write, “average wheat yields are likely to increase by 1.2 to 2 t/ha (15–23%) by the 2050s because of a CO₂-related increase in radiation use efficiency.”

Bernacchi *et al.* (2006) grew soybeans (*Glycine max* (L.) Merr.) for three years at the SoyFACE facility of the University of Illinois at Urbana-Champaign, Illinois (USA) at atmospheric CO₂ concentrations of either 375 or 550 ppm under natural field conditions with and without a 23% increase in ambient atmospheric ozone concentration, measuring a number of weather and plant physiological parameters from pre-dawn to post-dusk on several days during the three growing seasons. They determined the mean daily integral of leaf-level net photosynthesis (A) was enhanced by nearly 25% in the CO₂-enriched air under ambient ozone concentrations, but by a slightly smaller 20% in the high-ozone air. In addition, “there was a strong positive correlation between daytime maximum temperatures and mean daily integrated A at elevated CO₂.” From their graphical depiction of this relationship, it appears at a daily maximum temperature of approximately 26.5°C, A was stimulated by about 14%, and at a daily maximum temperature of approximately 34.5°C, it was stimulated by about 35%. The 11 researchers report “the effect of elevated CO₂ on photosynthesis tended to be greater under water stress conditions,” rising from an approximate 17% enhancement of A at the most favorable soil moisture condition encountered to an enhancement close to 30% under the driest of the conditions experienced by the crop.

Robredo *et al.* (2007) grew well-watered and well-fertilized barley (*Hordeum vulgare* L.) seedlings (seven per each 2.5-liter pot filled with perlite and vermiculite) in controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 350 or 700 ppm. At the conclusion of the 18th day after seedling emergence, the treatments were split, with one continuing to be watered three times a week and the other treatment receiving no further

water. At that time and on several following dates, researchers measured a number of soil and plant water parameters, along with rates of leaf transpiration and net photosynthesis. They found “during the period of drought, elevated CO₂ delayed by 3–4 days the depletion of soil water content,” because of “the lower rates of transpiration in plants grown under CO₂ enrichment.” As a result, “under elevated CO₂, plant water stress developed more slowly,” thanks to “a slower rate of soil water depletion.” They report “the stimulation of carbon assimilation by elevated CO₂ was even greater in droughted compared to well-watered plants,” even though “elevated CO₂ caused stomata closure.”

The seven Spanish researchers write, “exposure to high carbon dioxide concentration resulted in an increase in photosynthesis and in a reduction in whole plant transpiration, contributing to an increase in water use efficiency that was more noticeable when plants were subjected to elevated CO₂ in conjunction with drought.” They conclude, “growing plants under [an] elevated CO₂ environment mitigates or delays the effects of water stress in barley.”

Li *et al.* (2007) employed open-top chambers to determine net ecosystem CO₂ exchange (NEE) before, during, and after the severe Central Florida drought of 1998 in a scrub-oak ecosystem in ambient-CO₂ (AC) air and in elevated-CO₂ (EC) air enriched with an extra 350 ppm of CO₂ since May 1996. They focused on the ecosystem's dominant species (*Quercus myrtifolia* Willd.), for which they measured net photosynthetic rate (PN) throughout the daylight hours of several days. They found EC air generally increased PN, whereas drought decreased it. Under droughty conditions, PN peaked at around 0830 each day, after which it declined in a fairly steady fashion until solar noon and typically remained at a relatively low level throughout the remainder of the daylight hours. The scientists assessed the interactive impacts of elevated CO₂ and drought on tree PN by comparing the percentage reduction in PN from 0830 to 1230 in the two CO₂ treatments. They found in May 1998, PN was reduced by 77% from 0830 to 1230 at AC but by only 48% at EC, and in July 1998, when the drought had further intensified, PN was reduced by 82% at AC but by a lesser 69% at EC.

NEE responded in much the same way. In May and June 1998, for example, NEE's midday depression was 58% and 60% less at EC than at AC, and in July 1999 it was 66% less. In addition, Li *et al.* note, “the mitigation of the effects of water stress by EC was reflected in the aboveground biomass

growth,” such that “the relative effect of EC on biomass accumulation of the dominant species *Q. myrtifolia* was higher during the drought year (210% for 1998) compared to the non-drought years (67% for 1997).”

Manderscheid and Weigel (2007) grew spring wheat (*Triticum aestivum* cv. Minaret) in open-top chambers on an experimental field of the Federal Agricultural Research Center in Braunschweig, Germany, in two growing seasons at either current or future (current + 280 ppm) atmospheric CO₂ concentrations and under sufficient-water-supply (WET) or drought-stress (DRY) conditions. They imposed the latter just after the crop first-node stage was reached (approximately 35 days after emergence), by halving the subsequent water supplied to the plants. The researchers found, “in both years, biomass and grain yield were decreased by drought and increased by CO₂ enrichment,” with the positive CO₂ effect being greater under drought conditions. Averaged over both years, “CO₂ enrichment increased biomass and grain yield under WET conditions by $\leq 10\%$ and under DRY conditions by $\geq 44\%$.” The CO₂-induced increase in crop water-use efficiency was 20% in the sufficient-water-supply treatment and 43% in the drought-stress treatment.

Veisz *et al.* (2008) grew seven cereal grain crops—winter barley (*Hordeum vulgare*, cv. Petra), winter wheat (*Triticum aestivum*, cvs. Libellula, Mv Regiment, Mv Mambo), winter durum wheat (*Triticum durum*, cv. Mv Makaroni), spring wheat (*Triticum aestivum*, cv. Lona), and spring oats (*Avena sativa*, cv. Mv Pehely)—in a phytotron at the Agricultural Research Institute of the Hungarian Academy of Sciences at ambient and enriched atmospheric CO₂ concentrations (380 and 750 ppm, respectively) under both well-watered and drought conditions. For the latter condition they withheld water beginning at the 10th day after heading, and soil volumetric water content dropped from approximately 25% to 6%. They measured a number of crop characteristics at harvest.

Under the experimental conditions, the plants grown in the CO₂-enriched air “produced more organic matter, being taller, with more spikes and a higher grain number per plant than those grown at the present CO₂ level,” and “thanks to the more intensive incorporation of carbohydrate, there was an increase in the mean grain mass and in the grain yield per plant” in the CO₂-enriched air. However, there was a concomitant decrease in the protein concentration of the grains produced in the high-CO₂ treatment.

Nevertheless, the net effect was positive because, for the several cereal varieties averaged together, grain yield under the well-watered conditions rose by 12.37% (from 2.83 to 3.18 g/plant) in response to atmospheric CO₂ enrichment, and grain protein concentration dropped from 17.04% to 16.23%, resulting in a net increase of 7% in total grain protein production. Likewise, grain yield under the water-stressed conditions rose by 30.68% (from 1.76 to 2.30 g/plant) in response to atmospheric CO₂ enrichment, and the concentration of the grain protein dropped from 21.63% to 19.70%, leading to a net increase of 19% in total grain protein production.

Chun *et al.* (2011) grew corn plants from seed in naturally sunlit soil-plant-atmosphere-research (SPAR) units in which temperature, humidity, and CO₂ concentration were precisely controlled, the latter at either 400 ppm (ambient) or 800 ppm (elevated), beginning 21 days after emergence (DAE). These units were placed atop soil bins (2.0 m long by 0.5 m wide by 1.0 m deep) filled with a mixture of 75% coarse sand and 25% vermiculate, where soil water contents were monitored hourly by a time domain reflectometry (TDR) system that consisted of 15 TDR probes per chamber placed in three rows at depths of 0, 15, 30, 50, and 75 cm from the soil surface. By means of this system of soil water content assessment, combined with nightly “fertilization,” Chun *et al.* were able to provide the plants with the nitrogen they needed while maintaining four soil water stress levels—control, mild, moderate, and severe—which were also initiated at 21 DAE. Thereafter, the height, number of leaves, leaf lengths, and growth states of the corn plants were determined twice weekly, and samples of the plants were collected, dried, and analyzed for biomass accumulation at 21 and 60 DAE (the beginning and end of the different CO₂ and soil water content treatments).

The five researchers did not find the elevated CO₂ treatment had a strong effect on plant height, leaf area, or above-ground biomass. But under both well-watered and water-stressed conditions, higher soil water contents were maintained in the elevated CO₂ treatment, even though 20–49% less water was applied to the soil of the elevated CO₂ treatment. The five researchers conclude, “under increased CO₂ concentrations as generally predicted in the future, less water will be required for corn plants than at present.”

Robredo *et al.* (2011) write, “barley, an economically important and extensively cultivated

cereal worldwide, increases its yield in parallel with an increase in CO₂,” but “responds to drought stress through altered nitrogen metabolism and reduced productivity.” They explored these complexities by growing barley (*Hordeum vulgare* L. cv. Iranis) seedlings in 2.5-L pots containing a 3:1 mix of perlite:vermiculite in a controlled-environment growth chamber, first at ambient and then at elevated atmospheric CO₂ concentrations (350 and 700 ppm, respectively). Initially, they watered the pots twice a week with a complete Hoagland solution and with deionized water between each Hoagland solution application. They initiated drought when the seedlings were 18 days old, withholding water for intervals of 9, 13, and 16 days. They analyzed the effects of these actions at the end of each drought period and analyzed water recovery three days after rewatering the 13-day droughted plants, with each complete experiment being replicated three times.

The six Spanish scientists state their barley plants showed a reduction in water use, even though under elevated CO₂ the plants had a larger leaf area, much as others also have found (Owensby *et al.*, 1997; Niklaus *et al.*, 1998). In addition, “during the period of drought, the depletion of soil water content was delayed by 3–4 days in plants grown under elevated CO₂ conditions,” and in the CO₂-enriched plants “water stress also developed more slowly than at ambient CO₂ because of a slower rate of water depletion.” They report, “leaf water potential in plants subjected to drought but grown at elevated CO₂ was less negative than in their ambient CO₂ grown counterparts.”

Robredo *et al.* also note “absolute values for nitrogen uptake by barley plants were higher under elevated CO₂ compared to ambient CO₂.” In addition, they “observed high nitrate reductase activity in plants grown at elevated CO₂, which should parallel an increase in photosynthesis (Robredo *et al.*, 2007) and sugar content (Perez-Lopez *et al.*, 2010).” Also, “under ambient CO₂ conditions, protein content decreased as the water stress progressed,” but “when plants grew under elevated CO₂ conditions, the rate of photosynthesis was higher [and] drought had less effect on the protein content.” They report the barley plants “showed a greater content of proteins under elevated CO₂,” in harmony with Geiger *et al.* (1999), who they say “reported a similar outcome in tobacco with the same supra-optimal nitrogen concentration.” They further remark these findings also mesh with the results of studies reviewed by Idso and Idso (2001), who conclude any negative effects of elevated CO₂ on

crop protein content “could be ameliorated by increased use of nitrogen fertilizer.” Robredo *et al.* conclude “elevated CO₂ mitigates many of the effects of drought on nitrogen metabolism and allows more rapid recovery following water stress.”

Tohidimoghadam *et al.* (2011) grew two varieties (Okapi and Talaye) of canola (*Brassica napus* L.) plants over the 2008 and 2009 growing seasons out-of-doors at 35°59'N, 50°75'E beneath rigid frames covered with polyethylene plastic film in air maintained at ambient and elevated atmospheric CO₂ concentrations of 400 and 900 ppm, at ambient and elevated levels of UV radiation, and under well-watered and deficit-watered conditions, during and after which periods they measured numerous plant properties. They found “water stress significantly decreased yield and yield components, oil yield, protein percentage, height, specific leaf area and the number of branches,” but elevated CO₂ “increased the final yield, 1000-seed weight, oil percentage, oil yield, height, specific leaf area and number of branches.” They also found elevated UV radiation “decreased the yield, yield components, oil and protein percentages and growth parameters,” but elevated CO₂ once again ameliorated “the adverse effects of UV radiation in the final yield, seed weight, oil percentage, oil yield, plant height, specific leaf area and number of branches per plant.”

Varga *et al.* (2012) write, “as well as damaging numerous physiological functions, abiotic stress [such as drought] also leads to higher concentrations of reactive oxygen species, which are present in nature in all plants, but which may damage cell components and disturb metabolic processes when present in larger quantities,” citing Omran (1980), Larson (1988), and Dat *et al.* (2000). They note, “many authors have demonstrated that the [atmosphere’s] CO₂ concentration has a substantial influence on the stress sensitivity of plants via changes in antioxidant enzyme activity,” citing Fernandez-Trujillo *et al.* (2007), Ali *et al.* (2008), and Varga and Bencze (2009).

In an experiment designed to explore this subject further, Varga *et al.* grew two varieties of winter wheat in phytotrons maintained at either 380 or 750 ppm CO₂, where the potted plants were watered daily and supplied with nutrient solution twice a week until the start of drought treatments. They induced drought in three phases—at first node appearance, heading, and grain filling—by completely withholding water for seven days, which ultimately dropped the volumetric soil water content in the pots

from 20–25% to 3–5%. These actions, the four Hungarian researchers report, led to “changes in enzyme activity” that “indicated that enhanced CO₂ concentration delayed the development of drought stress up to first node appearance, and stimulated antioxidant enzyme activity when drought occurred during ripening, thus reducing the unfavorable effects of [drought] stress.” They conclude the increases in the antioxidant enzymes they analyzed “may help to neutralize the reactive oxygen species induced by stress during various parts of the vegetation period,” and this phenomenon should help crops cope with extremes of moisture insufficiency.

These peer-reviewed, scientific studies of the effects of water insufficiency on the productivity of the world’s major agricultural crops strongly support the earlier work of Idso and Idso (1994), who concluded the rise in the air’s CO₂ content likely will lead to substantial increases in the photosynthetic rates and biomass production of the world’s major agricultural crops, even in less-than-optimum soil moisture conditions.

References

- Alexandrov, V.A. and Hoogenboom, G. 2000. The impact of climate variability and change on crop yield in Bulgaria. *Agricultural and Forest Meteorology* **104**: 315–327.
- Ali, M.B., Dewir, Y.H., Hahn, E., and Peak, K. 2008. Effect of carbon dioxide on antioxidant enzymes and ginsenoside production in root suspension cultures of *Panax ginseng*. *Environmental and Experimental Botany* **63**: 297–304.
- Baker, J.T., Allen Jr., L.H., Boote, K.J., and Pickering, N.B. 1997. Rice responses to drought under carbon dioxide enrichment. 2. Photosynthesis and evapotranspiration. *Global Change Biology* **3**: 129–138.
- Bernacchi, C.J., Leakey, A.D.B., Heady, L.E., Morgan, P.B., Dohleman, F.G., McGrath, J.M., Gillespie, K.M., Wittig, V.E., Rogers, A., Long, S.P., and Ort, D.R. 2006. Hourly and seasonal variation in photosynthesis and stomatal conductance of soybean grown at future CO₂ and ozone concentrations for 3 years under fully open-air field conditions. *Plant, Cell and Environment* 10.1111/j.1365-3040.2006.01581.x.
- Bhattacharya, N.C., Hileman, D.R., Ghosh, P.P., Musser, R.L., Bhattacharya, S., and Biswas, P.K. 1990. Interaction of enriched CO₂ and water stress on the physiology of and biomass production in sweet potato grown in open-top chambers. *Plant, Cell and Environment* **13**: 933–940.
- Chaves, M.M. and Pereira, J.S. 1992. Water stress, CO₂ and climate change. *Journal of Experimental Botany* **43**: 1131–1139.
- Chun, J.A., Wang, Q., Timlin, D., Fleisher, D., and Reddy, V.R. 2011. Effect of elevated carbon dioxide and water stress on gas exchange and water use efficiency in corn. *Agricultural and Forest Meteorology* **151**: 378–384.
- Clifford, S.C., Stronach, I.M., Mohamed, A.D., Azam-Ali, S.N., and Crout, N.M.J. 1993. The effects of elevated atmospheric carbon dioxide and water stress on light interception, dry matter production and yield in stands of groundnut (*Arachis hypogaea* L.). *Journal of Experimental Botany* **44**: 1763–1770.
- Conley, M.M., Kimball, B.A., Brooks, T.J., Pinter Jr., P.J., Hunsaker, D.J., Wall, G.W., Adams, N.R., LaMorte, R.L., Matthias, A.D., Thompson, T.L., Leavitt, S.W., Ottman, M.J., Cousins, A.B., and Triggs, J.M. 2001. CO₂ enrichment increases water-use efficiency in sorghum. *New Phytologist* **151**: 407–412.
- Dat, J., Vandenabeele, S., Vranova, A., Van Montagu, M., Inze, D., and Van Breusegem, F. 2000. Dual action of the active oxygen species during plant stress responses. *Cellular and Molecular Life Sciences* **57**: 779–995.
- De Luis, J., Irigoyen, J.J., and Sanchez-Diaz, M. 1999. Elevated CO₂ enhances plant growth in droughted N₂-fixing alfalfa without improving water stress. *Physiologia Plantarum* **107**: 84–89.
- Ferris, R., Wheeler, T.R., Ellis, R.H., and Hadley, P. 1999. Seed yield after environmental stress in soybean grown under elevated CO₂. *Crop Science* **39**: 710–718.
- Ferris, R., Wheeler, T.R., Hadley, P., and Ellis, R.H. 1998. Recovery of photosynthesis after environmental stress in soybean grown under elevated CO₂. *Crop Science* **38**: 948–955.
- Fernandez-Trujillo, J.P., Nock, J.F., and Watkins, C.B. 2007. Antioxidant enzyme activities in strawberry fruit exposed to high carbon dioxide atmospheres during cold storage. *Food Chemistry* **104**: 1425–1429.
- Geiger, M., Haake, V., Ludewig, F., Sonnewald, U., and Stitt, M. 1999. The nitrate and ammonium nitrate supply have a major influence on the response of photosynthesis, carbon metabolism, nitrogen metabolism, and growth to elevated carbon dioxide in tobacco. *Plant, Cell and Environment* **22**: 1177–1199.
- Hudak, C., Bender, J., Weigel, H.-J., and Miller, J. 1999. Interactive effects of elevated CO₂, O₃, and soil water deficit on spring wheat (*Triticum aestivum* L. cv. Nandu). *Agronomie* **19**: 677–687.
- Idso, K.E. and Idso, S.B. 1994. Plant responses to

Climate Change Reconsidered II: Biological Impacts

- atmospheric CO₂ enrichment in the face of environmental constraints: A review of the past 10 years' research. *Agricultural and Forest Meteorology* **69**: 153–203.
- Idso, S.B. 1988. Three phases of plant response to atmospheric CO₂ enrichment. *Plant Physiology* **87**: 5–7.
- Idso, S.B. and Idso, K.E. 2001. Effects of atmospheric CO₂ enrichment on plant constituents related to animal and human health. *Environmental and Experimental Botany* **45**: 179–199.
- Jones, P., Jones, J.W., and Allen Jr., L.H. 1985. Seasonal carbon and water balances of soybeans grown under stress treatments in sunlit chambers. *Transactions of the American Society of Agricultural Engineers* **28**: 2021–2028.
- Kaddour, A.A. and Fuller, M.P. 2004. The effect of elevated CO₂ and drought on the vegetative growth and development of durum wheat (*Triticum durum* Desf.) cultivars. *Cereal Research Communications* **32**: 225–232.
- Larson, R.A. 1988. The antioxidants of higher plants. *Phytochemistry* **27**: 969–978.
- Li, A.-G., Hou, Y.-S., Wall, G.W., Trent, A., Kimball, B.A., and Pinter Jr., P.J. 2000. Free-air CO₂ enrichment and drought stress effects on grain filling rate and duration in spring wheat. *Crop Science* **40**: 1263–1270.
- Li, J.H., Johnson, D.P., Dijkstra, P., Hungate, B.A., Hinkle, C.R., and Drake, B.G. 2007. Elevated CO₂ mitigates the adverse effects of drought on daytime net ecosystem CO₂ exchange and photosynthesis in a Florida scrub-oak ecosystem. *Photosynthetica* **45**: 51–58.
- Lin, J.-S. and Wang, G.-X. 2002. Doubled CO₂ could improve the drought tolerance better in sensitive cultivars than in tolerant cultivars in spring wheat. *Plant Science* **163**: 627–637.
- Manderscheid, R. and Weigel, H.-J. 2007. Drought stress effects on wheat are mitigated by atmospheric CO₂ enrichment. *Agronomy for Sustainable Development* **27**: 79–87.
- Niklaus, P.A., Spinnler, D., and Korner, C. 1998. Soil moisture dynamics of calcareous grassland under elevated CO₂. *Oecologia* **117**: 201–208.
- Omran, R.G. 1980. Peroxide levels and the activities of catalase, peroxidase and indoleacetic acid oxidase during and after chilling cucumber seedlings. *Plant Physiology* **65**: 407–408.
- Ottman, M.J., Kimball, B.A., Pinter Jr., P.J., Wall, G.W., Vanderlip, R.L., Leavitt, S.W., LaMorte, R.L., Matthias, A.D., and Brooks, T.J. 2001. Elevated CO₂ increases sorghum biomass under drought conditions. *New Phytologist* **150**: 261–273.
- Owensby, C.E., Ham, J.M., Knapp, A.K., Breemer, D., and Auen, L.M. 1997. Water vapor fluxes and their impact under elevated CO₂ in a C₄-tallgrass prairie. *Global Change Biology* **3**: 189–195.
- Perez-Lopez, U., Robredo, A., Lacuesta, M., Munoz-Rueda, A., and Mena-Petite, A. 2010. Atmospheric CO₂ concentration influences the contributions of osmolyte accumulation and cell wall elasticity to salt tolerance in barley cultivars. *Journal of Plant Physiology* **167**: 15–22.
- Rabha, B.K. and Upreti, D.C. 1998. Effects of elevated CO₂ and moisture stress on *Brassica juncea*. *Photosynthetica* **35**: 597–602.
- Richter, G.M. and Semenov, M.A. 2005. Modeling impacts of climate change on wheat yields in England and Wales: assessing drought risks. *Agricultural Systems* **84**: 77–97.
- Robredo, A., Perez-Lopez, U., Miranda-Apodaca, J., Lacuesta, M., Mena-Petite, A., and Munoz-Rueda, A. 2011. Elevated CO₂ reduces the drought effect on nitrogen metabolism in barley plants during drought and subsequent recovery. *Environmental and Experimental Botany* **71**: 399–408.
- Robredo, A., Perez-Lopez, U., Sainz de le Maza, H., Gonzalez-Moro, B., Lacuesta, M., Mena-Petite, A., and Munoz-Rueda, A. 2007. Elevated CO₂ alleviates the impact of drought on barley improving water status by lowering stomatal conductance and delaying its effects on photosynthesis. *Environmental and Experimental Botany* **59**: 252–263.
- Rogers, H.H., Sionit, N., Cure, J.D., Smith, H.M., and Bingham, G.E. 1984. Influence of elevated CO₂ on water relations of soybeans. *Plant Physiology* **74**: 233–238.
- Schutz, M. and Fangmeier, A. 2001. Growth and yield responses of spring wheat (*Triticum aestivum* L. cv. Minaret) to elevated CO₂ and water limitation. *Environmental Pollution* **114**: 187–194.
- Serraj, R., Allen Jr., L.H., and Sinclair, T.R. 1999. Soybean leaf growth and gas exchange response to drought under carbon dioxide enrichment. *Global Change Biology* **5**: 283–291.
- Sgherri, C.L.M., Quartacci, M.F., Menconi, M., Raschi, A., and Navari-Izzo, F. 1998. Interactions between drought and elevated CO₂ on alfalfa plants. *Journal of Plant Physiology* **152**: 118–124.
- Tohidimoghdam, H.R., Ghooshchi, F., and Zahedi, H. 2011. Effect of UV radiation and elevated CO₂ on morphological traits, yield and yield components of canola (*Brassica napus* L.) grown under water deficit. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* **39**: 213–219.
- Triggs, J.M., Kimball, B.A., Pinter Jr., P.J., Wall, G.W.,

Conley, M.M., Brooks, T.J., LaMorte, R.L., Adam, N.R., Ottman, M.J., Matthias, A.D., Leavitt, S.W., and Cervený, R.S. 2004. Free-air CO₂ enrichment effects on the energy balance and evapotranspiration of sorghum. *Agricultural and Forest Meteorology* **124**: 63–79.

Varga, B. and Bencze, Sz. 2009. Comparative study of drought stress resistance in two winter wheat varieties raised at ambient and elevated CO₂ concentration. *Cereal Research Communications* **37**: 209–212.

Varga, B., Janda, T., Laszlo, E., and Veisz, O. 2012. Influence of abiotic stresses on the antioxidant enzyme activity of cereals. *Acta Physiologiae Plantarum* **34**: 849–858.

Veisz, O., Bencze, S., Balla, K., Vida, G., and Bedo, Z. 2008. Change in water stress resistance of cereals due to atmospheric CO₂ enrichment. *Cereal Research Communications* **36**: 10.1556/CRC.36.2008.Suppl.1.

Vu, J.C.V., Baker, J.T., Pennanen, A.H., Allen Jr., L.H., Bowes, G., and Boote, K.J. 1998. Elevated CO₂ and water deficit effects on photosynthesis, ribulose biphosphate carboxylase-oxygenase, and carbohydrate metabolism in rice. *Physiologia Plantarum* **103**: 327–339.

Wall, G.W. 2001. Elevated atmospheric CO₂ alleviates drought stress in wheat. *Agriculture, Ecosystems and Environment* **87**: 261–271.

Wechsung, G., Wechsung, F., Wall, G.W., Adamsen, F.J., Kimball, B.A., Pinter Jr., P.J., LaMorte, R.L., Garcia, R.L., and Kartschall, Th. 1999. The effects of free-air CO₂ enrichment and soil water availability on spatial and seasonal patterns of wheat root growth. *Global Change Biology* **5**: 519–529.

Widodo, W., Vu, J.C.V., Boote, K.J., Baker, J.T., and Allen Jr., L.H. 2003. Elevated growth CO₂ delays drought stress and accelerates recovery of rice leaf photosynthesis. *Environmental and Experimental Botany* **49**: 259–272.

3.15.2 Grasslands

- The peer-reviewed scientific literature demonstrates the historical and still-ongoing rise in the air's CO₂ content has led and likely will continue to lead to substantial increases in the photosynthetic rates and biomass production of various grassland plants, even under stressful environmental conditions imposed by less-than-optimum soil moisture.

As the air's CO₂ content rises, nearly all plants should exhibit increases in photosynthesis and biomass

production, but some researchers have claimed water stress will negate these benefits. In reviewing the scientific literature for 1983–1994, Idso and Idso (1994) concluded water stress will not in fact negate the CO₂-induced stimulation of plant productivity. They discovered the CO₂-induced percentage increase in plant productivity was nearly always greater under water-stressed conditions than when plants were well-watered. Seven years later, Poorter and Perez-Soba (2001) conducted a similar literature review and reached the same conclusion. This section provides background for this phenomenon and highlights some of the more important work that subsequently has been done in this area.

Elevated levels of atmospheric CO₂ tend to reduce the area of open stomatal pore space on leaf surfaces, thus reducing plant stomatal conductance. This phenomenon, in turn, effectively reduces the amount of water lost to the atmosphere via transpiration. Leymarie *et al.* (1999), for example, found twice-ambient levels of atmospheric CO₂ caused significant reductions in the stomatal conductance of water-stressed *Arabidopsis thaliana*. Similarly, Volk *et al.* (2000) reported several calcareous grassland species exposed to elevated atmospheric CO₂ concentrations (600 ppm) consistently exhibited reduced stomatal conductance, regardless of soil moisture availability.

In addition, CO₂-induced increases in root development and CO₂-induced reductions in leaf stomatal conductance often combine to maintain a more favorable plant water status during times of drought. In the case of four grassland species comprising a pasture characteristic of New Zealand, for example, Clark *et al.* (1999) report leaf water potential, a good indicator of plant water status, was consistently higher (less negative and, therefore, less stressful) under elevated atmospheric CO₂ concentrations. Leaf water potentials of the water-stressed C₄ grass *Panicum coloratum* grown at 1,000 ppm CO₂ were always higher than those of their water-stressed counterparts growing in ambient air (Seneweera *et al.*, 2001). Seneweera *et al.* (1998) had earlier reported leaf water potentials observed in CO₂-enriched water-stressed plants were three-and-a-half times greater than those observed in control plants grown at 350 ppm during drought conditions (Seneweera *et al.*, 1998).

If atmospheric CO₂ enrichment thus allows grassland plants to maintain better water status during times of water stress, it is logical to infer such plants will exhibit greater photosynthetic rates than similar

plants growing in ambient air. In a severe test of this concept, Ward *et al.* (1999) found extreme water stress caused 93 and 85% reductions in the photosynthetic rates of two CO₂-enriched grassland species, yet their rates of carbon fixation were still greater than those observed under ambient CO₂ conditions.

These observations demonstrate elevated CO₂ nearly always enhances photosynthetic rates during times of water stress. One thus would expect plant biomass production to be enhanced by elevated CO₂ concentrations under drought conditions.

On the American prairie, Owensby *et al.* (1999) observed tallgrass ecosystems exposed to twice-ambient concentrations of atmospheric CO₂ for eight years exhibited significant increases in above- and below-ground biomass only during years of less-than-average rainfall. Derner *et al.* (2001) observed a 150 ppm increase in the CO₂ content of the air increased shoot biomass in two C₄ grasses by 57%, regardless of soil water content. Seneweera *et al.* (2001) reported a 640 ppm increase in the air's CO₂ content increased shoot dry mass in a C₄ grass by 44 and 70% under well-watered and water-stressed conditions, respectively. Volk *et al.* (2000) grew calcareous grassland assemblages at 360 and 600 ppm CO₂ and documented 18 and 40% CO₂-induced increases in whole-community biomass under well-watered and water-stressed conditions, respectively.

Nelson *et al.* (2004) reported on a five-year study (1997–2001) conducted on the semi-arid shortgrass steppe (SGS) of Colorado (USA). Working at the USDA-ARS Central Plains Experimental Range in the northern portion of the SGS about 60 km northeast of Fort Collins, Colorado, they used large (15.5 m²) open-top chambers to examine the effects of elevated CO₂ (720 vs. 360 ppm) on plant water relations, ecosystem water use efficiency, soil moisture dynamics, and root distributions of the ecosystem's dominant C₃ (*Pascopyrum smithii* and *Stipa comata*) and C₄ (*Bouteloua gracilis*) grasses.

The five Agricultural Research Service scientists and their collaborator from Colorado State University report “seasonal average soil moisture throughout the soil profile (0–15, 15–45, 45–75, 75–105 cm) was increased under elevated CO₂ compared to ambient CO₂ for much of the study period,” with the greatest relative increase (16.4%) occurring in the 75–105 cm depth increment. This finding of “increased soil moisture under elevated CO₂ at the deepest soil depth suggests that water percolated deeper into the soil profile and that less moisture was lost to evapotranspiration under elevated CO₂.” Noting “this

phenomenon enhances water storage in the deep fine sandy loam soils underlying large portions of the SGS,” they state, “this increase in soil moisture has been shown to be the major controlling factor in improved carbon assimilation rates and increased total aboveground biomass in this system (LeCain *et al.*, 2003) and will likely decrease the susceptibility of the SGS to drought.”

The Colorado researchers also found, when averaged over the study period, “leaf water potential was enhanced 24–30% under elevated CO₂ in the major warm- and cool-season grass species of the SGS (*Bouteloua gracilis*, C₄, 28.5%; *Pascopyrum smithii*, C₃, 24.7%; *Stipa comata*, C₃, 30.4%).” They report these results are similar to those of “studies involving other C₃ and C₄ grass species (Owensby *et al.*, 1993; Jackson *et al.*, 1994),” and they say the enhanced leaf water potential—“which reflects improved plant water status and increased drought tolerance (Tyree and Alexander, 1993)” —may lead to increased leaf turgor and allow the grasses “to continue growth further into periods of drought.” Averaged over the five years of the study, Nelson *et al.* report, “water-use efficiency (grams aboveground biomass harvested / kilogram water consumed) was 43% higher in elevated than ambient CO₂ plots.”

Nelson *et al.* say their results “suggest that a future, elevated CO₂ environment may result not only in increased plant productivity due to improved water use efficiency, but also lead to increased water drainage and deep soil moisture storage in this semi-arid grassland ecosystem.” They add, “this, along with the ability of the major grass species to maintain a favorable water status under elevated CO₂, should result in the SGS being less susceptible to prolonged periods of drought.”

Nelson *et al.* note their findings are common, writing, “previous studies have reported increased soil moisture under elevated CO₂ in semi-arid C₃ annual grasslands in California (Fredeen *et al.*, 1997), mesic C₃/C₄ perennial tallgrass prairie in Kansas (Owensby *et al.*, 1993, 1999; Ham *et al.*, 1995; Bremer *et al.*, 1996), and mesic C₃ perennial grasslands in Switzerland (Niklaus *et al.*, 1998) and Sweden (Sindhoj *et al.*, 2000).” Taken together, these studies indicate the benefits of atmospheric CO₂ enrichment will apply to grasslands generally, as the air's CO₂ content rises to double-and-beyond its current concentration.

If air temperature rises concurrently, things could get even better. Nelson *et al.* note, for example, “air temperature was on average 2.6°C higher inside the

chambers than outside,” and this warming “was implicated in the 36% enhanced biomass production observed in chambered-ambient compared to non-chambered plots.” Consequently, since this already-enhanced biomass production was the starting point from which the 41% increase in biomass arising from the doubling of the air’s CO₂ content was calculated, the increase in biomass caused by the concurrent actions of both factors (increasing air temperature and CO₂ concentration) could be on the order of 90%.

The 15-member team of Morgan *et al.* (2004) reviewed the scientific literature on the role of water relations in the response of grassland and desert ecosystems to elevated levels of atmospheric CO₂. They found it suggests “atmospheric CO₂ enrichment may stimulate plant growth either directly through (1) enhanced photosynthesis or indirectly through (2) reduced plant water consumption and hence slower soil moisture depletion, or the combination of both.” They performed an analysis to determine “gas exchange, plant biomass and species responses of five native or semi-native temperate and Mediterranean grasslands and three semi-arid ecosystems to CO₂ enrichment, with an emphasis on water relations.”

The team found “increasing CO₂ led to decreased leaf conductance for water vapor, improved plant water status, altered seasonal evapotranspiration dynamics, and in most cases, periodic increases in soil water content.” As a result, “across the grasslands of the Kansas tallgrass prairie, Colorado shortgrass steppe and Swiss calcareous grassland, increases in aboveground biomass from CO₂ enrichment were relatively greater in dry years.” In contrast, they report, “CO₂-induced aboveground biomass increase in the Texas C₃/C₄ grassland and the New Zealand pasture seemed little or only marginally influenced by yearly variation in soil water, and plant growth in the Mojave Desert was stimulated by CO₂ in a relatively wet year.” In addition, “Mediterranean grasslands sometimes failed to respond to CO₂-related increased late-season water, whereas semiarid Negev grassland assemblages profited.”

Although they state “vegetative and reproductive responses to CO₂ were highly varied among species and ecosystems, and did not generally follow any predictable pattern in regard to function groups,” considered in their entirety, they conclude the literature results they reviewed (many of which they themselves had been instrumental in collecting) “suggest that the indirect effects of CO₂ on plant and soil water relations may contribute substantially to experimentally induced CO₂-effects.”

Lazzarotto *et al.* (2010) write, “white clover (*Trifolium repens* L.) is the most important pasture legume grown in temperate climates in association with a variety of grasses, notably perennial ryegrass (*Lolium perenne* L.),” adding, “white clover improves the nutritional quality and digestibility of the herbage” and “contributes substantially to the nitrogen status of the sward through biological nitrogen fixation.” They note some researchers have expressed concern future drought, such as is predicted by climate models to occur in tandem with CO₂-induced global warming, will damage clover more than the grass with which it is intermingled, thereby degrading the nutritional quality and digestibility of pasture swards.

Lazzarotto *et al.* conducted a study in which “mechanisms controlling transient responses to elevated CO₂ concentration and climate change in an unfertilized grassland on the Swiss Plateau were examined in light of simulations with PROGRASS.” They used a process-based model of grass-clover interactions developed by Lazzarotto *et al.* (2009), in which “daily weather for a series of transient climate scenarios spanning the 21st century were developed for the study site with the help of the LARS-WG weather generator,” as described by Semenov and Barrow (1997) and Semenov *et al.* (1998), and “changes in the length of dry and wet spells, temperature, precipitation and solar radiation defining the scenarios were obtained from regional climate simulations carried out in the framework of the PRUDENCE project,” as described by Christensen and Christensen (2007).

“Compared to 1961–1990,” the Swiss and UK scientists write, the climate scenarios they developed for a CO₂ increase from 370 to 860 ppm “indicated that for 2071–2100 there would be a noticeable increase in temperature (roughly 3°C in winter and 5°C in summer), a significant drop in summer precipitation (of the order of -30%) and a nearly 2-fold increase in the length of dry spells.” They report “clover abundance did not decline even in the absence of CO₂ stimulation.” When the atmospheric CO₂ concentration was programmed to gradually rise from an initial value of 370 ppm to a final value of 860 ppm, “clover development benefited from the overall positive effects of CO₂ on nitrogen acquisition,” which they note was “the reason for increasing productivity of the [entire] sward.”

These findings indicate the rather large increases in temperature and decreases in precipitation projected for the remainder of the twenty-first

century, even if they come to pass, will not have much of an effect on Swiss grass-clover swards, but the concomitant increase in the air's CO₂ content will benefit them considerably. Lazzarotto *et al.* opine it is likely "technical progress in the management of grasslands and pastures," which will surely occur, will help such pastures even more.

Noting "grassland communities constitute an important fraction of the green surface of the Earth, and are worldwide an important source of cattle-food (Carlier *et al.*, 2009; Ciais *et al.*, 2011)," Farfan-Vignolo and Asard (2012) investigated several physiological and molecular (antioxidant) responses to water deficit in two major grassland species (*Lolium perenne* L. and *Medicago lupulina* L.) under current ambient (A) and future elevated (E) atmospheric CO₂ concentrations and air temperatures (T), where ECO₂ = ACO₂ + 375 ppm, and ET = AT + 3°C. The researchers found "drought caused significant increases in oxidative damage, i.e., in protein oxidation and lipid peroxidation levels." They also report, "in both species the impact of drought on protein oxidation was reduced in future climate conditions [ECO₂ and ET]." As to the stress-reducing effect of ECO₂, they state "this 'CO₂-protection effect' is reported for a variety of abiotic stress conditions and species," citing Schwanz and Polle (1998), Sgherri *et al.* (2000), Geissler *et al.* (2009), Perez-Lopez *et al.* (2009), Vurro *et al.* (2009), and Salazar-Parra *et al.* (2012). They say they too "find support for this effect at the level of oxidative cell damage and protein oxidation in water-deficit responses of *L. perenne* and *M. lupulina*." Even under drought stress, they note, "elevated CO₂ significantly affected shoot production in *L. perenne* (increase by 27–32%)," and "also in *M. lupulina* a biomass increase was observed (26–38%)."

Thus the conclusions of Idso and Idso (1994), based on the pre-1994 literature, are well supported by the subsequent peer-reviewed scientific literature, which indicates the rise in the air's CO₂ content likely will lead to substantial increases in plant photosynthetic rates and biomass production, even with stressful environmental conditions imposed by less-than-optimum soil moisture conditions.

References

- Bremer, D.J., Ham, J.M., and Owensby C.E. 1996. Effect of elevated atmospheric carbon dioxide and open-top chambers on transpiration in a tallgrass prairie. *Journal of Environmental Quality* 25: 691–701.
- Carlier, L., Rotar, I., Vlahova, M., and Vidican, R. 2009. Importance and functions of grasslands. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* 37: 25–30.
- Christensen, J.H. and Christensen, O.B. 2007. A summary of the PRUDENCE model projections of changes in European climate by the end of this century. *Climatic Change* 81: 7–30.
- Ciais, P., Gervois, S., Vuichard, N., Piao, S.L., and Viovy, N. 2011. Effects of land use change and management on the European cropland carbon balance. *Global Change Biology* 17: 320–338.
- Clark, H., Newton, P.C.D., and Barker, D.J. 1999. Physiological and morphological responses to elevated CO₂ and a soil moisture deficit of temperate pasture species growing in an established plant community. *Journal of Experimental Botany* 50: 233–242.
- Derner, J.D., Polley, H.W., Johnson, H.B., and Tischler, C.R. 2001. Root system response of C₄ grass seedlings to CO₂ and soil water. *Plant and Soil* 231: 97–104.
- Farfan-Vignolo, E.R. and Asard, H. 2012. Effect of elevated CO₂ and temperature on the oxidative stress response to drought in *Lolium perenne* L. and *Medicago sativa* L. *Plant Physiology and Biochemistry* 59: 55–62.
- Fredeen, A.L., Randerson, J.T., Holbrook, N.M., and Field, C.B. 1997. Elevated atmospheric CO₂ increases water availability in a water-limited grassland ecosystem. *Journal of the American Water Resources Association* 33: 1033–1039.
- Geissler, N., Hussin, S., and Koyro, H.-W. 2009. Elevated atmospheric CO₂ concentration ameliorates effects of NaCl salinity on photosynthesis and leaf structure of *Aster tripolium* L. *Journal of Experimental Botany* 60: 137–151.
- Ham, J.M., Owensby, C.E., Coyne, P.I., and Bremer, D.J. 1995. Fluxes of CO₂ and water vapor from a prairie ecosystem exposed to ambient and elevated atmospheric CO₂. *Agricultural and Forest Meteorology* 77: 73–93.
- Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: A review of the past 10 years' research. *Agricultural and Forest Meteorology* 69: 153–203.
- Jackson, R.B., Sala, O.E., Field, C.B., and Mooney, H.A. 1994. CO₂ alters water use, carbon gain, and yield for the dominant species in a natural grassland. *Oecologia* 98: 257–262.
- Lazzarotto, P., Calanca, P., and Fuhrer, J. 2009. Dynamics of grass-clover mixtures—an analysis of the response to management with the PROductive GRASSland Simulator (PROGRASS). *Ecological Modeling* 220: 703–724.
- Lazzarotto, P., Calanca, P., Semenov, M., and Fuhrer, J.

2010. Transient responses to increasing CO₂ and climate change in an unfertilized grass-clover sward. *Climate Research* **41**: 221–232.
- LeCain, D.R., Morgan, J.A., Mosier, A.R., and Nelson, J.A. 2003. Soil and plant water relations determine photosynthetic responses of C₃ and C₄ grasses in a semi-arid ecosystem under elevated CO₂. *Annals of Botany* **92**: 41–52.
- Leymarie, J., Lasceve, G., and Vavasour, A. 1999. Elevated CO₂ enhances stomatal responses to osmotic stress and abscisic acid in *Arabidopsis thaliana*. *Plant, Cell and Environment* **22**: 301–308.
- Morgan, J.A., Pataki, D.E., Korner, C., Clark, H., Del Grosso, S.J., Grunzweig, J.M., Knapp, A.K., Mosier, A.R., Newton, P.C.D., Niklaus, P.A., Nippert, J.B., Nowak, R.S., Parton, W.J., Polley, H.W., and Shaw, M.R. 2004. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO₂. *Oecologia* **140**: 11–25.
- Nelson, J.A., Morgan, J.A., LeCain, D.R., Mosier, A.R., Milchunas, D.G., and Parton, B.A. 2004. Elevated CO₂ increases soil moisture and enhances plant water relations in a long-term field study in semi-arid shortgrass steppe of Colorado. *Plant and Soil* **259**: 169–179.
- Niklaus, P.A., Spinnler, D., and Korner, C. 1998. Soil moisture dynamics of calcareous grassland under elevated CO₂. *Oecologia* **117**: 201–208.
- Owensby, C.E., Coyne, P.I., Ham, J.H., Auen, L.M., and Knapp, A.K. 1993. Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO₂. *Ecological Applications* **3**: 644–653.
- Owensby, C.E., Ham, J.M., Knapp, A.K., and Auen, L.M. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO₂. *Global Change Biology* **5**: 497–506.
- Perez-Lopez, U., Robredo, A., Lacuesta, M., Sgherri, C., Munoz-Rueda, A., Navari-Izzo, F., and Mena-Petite, A. 2009. The oxidative stress caused by salinity in two barley cultivars is mitigated by elevated CO₂. *Physiologia Plantarum* **135**: 29–42.
- Poorter, H. and Perez-Soba, M. 2001. The growth response of plants to elevated CO₂ under non-optimal environmental conditions. *Oecologia* **129**: 1–20.
- Salazar-Parra, C., Aguirreolea, J., Sanchez-Diaz, M., Irigoyen, J.J., and Morales, F. 2012. Climate change (elevated CO₂, elevated temperature and moderate drought) triggers the antioxidant enzymes' response of grapevine cv. Tempranillo, avoiding oxidative damage. *Physiologia Plantarum* **144**: 99–110.
- Schwanz, P. and Polle, A. 1998. Antioxidative systems, pigment and protein contents in leaves of adult Mediterranean oak species (*Quercus pubescens* and *Q. ilex*) with lifetime exposure to elevated CO₂. *New Phytologist* **140**: 411–423.
- Semenov, M.A. and Barrow, E.M. 1997. Use of a stochastic weather generator in the development of climate change scenarios. *Climatic Change* **35**: 397–414.
- Semenov, M.A., Books, R.J., Barrow, E.M., and Richardson, C.W. 1998. Comparison of the WGEN and LARS-WG stochastic weather generators for diverse climates. *Climate Research* **10**: 95–107.
- Seneweera, S.P., Ghannoum, O., and Conroy, J. 1998. High vapor pressure deficit and low soil water availability enhance shoot growth responses of a C₄ grass (*Panicum coloratum* cv. Bambatsi) to CO₂ enrichment. *Australian Journal of Plant Physiology* **25**: 287–292.
- Seneweera, S., Ghannoum, O., and Conroy, J.P. 2001. Root and shoot factors contribute to the effect of drought on photosynthesis and growth of the C₄ grass *Panicum coloratum* at elevated CO₂ partial pressures. *Australian Journal of Plant Physiology* **28**: 451–460.
- Sgherri, C.L.M., Salvateci, P., Menconi, M., Raschi, A., and Navari-Izzo, F. 2000. Interaction between drought and elevated CO₂ in the response of alfalfa plants to oxidative stress. *Journal of Plant Physiology* **156**: 360–366.
- Sindhoj, E., Hansson, A.C., Andren, O., Katterer, T., Marissink, M., and Pettersson, R. 2000. Root dynamics in a semi-natural grassland in relation to atmospheric carbon dioxide enrichment, soil water and shoot biomass. *Plant and Soil* **223**: 253–263.
- Tyree, M.T. and Alexander, J.D. 1993. Plant water relations and the effects of elevated CO₂: A review and suggestions for future research. *Vegetatio* **104/105**: 47–62.
- Volk, M., Niklaus, P.A., and Korner, C. 2000. Soil moisture effects determine CO₂ responses of grassland species. *Oecologia* **125**: 380–388.
- Vurro, E., Bruni, R., Bianchi, A., and di Toppi, L.S. 2009. Elevated atmospheric CO₂ decreases oxidative stress and increases essential oil yield in leaves of *Thymus vulgaris* grown in a mini-FACE system. *Environmental and Experimental Botany* **65**: 99–106.
- Ward, J.K., Tissue, D.T., Thomas, R.B., and Strain, B.R. 1999. Comparative responses of model C₃ and C₄ plants to drought in low and elevated CO₂. *Global Change Biology* **5**: 857–867.

3.15.3 Woody Plants

- The rise in the air's CO₂ concentration likely will lead to substantial increases in the photosynthetic rates and biomass production of trees and shrubs, even with stressful environmental conditions imposed by suboptimal soil moisture availability.

It is widely acknowledged that as the CO₂ content of the air rises, nearly all plant types will exhibit increases in photosynthesis and biomass production, but some researchers claim future water stress will negate these benefits of atmospheric CO₂ enrichment. Much of the pertinent scientific literature of the 10-year period 1983–1994, reviewed by Idso and Idso (1994), calls that claim into question, showing water stress will generally not negate the CO₂-induced stimulation of plant growth. Idso and Idso's literature review found the CO₂-induced percentage increase in plant productivity was nearly always greater under water-stressed conditions than when plants were well-watered. This section discusses subsequent relevant literature as it pertains to woody species.

It is well-known that during times of water stress, atmospheric CO₂ enrichment often stimulates the development of larger-than-usual and more robust root systems in woody plants, enabling them to probe greater volumes of soil for scarce and much-needed moisture. Tomlinson and Anderson (1998), for example, found greater root development in water-stressed red oak seedlings grown at 700 ppm CO₂ helped them effectively deal with the reduced availability of moisture, and these trees eventually produced just as much biomass as well-watered controls exposed to air containing 400 ppm CO₂. Polley *et al.* (1999) report water-stressed honey mesquite trees exposed to an atmospheric CO₂ concentration of 700 ppm produced 37% more root biomass than water-stressed seedlings in air of 370 ppm.

Elevated levels of atmospheric CO₂ also tend to reduce the area of open stomatal pore space on leaf surfaces, thus reducing plant stomatal conductance. This phenomenon, in turn, reduces the amount of water lost to the atmosphere via transpiration. Tognetti *et al.* (1998) determined the stomatal conductances of mature oak trees growing near natural CO₂ springs in central Italy were significantly lower than those of similar trees growing farther away from the springs during periods of severe summer drought, which allowed the CO₂-enriched trees to better conserve what little water was available to

them.

Working together, CO₂-induced increases in root development and CO₂-induced reductions in stomatal conductance often contribute to the maintenance of a more favorable plant water status during times of drought. In the case of three Mediterranean shrubs, for example, Tognetti *et al.* (2002) found leaf water potential, a good indicator of plant water status, was consistently higher (less negative and, hence, less stressful) under twice-ambient CO₂ concentrations. Polley *et al.* (1999) observed leaf water potentials of water-stressed mesquite seedlings grown at 700 ppm CO₂ were 40% higher than those of their water-stressed counterparts growing in ambient air, comparable to the values of -5.9 and -3.4 MPa observed in water-stressed evergreen shrubs (*Larrea tridentata*) exposed to 360 and 700 ppm CO₂, respectively, as documented by Hamerlynck *et al.* (2000).

If atmospheric CO₂ enrichment allows plants to maintain a better water status during times of water stress, it is only logical to surmise plants growing under such conditions will exhibit CO₂-induced increases in photosynthesis. Palanisamy (1999) found water-stressed Eucalyptus seedlings grown at 800 ppm CO₂ had greater net photosynthetic rates than their ambient-grown and water-stressed counterparts. Runion *et al.* (1999) found the CO₂-induced photosynthetic stimulation of water-stressed pine seedlings grown at 730 ppm CO₂ was nearly 50% greater than similar water-stressed pine seedlings grown at 365 ppm CO₂. Similarly, Centritto *et al.* (1999a) report water-stressed cherry trees grown at 700 ppm CO₂ displayed net photosynthetic rates 44% greater than those of water-stressed trees grown at 350 ppm CO₂. And Anderson and Tomlinson (1998) determined a 300-ppm increase in the air's CO₂ concentration boosted photosynthetic rates in well-watered and water-stressed red oak seedlings by 34 and 69%, respectively, demonstrating the CO₂-induced enhancement in net photosynthesis in this species was essentially twice as great in water-stressed seedlings as in well-watered ones.

Nevertheless, plants sometimes suffer drastically when subjected to extreme water stress, but the addition of CO₂ to the air often induces plants to react better to stress than plants growing in normal air. Tuba *et al.* (1998), for example, reported leaves of a water-stressed woody shrub exposed to an atmospheric CO₂ concentration of 700 ppm continued to maintain positive rates of net carbon fixation for a period that lasted three times longer than did leaves of

equally water-stressed control plants growing in ambient air. Fernandez *et al.* (1998) discovered herb and tree species growing near natural CO₂ vents in Venezuela continued to maintain positive rates of net photosynthesis during that location's dry season, and the same species growing some distance away from the CO₂ source displayed net losses of carbon during this stressful time. Likewise, Fernandez *et al.* (1999) note that after four weeks of drought, the deciduous Venezuelan shrub *Ipomoea carnea* continued to exhibit positive carbon gains under elevated CO₂ conditions, whereas ambient-growing plants displayed net carbon losses. Polley *et al.* (2002) reported seedlings of five woody species grown at twice-ambient CO₂ concentrations survived 11 days longer (on average) than control seedlings when subjected to maximum drought conditions.

Since elevated CO₂ enhances photosynthetic rates during times of water stress, one would expect tree and shrub biomass production to be enhanced by elevated CO₂ concentrations under drought conditions. That was demonstrated by Arp *et al.* (1998), who reported six perennial plants common to the Netherlands increased their biomass under CO₂-enriched conditions even when suffering from lack of water. In some cases, the CO₂-induced percentage biomass increase is greater for water-stressed plants than for well-watered plants. Catovsky and Bazzaz (1999), for example, reported the CO₂-induced biomass increase for paper birch was 27% and 130% for well-watered and water-stressed seedlings, respectively. Schulte *et al.* (1998) noted the CO₂-induced biomass increase of oak seedlings was greater under water-limiting conditions than under well-watered conditions (128% vs. 92%), as did Centritto *et al.* (1999b) for basal trunk area in cherry seedlings (69% vs. 22%).

Knapp *et al.* (2001) developed tree-ring index chronologies from western juniper stands in Oregon (USA), finding the trees recovered better from the effects of drought in the 1990s, when the air's CO₂ concentration was around 340 ppm, than they did in 1900–1930, when the atmospheric CO₂ concentration was around 300 ppm.

In a loosely related study, Osborne *et al.* (2000) looked at the warming and reduced precipitation experienced in Mediterranean shrublands over the last century and concluded primary productivity should have been negatively impacted in those areas. However, when the concurrent increase in atmospheric CO₂ concentration was factored into their mechanistic model, a 25% increase in primary

productivity was projected.

Centritto (2002) grew peach seedlings for two growing seasons in pots in open-top chambers of either ambient or CO₂-enriched air (350 or 700 ppm, respectively) inside a glasshouse, where all plants were continuously maintained at optimum soil fertility and, for the entire first growing season, at optimum soil water availability. In the second growing season, half of the seedlings had water withheld from them for four weeks. At the end of the study, there was no evidence of any downward acclimation of photosynthesis in the seedlings grown at elevated CO₂, nor was there any downward acclimation in rubisco carboxylation efficiency or in the maximum RuBP regeneration capacity mediated by electron transport.

Xiao *et al.* (2005) experimented with *Caragana intermedia* Kuanget H.C. Fu, a deciduous shrub of semi-arid northern China that occurs primarily in the country's Maowusu sandland as well as parts of Inner Mongolia, where they state it is "used by local people as feed for livestock, and as shelter for protection of soils (Zhang, 1994)," noting "it is one of the dominant shrubs that fix soil and reduce wind speed, thus actively mitigating desertification." The five Chinese scientists grew seedlings of this species for 3.5 months in 10-cm-diameter by 10-cm-deep pots filled with sand and maintained at three water regimes—well-watered (60–70% field capacity), moderate-watered (45–55% field capacity), and drought-stressed (30–40% field capacity)—in greenhouse compartments maintained at atmospheric CO₂ concentrations of either 350 or 700 ppm. Near the end of this period, they measured leaf water potentials and several plant growth parameters.

Xiao *et al.* found, "elevated CO₂ significantly increased leaf water potential" while also increasing tree height, basal diameter, shoot biomass, root biomass, and total biomass, which was increased by 79% under the well-watered condition, by 61% under the moderate-watered condition, and by 53% under the drought-stressed condition. They report the Canopy Productivity Index (CPI, total growth per unit leaf area) was also "significantly increased by elevated CO₂, and the increase in CPI became stronger as the level of drought stress increased." They conclude their study "confirmed the beneficial effects of elevated CO₂ on *C. intermedia* seedlings exposed to drought-stressed conditions," and these findings "suggest that elevated CO₂ may enhance drought avoidance and improved water relations, thus weakening the effect of drought stress on growth of

C. intermedia seedlings.”

Soule and Knapp (2006) write, “two major environmental issues have arisen regarding the increasingly CO₂-rich world of the late 20th and early 21st centuries: climatic change, and plant responses to the environment,” and they note, “while the implications of atmospheric CO₂ for potential climatic change have received the majority of attention, the potential role of atmospheric CO₂ fertilization in plant growth and subsequent ecosystem dynamics may be equally important.” They studied ponderosa pine trees growing at eight sites in the Pacific Northwest of the United States to see how they may have responded to the increase in the atmosphere’s CO₂ concentration that occurred after 1950.

The two geographers say they chose study sites that “fit several criteria designed to limit potential confounding influences associated with anthropogenic disturbance,” with “a variety of climatic and topo-edaphic conditions, ranging from extremely water-limiting environments ... to areas where soil moisture should be a limiting factor for growth only during extreme drought years.” They note all their study sites were located in areas “where ozone concentrations and nitrogen deposition are typically low.”

At each of the eight sites, Soule and Knapp obtained core samples from about 40 mature trees that included “the potentially oldest trees on each site,” so their results would indicate “the response of mature, naturally occurring ponderosa pine trees that germinated before anthropogenically elevated CO₂ levels, but where growth, particularly post-1950, has occurred under increasing and substantially higher atmospheric CO₂ concentrations.” Utilizing meteorological evaluations of the Palmer Drought Severity Index, they compared ponderosa pine (*Pinus ponderosa* Laws. var. *ponderosa*) radial growth rates during matched wet and dry years pre- and post-1950.

The two researchers report finding a post-1950 radial growth enhancement “more pronounced during drought years compared with wet years,” and they add, “the greatest response occurred at the most stressed site.” They write, “the relative change in growth [was] upward at seven of our [eight] sites, ranging from 11 to 133%.”

Soule and Knapp state their results, “showing that radial growth has increased in the post-1950s period ... while climatic conditions have generally been unchanged, suggest that nonclimatic driving forces are operative.” In addition, “these radial growth responses are generally consistent with what has been

shown in long-term open-top chamber (Idso and Kimball, 2001) and FACE studies (Ainsworth and Long, 2005).” They state their findings suggest “elevated levels of atmospheric CO₂ are acting as a driving force for increased radial growth of ponderosa pine, but that the overall influence of this effect may be enhanced, reduced or obviated by site-specific conditions.”

Soule and Knapp recount how they “hypothesized that ponderosa pine ... would respond to gradual increases in atmospheric CO₂ over the past 50 years, and that these effects would be most apparent during drought stress and on environmentally harsh sites,” and in the following sentence they state their results “support these hypotheses.” They conclude it is likely “an atmospheric CO₂-driven growth-enhancement effect exists for ponderosa pine growing under specific natural conditions in the [USA’s] interior Pacific Northwest.”

Wang *et al.* (2006) conducted a similar study, seeking to ascertain how the historical increase in atmospheric CO₂ concentration had affected the growth of trees in the real world rather than experimental settings. They examined ring-width development in cohorts of young and old white spruce (*Picea glauca*) trees in a mixed grass-prairie ecosystem in southwestern Manitoba, Canada, where a 1997 wildfire killed most of the older trees growing in high-density spruce islands, but where younger trees slightly removed from the islands were not affected by the flames. “Within each of a total of 24 burned islands,” the three researchers write, “the largest dominant tree (dead) was cut down and a disc was then sampled from the stump height,” and “adjacent to each sampled island, a smaller, younger tree (live) was also cut down, and a disc was sampled from the stump height.”

After removing size-, age-, and climate-related trends in radial growth from the ring-width histories of the trees, Wang *et al.* plotted the residuals as functions of time for the 30-year periods for which both the old and young trees would have been approximately the same age: 1900–1929 for the old trees and 1970–1999 for the young trees. During the first of these periods, the atmosphere’s CO₂ concentration averaged 299 ppm, and during the second it averaged 346 ppm. The mean rate-of-rise of the atmosphere’s CO₂ concentration was 0.37 ppm/year for the first period and 1.43 ppm/year for the second.

In comparison to the 1900–1929 period, the slope of the linear regression describing the rate-of-growth of the ring-width residuals for the 1970–1999 period

(when the air's CO₂ concentration was 15% greater and its rate-of-rise was 285% greater) was more than twice the linear regression describing the rate-of-growth of the ring-width residuals for the 1900–1929 period. As the researchers observe, these results show “at the same developmental stage, a greater growth response occurred in the late period when atmospheric CO₂ concentration and the rate of atmospheric CO₂ increase were both relatively high,” and “these results are consistent with expectations for CO₂-fertilization effects.” They write, “the response of the studied young trees can be taken as strong circumstantial evidence for the atmospheric CO₂-fertilization effect.”

Wang *et al.* also learned “postdrought growth response was much stronger for young trees (1970–1999) compared with old trees at the same development stage (1900–1929).” They add, “higher atmospheric CO₂ concentration in the period from 1970–1999 may have helped white spruce recover from severe drought.” Similarly, young trees showed a weaker relationship to precipitation than did old trees, noting “more CO₂ would lead to greater water-use efficiency, which may be dampening the precipitation signal in young trees.” Wang *et al.*'s unique study provides an exciting real-world example of the benefits the historical rise in the air's CO₂ content likely has conferred on long-lived woody species.

Davi *et al.* (2006) used a meteorological model following “a moderate CO₂ emission scenario” (B2 of IPCC) to calculate a 1960–2100 average temperature increase of 3.1°C and a mean summer rainfall decrease of 27%, which they used as input to a physiologically based multilayer process-based ecosystem productivity model (which contained a carbon allocation sub-model coupled with a soil model) to evaluate net productivity changes of six French forest ecosystems representative of oceanic, continental, and Mediterranean climates dominated, respectively, by deciduous species (*Fagus sylvatica*, *Quercus robur*), coniferous species (*Pinus pinaster*, *Pinus sylvestris*), and sclerophyllous evergreen species (*Quercus ilex*). These ecosystems, they write, “are representative of a significant proportion of forests in western Europe.”

“By comparing runs with and without CO₂ effects,” according to the researchers, they found “CO₂ fertilization is responsible from 1960 to 2100 for an NEP [net ecosystem productivity] enhancement of about 427 g(C) on average for all sites (= 3.05 g(C) m⁻² year⁻¹),” and “the CO₂ fertilization effect” turns a

warming- and drying-induced “decrease of NEP into an increase.” In addition, they report, “no saturation of this effect on NEP is found because the differences between the simulations with and without CO₂ fertilization continuously increase with time.” Consequently, the real-world physiological effects of atmospheric CO₂ enrichment included in the ecosystem productivity model employed by Davi *et al.* are able to more than compensate for the deleterious effects of the dramatic climate-change scenario on the productivity of major European forests.

Pardos *et al.* (2006) grew seedlings of cork oak (*Quercus suber* L., which they describe as “a typical Mediterranean species”) germinated from acorns they collected from trees near Toledo, Spain, and maintained for five months, one per each 3-L pot filled with a mixture of fine sand and peat. The seedlings were maintained at either high (83%) or low (32–34%) growing medium moisture, under either high (600 μmol m⁻² s⁻¹) or low (60 μmol m⁻² s⁻¹) light intensity, in growth chambers maintained at either ambient (360 ppm) or elevated (700 ppm) atmospheric CO₂ concentrations. The four Spanish researchers state “elevated CO₂ caused the cork oak seedlings to improve their performance in dry and high light environments to a greater extent than under well-irrigated and low-light conditions, thus ameliorating the effects of soil water stress and high light loads on growth.” Consequently, and because they assume these latter two stressful conditions are what “global change is likely to produce in the Mediterranean basin in the next decades,” the rise in the air's CO₂ concentration should help the cork oak species deal successfully with those stresses, if and when they occur.

Saleska *et al.* (2007) note “large-scale numerical models that simulate the interactions between changing global climate and terrestrial vegetation predict substantial carbon loss from tropical ecosystems, including the drought-induced collapse of the Amazon forest and conversion to savanna.” They used Terra satellite data—Enhanced Vegetation Index (EVI) derived from the Moderate Resolution Imaging Spectroradiometer (MODIS)—to determine whether the widespread Amazon drought of 2005, which peaked during the dry season onset (July–September), did indeed reduce whole-canopy forest photosynthesis as predicted, which they said “should have been especially observable during this period, when anomalous interannual drought coincided with the already seasonally low precipitation.”

Strongly contradicting the model predictions, the

four researchers found intact forest “greenness” in the region was “dominated by a significant increase ($P < 0.0001$), not a decline.” They say the trees of the Amazon forest may be utilizing deep roots to “access and sustain” water availability during drought. Another possibility is the historical increase in the air’s CO_2 content has significantly enhanced the trees’ water use efficiency, enabling them to produce considerably more biomass per unit of water transpired and thereby conserve water. And yet another possibility is the phenomenon described in Soule and Knapp (2006), Wang *et al.* (2006), Davi *et al.* (2006), and Pardos *et al.* (2006), discussed above.

Huang *et al.* (2007) compared, synthesized, and evaluated the scientific literature describing atmospheric CO_2 enrichment experiments conducted on trees and empirical tree-ring studies designed to ascertain whether the growth-promoting effects of rising atmospheric CO_2 concentrations occur in natural forests. They found numerous CO_2 -enrichment experiments have “demonstrated significantly positive physiological and growth responses of trees to CO_2 , providing strong evidence to support the direct CO_2 fertilization effect (increased photosynthesis, water use efficiency, above- and below-ground growth) and thus allowing prediction of which ecosystems might be most responsive to CO_2 .” They conclude the latter will be “warm, moderately drought-stressed ecosystems with an ample nitrogen supply,” because “drought-stressed trees could benefit from increased water use efficiency to enhance growth.” They also note tree-ring studies on the cold and arid Tibetan Plateau “showed significant growth enhancements as well as increased water use efficiency (24.7% and 33.6% for each species, respectively) in Qilian juniper and Qinghai spruce since the 1850s,” citing Zhang *et al.* (2003), Shao *et al.* (2005), Liang *et al.* (2006), Huang and Zhang (2007), and Zhang and Qiu (2007).

Wyckoff and Bowers (2010) note, “with continued increases in global greenhouse gas emissions, climate models predict that, by the end of the 21st century, Minnesota [USA] summer temperature will increase by 4–9°C and summer precipitation will slightly decrease,” citing Kling *et al.* (2003) and Christensen *et al.* (2007). They state certain “forest models and extrapolations from the paleoecological record suggest that, in response to increased temperature and/or drought, forests may retreat to the extreme north-eastern parts of the state,” citing Pastor and Post (1998), Hamilton and Johnson (2002), and Galatowitsch *et al.* (2009). Working with bur oak

(*Quercus macrocarpa*) trees, Wyckoff and Bowers explored the likelihood of this scenario by: “(i) using tree rings to establish the relationship between drought and *Q. macrocarpa* growth for three sites along Minnesota’s prairie-forest border, (ii) calculating the current relationship between growth and mortality for adult *Q. macrocarpa* and (iii) using the distributions of current growth rates for *Q. macrocarpa* to predict the susceptibility of current populations to droughts of varying strength.” In addition, they looked for “temporal trends in the correlation between *Q. macrocarpa* growth and climate, hypothesizing that increases in CO_2 may lead to weaker relationships between drought and tree growth over time,” because atmospheric CO_2 enrichment typically leads to increases in plant water use efficiency, which generally makes them less susceptible to the deleterious impact of drought on growth.

The two University of Minnesota researchers report “the sensitivity of annual growth rates to drought has steadily declined over time as evidenced by increasing growth residuals and higher growth rates for a given PDSI [Palmer Drought Severity Index] value after 1950 [when the atmosphere’s CO_2 concentration rose by 57 ppm from 1950 to 2000] compared with the first half of the century [when the CO_2 increase was only 10 ppm].” They state “for *Q. macrocarpa*, declining sensitivity of growth to drought translates into lower predicted mortality rates at all sites,” and at one such site, “declining moisture sensitivity yields a 49% lower predicted mortality from a severe drought (PDSI = -8, on a par with the worst 1930s ‘American Dust Bowl’ droughts).” Wyckoff and Bowers conclude “the decreasing drought sensitivity of established trees may act as a buffer and delay the movement of the prairie-forest ecotone for many decades even in the face of climate change.”

Noting climate models “consistently project significant increases in temperature and decreases in precipitation in the Mediterranean basin,” Keenan *et al.* (2011) report these changes may have a large impact on current Mediterranean forests and the related ecosystem services they provide. They note niche-based models—also known as bioclimatic envelope models or habitat models—are the most commonly used method for predicting potential species distribution responses to future climatic changes. These models typically predict significant negative consequences for terrestrial plants and animals in the face of continued increases in

atmospheric CO₂ concentrations.

Keenan *et al.* say they preferred process-based models, which describe eco-physiological processes ranging from purely empirical relationships to mechanistic descriptions based on physical laws. These models—supported by experiments and growth and yield surveys—“suggest that global warming will have a positive impact on forest productivity (van der Meer *et al.*, 2002; Nigh *et al.*, 2004; Norby and Luo, 2004; Briceño-Elizondo *et al.*, 2006; Gaucharel *et al.*, 2008), due to the direct fertilization effect of increased CO₂ and indirect effects such as lengthening of the growing period.”

To demonstrate the difference in results obtained by these two approaches to forecasting, the five researchers assessed and compared the projections of each when applied to stands of three common forest species (*Quercus ilex*, *Pinus halepensis*, and *Pinus sylvestris*) with widely contrasting distributions in continental Spain. This procedure revealed, they write, “CO₂ fertilization through projected increased atmospheric CO₂ concentrations is shown to increase forest productivity in the mechanistic process-based model (despite increased drought stress) by up to three times the non-CO₂ fertilization scenario by the period 2050–2080, which is in stark contrast to projections of reduced habitat suitability from the niche-based models by the same period.”

Thus the Spanish and U.S. scientists write, “previous reports of species decline in continental Spain (e.g. Benito-Garzon *et al.*, 2008) may be overestimated due to two reasons: the use of only one predictive niche-based model, and the failure to account for possible effects of CO₂ fertilization.” They add, “similar studies in other regions, which do not consider these two aspects, are also potentially overestimating species decline due to climate change.” They note, “niche-based model results also likely overestimate the decline in [habitat] suitability,” and they therefore conclude “an organism’s niche must be modeled mechanistically if we are to fully explain distribution limits,” citing Kearney (2006).

Osorio *et al.* (2011) write, “water deficits and high temperature are major abiotic stress factors restricting plant growth and productivity in many regions,” and “the impact of climate change on temperature and rainfall patterns is of great importance in determining the future response of tree crops to new environmental conditions.” They studied the Carob or St. John’s tree (*Ceratonia siliqua*), which grows in the Mediterranean, where they

contend water stress will be the most important factor limiting plant growth throughout the remainder of this century. They investigated the impacts of drought and high-temperature stresses on photosynthesis, energy partitioning, and membrane lipids, as well as the potential ability of Carob trees to attenuate oxidative damage, in young seedlings growing in controlled-environment chambers. They rooted the plants in 3-dm³ pots filled with a 2:1 mixture of a fertilized substrate and natural soil and maintained them under two thermal regimes—low and high temperature (LT: 25/18°C; HT: 32/21°C)—and three soil water conditions (control, water stress, and rewetting), monitoring numerous physiological and biochemical plant properties and processes.

Osorio *et al.* report the decrease in net photosynthesis (PN) caused by drought was 33% in the LT chamber and 84% in the HT chamber. They say “the negative effects of soil drying on PN and stomatal conductance of HT plants were no longer detected 36 hours following rewatering.” The five Portuguese scientists remark, “although *C. siliqua* seedlings exhibit clear signs of oxidative stress under drought and high temperature, they retain a remarkable ability to quickly restore normal physiological activity on rehydration, which let us believe that they can satisfactorily deal with predicted climate warming and increased soil drying in the Mediterranean area.”

Soule and Knapp (2011) write, “in 2008, atmospheric CO₂ concentrations from the Mauna Loa, Hawaii, Observatory records exceeded 385 ppm, representing a 22% increase since 1959.” They note, “as CO₂ has increased, most tree species have been able to use water more efficiently” as their “leaf stomatal apertures narrow during photosynthesis,” resulting in “less transpirational water loss per biomass gained.” The parameter representing this phenomenon is referred to as intrinsic water-use efficiency (iWUE), defined as the ratio of net CO₂ assimilation to stomatal conductance, and it has been documented, they write, “for various tree species in many parts of the world,” citing Bert *et al.* (1997), Feng (1999), Tang *et al.* (1999), Arneth *et al.* (2002), Saurer *et al.* (2004), Waterhouse *et al.* (2004), and Liu *et al.* (2007).

They examined changes in, and relationships between, radial growth rates and the iWUE of ponderosa pine (*Pinus ponderosa*) trees, climate, and atmospheric CO₂ concentration in the western United States since the mid-nineteenth century, developing tree-ring chronologies for eight sites in three climate

regions, and using carbon isotope data to calculate pentadal values of iWUE. They examined relationships among radial growth, climate, iWUE, and CO₂ via correlation and regression analyses.

Soule and Knapp report finding significant upward trends in iWUE at all sites, and they state “despite an absence of climate changes that would favor growth,” upward radial growth trends occurred at five sites. The highest iWUE values “were recorded in the last pentad at six of eight sites and follow a positive quadratic progression at all sites, suggesting that future increases in iWUE are likely for ponderosa pine within our study regions as CO₂ levels increase.” They also found “significant improvements in radial growth rates during drought years after 1950,” when the air’s CO₂ content rose at an accelerating rate.

The two researchers say their findings suggest “increased iWUE associated with rising CO₂ can positively impact tree growth rates in the western United States and are thus an evolving component of forest ecosystem processes.” They conclude, “if potential climate changes lead to increasing aridity in the western United States, additional increases in iWUE associated with future increases in CO₂ might ameliorate growth declines associated with drought conditions.”

The peer-reviewed scientific studies described in this section support the earlier conclusions of Idso and Idso (1994), who found the rise in the air’s CO₂ content likely will lead to substantial increases in photosynthetic rates and biomass production in Earth’s many woody species, even under stressful conditions imposed by suboptimal soil moisture.

References

- Ainsworth, E.A. and Long, S.P. 2005. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytologist* **165**: 351–372.
- Anderson, P.D. and Tomlinson, P.T. 1998. Ontogeny affects response of northern red oak seedlings to elevated CO₂ and water stress. I. Carbon assimilation and biomass production. *New Phytologist* **140**: 477–491.
- Arneth, A., Lloyd, J., Santruckova, H., Bird, M., Girgoryev, S., Kalaschnikov, Y.N., Gleixner, G., and Schulze, E. 2002. Response of central Siberian Scots pine to soil water deficit and long-term trends in atmospheric CO₂ concentration. *Global Biogeochemical Cycles* **16**: 10.1029/2000GB001374.
- Arp, W.J., Van Mierlo, J.E.M., Berendse, F., and Snijders, W. 1998. Interactions between elevated CO₂ concentration, nitrogen and water: effects on growth and water use of six perennial plant species. *Plant, Cell and Environment* **21**: 1–11.
- Benito-Garzon, M., Sanchez de Dios, R., and Sainz Ollero, H. 2008. Effects of climate change on the distribution of Iberian tree species. *Applied Vegetation Science* **11**: 169–178.
- Bert, D., Leavitt, S., and Dupouey, J.-L. 1997. Variations of wood $\delta^{13}\text{C}$ and water-use efficiency of *Abies alba* during the last century. *Ecology* **78**: 1588–1596.
- Briceño-Elizondo, R., Garcia-Gonzalo, J., Peltola, H., Matala, J., and Kellomaki, S. 2006. Sensitivity of growth of Scots pine, Norway spruce and silver birch to climate change and forest management in boreal conditions. *Forest Ecology and Management* **232**: 152–167.
- Catovsky, S. and Bazzaz, F.A. 1999. Elevated CO₂ influences the responses of two birch species to soil moisture: implications for forest community structure. *Global Change Biology* **5**: 507–518.
- Centritto, M. 2002. The effects of elevated [CO₂] and water availability on growth and physiology of peach (*Prunus persica*) plants. *Plant Biosystems* **136**: 177–188.
- Centritto, M., Lee, H.S.J., and Jarvis, P.G. 1999b. Interactive effects of elevated [CO₂] and drought on cherry (*Prunus avium*) seedlings. I. Growth, whole-plant water use efficiency and water loss. *New Phytologist* **141**: 129–140.
- Centritto, M., Magnani, F., Lee, H.S.J., and Jarvis, P.G. 1999a. Interactive effects of elevated [CO₂] and drought on cherry (*Prunus avium*) seedlings. II. Photosynthetic capacity and water relations. *New Phytologist* **141**: 141–153.
- Christensen, J.H., Hewitson, B., Bisuioc, A., Chen, A., Gao, X., and Held, I. *et al.* 2007. Regional climate projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Avery, K.B., Tignor, M., and Miller, H.L. (Eds.) *Climate Change 2007: The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (Cambridge University Press, Cambridge, UK/New York, New York, USA, pp. 847–940.
- Davi, H., Dufrene, E., Francois, C., Le Maire, G., Loustau, D., Bosc, A., Rambal, S., Granier, A., and Moors, E. 2006. Sensitivity of water and carbon fluxes to climate changes from 1960–2100 in European forest ecosystems. *Agricultural and Forest Meteorology* **141**: 35–56.
- Feng, X. 1999. Trends in intrinsic water-use efficiency of natural trees for the past 100–200 years: A response to atmospheric CO₂ concentration. *Geochimica et Cosmochimica Acta* **63**: 1891–1903.

Plants Under Stress

- Fernandez, M.D., Pieters, A., Azuke, M., Rengifo, E., Tezara, W., Woodward, F.I., and Herrera, A. 1999. Photosynthesis in plants of four tropical species growing under elevated CO₂. *Photosynthetica* **37**: 587–599.
- Fernandez, M.D., Pieters, A., Donoso, C., Tezara, W., Azuke, M., Herrera, C., Rengifo, E., and Herrera, A. 1998. Effects of a natural source of very high CO₂ concentration on the leaf gas exchange, xylem water potential and stomatal characteristics of plants of *Spatiphyllum cannifolium* and *Bauhinia multinervia*. *New Phytologist* **138**: 689–697.
- Galatowitsch, S., Frelich, L., and Phillips-Mao, L. 2009. Regional climate change adaptation strategies for biodiversity conservation in a mid-continental region of North America. *Biological Conservation* **142**: 2012–2022.
- Gaucharel, C., Guiot, J., and Misson, L. 2008. Changes of the potential distribution area of French Mediterranean forests under global warming. *Biogeosciences* **5**: 1493–1503.
- Hamerlynck, E.P., Huxman, T.E., Loik, M.E., and Smith, S.D. 2000. Effects of extreme high temperature, drought and elevated CO₂ on photosynthesis of the Mojave Desert evergreen shrub, *Larrea tridentata*. *Plant Ecology* **148**: 183–193.
- Hamilton, J.D. and Johnson, S. 2002. *Playing with Fire: Climate Change in Minnesota*. Minnesotans for an Energy-Efficient Economy. St Paul, Minnesota, USA.
- Huang, J.-G., Bergeron, Y., Denneler, B., Berninger, F., and Tardif, J. 2007. Response of forest trees to increased atmospheric CO₂. *Critical Reviews in Plant Sciences* **26**: 265–283.
- Huang, J.G. and Zhang, Q.B. 2007. Tree-rings and climate for the last 680 years in Wulan area of northeastern Qinghai-Tibetan Plateau. *Climatic Change* **80**: 369–377.
- Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: A review of the past 10 years' research. *Agricultural and Forest Meteorology* **69**: 153–203.
- Idso, S.B. and Kimball, B.A. 2001. CO₂ enrichment of sour orange trees: 13 years and counting. *Environmental and Experimental Botany* **46**: 147–153.
- Kearney, M. 2006. Habitat, environment and niche: what are we modeling? *Oikos* **115**: 186–191.
- Keenan, T., Serra, J.M., Lloret, F., Ninyerola, M., and Sabate, S. 2011. Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO₂ matters! *Global Change Biology* **17**: 565–579.
- Kling, G.W., Hayhoe, K., Johnson, L.B., Magnuson, J.J., Polasky, S., and Robinson, S.K., et al. 2003. *Confronting Climate Change in the Great Lakes Region: Impacts on our Communities and Ecosystems*. Union of Concerned Scientists and Ecological Society of America, Washington, DC, USA.
- Knapp, P.A., Soule, P.T., and Grissino-Mayer, H.D. 2001. Post-drought growth responses of western juniper (*Juniperus occidentalis* var. *occidentalis*) in central Oregon. *Geophysical Research Letters* **28**: 2657–2660.
- Liang, E.Y., Shao, X.M., Eckstein, D., Huang, L., and Liu, X.H. 2006. Topography- and species-dependent growth response of *Sabina przewalskii* and *Picea crassifolia* to climate on the northeast Tibetan Plateau. *Forest Ecology and Management* **236**: 268–277.
- Liu, X., Shao, X., Liang, E., Zhao, L., Chen, T., Qin, D., and Ren, J. 2007. Species dependent responses of juniper and spruce to increasing CO₂ concentration and to climate in semi-arid and arid areas of northwestern China. *Plant Ecology* **193**: 195–209.
- Nigh, G.D., Ying, C.C., and Qian, H. 2004. Climate and productivity of major conifer species in the interior of British Columbia, Canada. *Forest Science* **50**: 659–671.
- Norby, R.J. and Luo, Y. 2004. Evaluating ecosystem responses to rising atmospheric CO₂ and global warming in a multi-factor world. *New Phytologist* **162**: 281–293.
- Osorio, M.L., Osorio, J., Vieira, A.C., Goncalves, S., and Romano, A. 2011. Influence of enhanced temperature on photosynthesis, photooxidative damage, and antioxidant strategies in *Ceratonia siliqua* L. seedlings subjected to water deficit and rewatering. *Photosynthetica* **49**: 3–12.
- Osborne, C.P., Mitchell, P.L., Sheehy, J.E., and Woodward, F.I. 2000. Modeling the recent historical impacts of atmospheric CO₂ and climate change on Mediterranean vegetation. *Global Change Biology* **6**: 445–458.
- Palanisamy, K. 1999. Interactions of elevated CO₂ concentration and drought stress on photosynthesis in *Eucalyptus cladocalyx* F. Muell. *Photosynthetica* **36**: 635–638.
- Pardos, M., Puertolas, J., Aranda, I., and Pardos, J.A. 2006. Can CO₂ enrichment modify the effect of water and high light stress on biomass allocation and relative growth rate of cork oak seedlings? *Trees* **20**: 713–724.
- Pastor, J. and Post, W.M. 1988. Response of northern forests to CO₂-induced climate change. *Nature* **334**: 55–58.
- Polley, H.W., Tischler, C.R., Johnson, H.B., and Derner, J.D. 2002. Growth rate and survivorship of drought: CO₂ effects on the presumed tradeoff in seedlings of five woody legumes. *Tree Physiology* **22**: 383–391.

Climate Change Reconsidered II: Biological Impacts

- Polley, H.W., Tischler, C.R., Johnson, H.B., and Pennington, R.E. 1999. Growth, water relations, and survival of drought-exposed seedlings from six maternal families of honey mesquite (*Prosopis glandulosa*): responses to CO₂ enrichment. *Tree Physiology* **19**: 359–366.
- Runion, G.B., Mitchell, R.J., Green, T.H., Prior, S.A., Rogers, H.H., and Gjerstad, D.H. 1999. Longleaf pine photosynthetic response to soil resource availability and elevated atmospheric carbon dioxide. *Journal of Environmental Quality* **28**: 880–887.
- Saleska, S.R., Didan, K., Huete, A.R., and da Rocha, H.R. 2007. Amazon forests green-up during 2005 drought. *Scienceexpress*: 10.1126/science.1146663.
- Saurer, M., Siegwolf, R., and Schweingruber, F. 2004. Carbon isotope discrimination indicates improving water-use efficiency of trees in northern Eurasia over the last 100 years. *Global Change Biology* **10**: 2109–2120.
- Schulte, M., Herschbach, C., and Rennenberg, H. 1998. Interactive effects of elevated atmospheric CO₂, mycorrhization and drought on long-distance transport of reduced sulfur in young pedunculate oak trees (*Quercus robur* L.). *Plant, Cell and Environment* **21**: 917–926.
- Shao, X.M., Huang, L., Liu, H.B., Liang, E.Y., Fang, X.Q., and Wang, L.L. 2005. Reconstructions of precipitation variation from tree-rings in recent 1000 years in Delingha, Qinghai. *Science in China* **48**: 939–949.
- Soule, P.T. and Knapp, P.A. 2006. Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century CO₂ fertilization effect? *New Phytologist* doi: 10.1111/j.1469-8137.2006.01746.x.
- Soule, P.T. and Knapp, P.A. 2011. Radial growth and increased water-use efficiency for ponderosa pine trees in three regions in the western United States. *The Professional Geographer* **63**: 370–391.
- Tang, K., Feng, X., and Funkhouser, G. 1999. The $\delta^{13}\text{C}$ of trees in full-bark and strip-bark bristlecone pine trees in the White Mountains of California. *Global Change Biology* **5**: 33–40.
- Tognetti, R., Longobucco, A., Miglietta, F., and Raschi, A. 1998. Transpiration and stomatal behaviour of *Quercus ilex* plants during the summer in a Mediterranean carbon dioxide spring. *Plant, Cell and Environment* **21**: 613–622.
- Tognetti, R., Raschi, A., and Jones M.B. 2002. Seasonal changes in tissue elasticity and water transport efficiency in three co-occurring Mediterranean shrubs under natural long-term CO₂ enrichment. *Functional Plant Biology* **29**: 1097–1106.
- Tomlinson, P.T. and Anderson, P.D. 1998. Ontogeny affects response of northern red oak seedlings to elevated CO₂ and water stress. II. Recent photosynthate distribution and growth. *New Phytologist* **140**: 493–504.
- Tuba, Z., Csintalan, Z., Szente, K., Nagy, Z., and Grace, J. 1998. Carbon gains by desiccation-tolerant plants at elevated CO₂. *Functional Ecology* **12**: 39–44.
- van der Meer, P.J., Jorritsma, I.T.M., and Kramer, J.K. 2002. Assessing climate change effects on long-term forest development: adjusting growth, phenology and seed production in a gap model. *Forest Ecology and Management* **162**: 39–52.
- Wang, G.G., Chhin, S. and Bauerle, W.L. 2006. Effect of natural atmospheric CO₂ fertilization suggested by open-grown white spruce in a dry environment. *Global Change Biology* **12**: 601–610.
- Waterhouse, J., Switsur, V., Barker, A., Carter, A., Hemming, D., Loader, N., and Robertson, I. 2004. Northern European trees show a progressively diminishing response to increasing atmospheric carbon dioxide concentrations. *Quaternary Science Reviews* **23**: 803–810.
- Wyckoff, P.H. and Bowers, R. 2010. Response of the prairie-forest border to climate change: impacts of increasing drought may be mitigated by increasing CO₂. *Journal of Ecology* **98**: 197–208.
- Xiao, C.-W., Sun, O.J., Zhou, G.-S., Zhao, J.-Z., and Wu, G. 2005. Interactive effects of elevated CO₂ and drought stress on leaf water potential and growth in *Caragana intermedia*. *Trees* **19**: 711–720.
- Zhang, Q.B., Cheng, G.D., Yao, T.D., Kang, X.C., and Huang, J.G. 2003. A 2,326-year tree-ring record of climate variability on the northeastern Qinghai-Tibetan Plateau. *Geophysical Research Letters* **30**: 10.1029/2003GL017425.
- Zhang, Q.B. and Qiu, H.Y. 2007. A millennium-long tree-ring chronology of *Sabina przewalskii* on northeastern Qinghai-Tibetan Plateau. *Dendrochronologia* **24**: 91–95.
- Zhang, X.S. 1994. The ecological background of the Maowusu sandland: the principles and optimal models for grass land management. *Acta Photoecologica Sinica* **18**: 1–6.

3.16 Weeds

Some researchers suggest weeds will become more aggressive as the air's CO₂ content climbs, making them greater threats to the wellbeing of natural ecosystems and farming operations. The subsections below investigate the merits of this claim regarding non-parasitic and parasitic weeds.

3.16.1 Non-Parasitic

- Non-parasitic weeds likely will be no more competitive in a high-CO₂ environment than they are today, and many could become less competitive. Atmospheric CO₂ enrichment may provide non-weeds with greater protection against weed-induced decreases in productivity, thereby increasing the competitiveness of non-weeds over weeds. And although atmospheric CO₂ enrichment increases the growth of many weeds, the fraction helped is probably not as large as non-weeds.

3.16.1.1 Competitiveness

- Non-parasitic weeds likely will be no more competitive in a high-CO₂ environment than they are today, and many could become less competitive.

Wayne *et al.* (1999) grew a common agricultural weed (field mustard) at six densities in pots exposed to atmospheric CO₂ concentrations of 350 and 700 ppm, sequentially harvesting them during the growing season. Early in stand development, the extra CO₂ increased above-ground biomass in a density-dependent manner; with the greatest stimulation (141%) occurring at the lowest weed density (20 plants per square meter) and the smallest stimulation (59%) occurring at the highest weed density (652 plants per square meter), the authors report. As the stands matured, the density-dependence of the growth response disappeared, and the CO₂-enriched weeds exhibited an average above-ground biomass 34% greater than those grown in ambient air. That response is similar to those of most herbaceous plants (a 30 to 50% increase for a doubling of the air's CO₂ content) and less than those of most woody species (50% and up). Consequently, in currently farmed or abandoned agricultural fields, as well as in regenerating forests, it is unlikely field mustard plants will benefit relative to other plants from Earth's rising atmospheric CO₂ concentration.

Caporn *et al.* (1999) grew bracken—a serious weed and potential threat to human health in the United Kingdom and elsewhere—for 19 months in controlled-environment chambers maintained at atmospheric CO₂ concentrations of 370 and 570 ppm and normal or high levels of fertilization. They found the extra 200 ppm of CO₂ increased rates of net

photosynthesis by 30 to 70%, depending on soil fertility and time of year. The elevated CO₂ did not increase total plant biomass, nor did it increase the biomass of any plant organs, including rhizomes, roots, and fronds. The only significant effect of elevated CO₂ on plant growth was observed in the normal nutrient regime, where it reduced average frond area.

Gavazzi *et al.* (2000) grew one-year-old loblolly pine seedlings for four months in pots seeded with a variety of C₃ and C₄ weeds and maintained at adequate and inadequate levels of soil moisture in growth chambers maintained at atmospheric CO₂ concentrations of 360 and 660 ppm. The elevated CO₂ increased pine seedling biomass by 22%, decreased total weed biomass by 22%, and reduced the percentage of weed biomass composed of C₄ species from 53 to 35%. The additional CO₂ induced an increase in root-to-shoot ratio under water-stressed conditions in the pine seedlings, which Gavazzi *et al.* opine could “contribute to an improved ability of loblolly pine to compete against weeds on dry sites under elevated CO₂ levels.”

Ziska (2003) grew Canada thistle, “the most frequently listed noxious weed species in surveys of the continental United States and southern Canada,” in pots watered to the drip point daily with one of three complete nutrient solutions that differed only in nitrogen (N) concentration (3.0, 6.0, or 14.5 mM) in controlled-environment chambers maintained at 287 and 373 ppm CO₂ from seeding until flowering, which occurred at 77 days after seeding (DAS). He reports, “N supply did not affect the relative response to CO₂ for any measured vegetative parameter up to 77 DAS.” Averaged across the three nitrogen treatments, the 86 ppm increase in atmospheric CO₂ concentration increased total plant biomass by 65.5%, which for the full 100 ppm CO₂ increase experienced over the course of the Industrial Revolution (initial value ~275 ppm, current value ~375 ppm) translates into an approximate 76% biomass increase.

To assess the significance of this CO₂-induced increase in weed biomass, it is necessary to compare it with what would have been expected for crops with which Canada thistle competes. Mayeux *et al.* (1997) obtained data indicating the 100-ppm increase in atmospheric CO₂ concentration experienced over the course of the Industrial Revolution should have produced yield increases of 70 and 74% in the two wheat varieties they studied when grown under well-watered conditions comparable to those studied by Ziska. In addition, based on the voluminous data Idso

and Idso (2000) summarized, we can scale these results to derive comparable CO₂-induced growth enhancements of 84% for other C₃ cereals, 74% for legumes, and 80% for root and tuber crops. Thus the CO₂-induced growth enhancement likely experienced by Canada thistle over the course of the Industrial Revolution was not much different from the growth enhancements of most of the crops with which it competes, suggesting the competitive ability of this noxious weed against these crops has remained largely unaffected by the historical increase in the air's CO₂ content.

Ziska and Goins (2006) grew genetically modified (Round-up Ready) soybean plants in the field in aluminum chambers maintained at ambient and ambient + 250 ppm atmospheric CO₂ concentrations for two full growing seasons under conditions allowing a variety of different weed densities to develop among the soybeans. The elevated CO₂ conditions advanced soybean seed yields by 25, 33, 50, 90, and 250% when chamber weed biomass densities were 0, 200, 400, 600, and 800 gm⁻², respectively. Soybean seed yield in the ambient-air treatment fell to a value of zero at a weed density of approximately 920 gm⁻², whereas calculations reveal it would not drop that far in the CO₂-enriched treatment until a weed density of approximately 1,250 gm⁻² was reached. Consequently, the atmospheric CO₂ enrichment of this study boosted crop yield by an increasing percentage as the stress of the expanding weed population grew larger, benefiting the soybean plants most when they needed it most. This phenomenon also has been shown to be true of other environmental stressors, such as plant diseases, lack of water, and high temperatures.

Kao-Kniffin and Balser (2007) grew invasive reed canary grass from seed for four months in well-watered mesocosms located in greenhouses maintained at atmospheric CO₂ concentrations of either 365 or 600 ppm in soils of either low or high nitrogen (N) supply (5 mg N l⁻¹ or 30 mg N l⁻¹) under conditions where the invading species was either dominant (high invasion: >90% cover) or subdominant (low invasion: <50% cover), and where the remaining surface portions of the mesocosms were covered with native graminoids (grasses, sedges, and bulrushes) and native forbs also grown from seed. Elevating the air's CO₂ content increased below-ground biomass only in the plant communities moderately invaded by reed canary grass, and the only plants to show a significant increase in above-ground biomass were the native graminoids in the

moderately invaded low N treatment. The scientists conclude, "when CO₂ concentrations rise in the future, wetland plant communities comprised of native graminoids may be better able to hinder reed canary grass invasion, particularly under low N environments."

Williams *et al.* (2007) studied the impacts of a 170 ppm increase in atmospheric CO₂ concentration and a 2°C rise in air temperature at the Tasmanian free-air CO₂ enrichment (TasFACE) facility, located in a native lowland grassland in the southern midlands region of Tasmania, Australia. Between spring 2003 and summer 2006, they documented annual seed production, seedling emergence, seedling survival, and adult survival of four abundant perennial species, including the two most dominant invading weeds: *Hypochaeris radicata* L. and *Leontodon taraxacoides* (Vill.) Merat, members of the Asteraceae family. They found no significant CO₂-induced differences in the population growth rates of either weed species, but the population growth rates of both "were substantially reduced by warming." The six researchers conclude "global warming may be a more important determinant of the success of invasive species than CO₂ concentration," and both the invading weed species they studied "are likely to be excluded from the grassland community by increasing temperatures."

McPeck and Wang (2007) collected seeds from a single dandelion plant in Speedway, Indiana (USA), which they allowed to sprout and grow until reaching reproductive maturity in pots placed in each of two controlled-environment chambers, one continually flushed with ambient air of 370 ppm CO₂ and the other maintained at an elevated atmospheric CO₂ concentration of 730 ppm. After harvesting the plants and measuring numerous parameters of reproductive fitness, the two scientists conducted a second experiment in which they measured various parameters of the germination of the seeds produced in the two CO₂ treatments, along with the physical characteristics of the second-generation plants 35 days after planting.

McPeck and Wang state the dandelion plants "produced 83% more inflorescences and 32% more achenes, i.e., single-seed fruits, per plant at elevated than at ambient CO₂," and the "seeds from elevated CO₂-grown plants were significantly heavier and had a higher germination percentage, leading to larger seedlings and earlier establishment in the subsequent generation." Furthermore, "achenes from plants grown at elevated CO₂ had characteristics, such as higher stalks at seed maturity, longer beaks, and

larger pappi, which would increase the distance of seed dispersal by wind.”

The two researchers conclude “dandelion can potentially become more widespread and noxious as atmospheric CO₂ continues to rise.”

References

Caporn, S.J.M., Brooks, A.L., Press, M.C., and Lee, J.A. 1999. Effects of long-term exposure to elevated CO₂ and increased nutrient supply on bracken (*Pteridium aquilinum*). *Functional Ecology* **13**: 107–115.

Gavazzi, M., Seiler, J., Aust, W., and Zedaker, S. 2000. The influence of elevated carbon dioxide and water availability on herbaceous weed development and growth of transplanted loblolly pine (*Pinus taeda*). *Environmental and Experimental Botany* **44**: 185–194.

Idso, C.D. and Idso, K.E. 2000. Forecasting world food supplies: The impact of the rising atmospheric CO₂ concentration. *Technology* **7S**: 33–56.

Kao-Kniffin, J. and Balser, T.C. 2007. Elevated CO₂ differentially alters belowground plant and soil microbial community structure in reed canary grass-invaded experimental wetlands. *Soil Biology & Biochemistry* **39**: 517–525.

Mayeux, H.S., Johnson, H.B., Polley, H.W., and Malone, S.R. 1997. Yield of wheat across a subambient carbon dioxide gradient. *Global Change Biology* **3**: 269–278.

McPeck, T.M. and Wang, X. 2007. Reproduction of dandelion (*Taraxacum officinale*) in a higher CO₂ environment. *Weed Science* **55**: 334–340.

Wayne, P.M., Carnelli, A.L., Connolly, J., and Bazzaz, F.A. 1999. The density dependence of plant responses to elevated CO₂. *Journal of Ecology* **87**: 183–192.

Williams, A.L., Wills, K.E., Janes, J.K., Vander Schoor, J.K., Newton, P.C.D., and Hovenden, M.J. 2007. Warming and free-air CO₂ enrichment alter demographics in four co-occurring grassland species. *New Phytologist* **176**: 365–374.

Ziska, L.H. 2003. The impact of nitrogen supply on the potential response of a noxious, invasive weed, Canada thistle (*Cirsium arvense*) to recent increases in atmospheric carbon dioxide. *Physiologia Plantarum* **119**: 105–112.

Ziska, L.H. and Goins, E.W. 2006. Elevated atmospheric carbon dioxide and weed populations in glyphosate treated soybean. *Crop Science* **46**: 1354–1359.

3.16.1.2 Biodiversity Impacts

- Rising atmospheric CO₂ concentrations will not favor the growth of non-parasitic weeds over crops and native plants. A CO₂ increase may provide the latter with greater protection against weed-induced decreases in productivity, thereby increasing the competitiveness of non-weeds over weeds.

Elevated CO₂ typically stimulates the growth of nearly all plant species in monoculture, including weeds. Consequently, it is important to determine how future increases in the air's CO₂ content may influence relationships between weeds and non-weeds when they grow competitively in mixed-species stands.

Dukes (2002) grew model serpentine grasslands common to California (USA) in competition with the invasive forb *Centaurea solstitialis* at atmospheric CO₂ concentrations of 350 and 700 ppm for one year. They found elevated CO₂ increased the biomass proportion of this weedy species in the community by 1.2%, while total community biomass increased by 28%. Similarly, Gavazzi *et al.* (2000) grew loblolly pine seedlings for four months in competition with C₃ and C₄ weeds at atmospheric CO₂ concentrations of 260 and 660 ppm, reporting elevated CO₂ increased pine biomass by 22% while eliciting no response from either type of weed. In a study of pasture ecosystems near Montreal, Canada, Taylor and Potvin (1997) determined elevated CO₂ concentrations did not influence the number of native species returning after their removal (to simulate disturbance), even in the face of the introduced presence of the C₃ weed *Chenopodium album*, which normally competes quite effectively with several slower-growing crops in ambient air. Atmospheric CO₂ enrichment did not impact the growth of this weed in any measurable way.

Ziska *et al.* (1999) studied the C₃ weed *C. album*, along with the C₄ weed *Amaranthus retroflexus*, in glasshouses maintained at atmospheric CO₂ concentrations of 360 and 720 ppm. Elevated CO₂ significantly increased the photosynthetic rate and total dry weight of the C₃ weed but had no effect on the C₄ weed. They report the growth response of the C₃ weed to a doubling of the air's CO₂ content was approximately 51%, about the same as the average 52% growth response tabulated by Idso (1992) and by Poorter (1993) for rapidly growing wild C₃ species (54%), suggesting a CO₂-enriched environment does not cause enhanced dominance of the C₃ weed over

other C₃ plants.

Wayne *et al.* (1999) studied another agricultural weed, field mustard (*Brassica kaber*), which they sowed in pots at six densities, placed in atmospheric CO₂ concentrations of 350 and 700 ppm, and sequentially harvested during the growing season. Early in stand development, elevated CO₂ increased aboveground weed biomass in a density-dependent manner, with the greatest stimulation (141%) occurring at the lowest density (20 plants per square meter) and the smallest stimulation (59%) occurring at the highest density (652 plants per square meter). As these stands matured, the density-dependence of the CO₂-induced growth response disappeared, and CO₂-enriched plants exhibited an average above-ground biomass 34% greater than ambient-grown plants across a broad range of plant densities. This final growth stimulation was similar to those of most other herbaceous plants exposed to atmospheric CO₂ enrichment (30 to 50% biomass increases for a doubling of the air's CO₂ content), demonstrating atmospheric CO₂ enrichment confers no undue advantage on weeds at the expense of other plants.

In a study of a weed that affects both plants and animals, Caporn *et al.* (1999) examined bracken (*Pteridium aquilinum*), which poses a serious weed problem and potential threat to human health in the United Kingdom and other regions, growing specimens for 19 months in controlled-environment chambers maintained at atmospheric CO₂ concentrations of 370 and 570 ppm and normal or high levels of soil fertility. The high-CO₂ treatment consistently increased rates of net photosynthesis by 30 to 70%, depending on soil fertility and time of year. Elevated CO₂ did not increase total plant dry mass or the dry mass of any plant organ, including rhizomes, roots, and fronds. The only significant effect of elevated CO₂ on bracken growth was observed in the normal nutrient regime, where elevated CO₂ reduced mean frond area.

These studies suggest atmospheric CO₂ enrichment will not favor the growth of non-parasitic weeds over crops and native plants.

References

Caporn, S.J.M., Brooks, A.L., Press, M.C., and Lee, J.A. 1999. Effects of long-term exposure to elevated CO₂ and increased nutrient supply on bracken (*Pteridium aquilinum*). *Functional Ecology* **13**: 107–115.

Dale, H. and Press, M.C. 1999. Elevated atmospheric CO₂

influences the interaction between the parasitic angiosperm *Orobanche minor* and its host *Trifolium repens*. *New Phytologist* **140**: 65–73.

Dukes, J.S. 2002. Comparison of the effect of elevated CO₂ on an invasive species (*Centaurea solstitialis*) in monoculture and community settings. *Plant Ecology* **160**: 225–234.

Gavazzi, M., Seiler, J., Aust, W., and Zedaker, S. 2000. The influence of elevated carbon dioxide and water availability on herbaceous weed development and growth of transplanted loblolly pine (*Pinus taeda*). *Environmental and Experimental Botany* **44**: 185–194.

Idso, K.E. 1992. Plant responses to rising levels of carbon dioxide: A compilation and analysis of the results of a decade of international research into the direct biological effects of atmospheric CO₂ enrichment. *Climatological Publications Scientific Paper #23*, Office of Climatology, Arizona State University, Tempe, AZ.

Poorter, H. 1993. Interspecific variation in the growth response of plants to an elevated and ambient CO₂ concentration. *Vegetatio* **104/105**: 77–97.

Taylor, K. and Potvin, C. 1997. Understanding the long-term effect of CO₂ enrichment on a pasture: the importance of disturbance. *Canadian Journal of Botany* **75**: 1621–1627.

Wayne, P.M., Carnelli, A.L., Connolly, J., and Bazzaz, F.A. 1999. The density dependence of plant responses to elevated CO₂. *Journal of Ecology* **87**: 183–192.

Ziska, L.H., Teasdale, J.R., and Bunce, J.A. 1999. Future atmospheric carbon dioxide may increase tolerance to glyphosate. *Weed Science* **47**: 608–615.

3.16.1.3 Miscellaneous Weeds

- Atmospheric CO₂ enrichment tends to increase the growth of many weeds, but possibly not by quite as great a percentage as it does for non-weeds.

Lewis *et al.* (2002) grew the common cocklebur (*Xanthium strumarium* L.) in controlled-environment growth chambers maintained at atmospheric CO₂ concentrations of 365 and 730 ppm for 70 days post-emergence. During the weed's vegetative growth phase, the photosynthetic rates of the CO₂-enriched plants were 30% greater than those of the plants growing in ambient air. During the flowering period that ensued shortly thereafter, this stimulation was reduced to 10%, after which it rose to 20% during the weed's fruiting period.

Gibeaut *et al.* (2001) grew the common weed *Arabidopsis thaliana* for seven weeks in controlled-environment chambers maintained at atmospheric CO₂ concentrations of 360 and 1,000 ppm, finding the 640 ppm increase in the air's CO₂ concentration increased the relative growth rate of the plants by about 20% during the first three weeks of the study. The extra CO₂ also increased the activity of the enzyme UDP-glucose dehydrogenase (an important enzyme involved in cell wall biosynthesis) by approximately 25%. Thereafter, relative growth rates were the same in both CO₂ treatments. Nevertheless, by the end of the study the CO₂-enriched plants had produced 2.3 times more biomass than the ambient-grown plants.

Ziska (2002) grew Canadian thistle (*Cirsium arvense* L. Scop.) plants in controlled-environment chambers maintained at atmospheric CO₂ concentrations of 280, 380, and 720 ppm for about two months. They determined the first increment of extra CO₂ enhanced photosynthesis rates and total plant biomass production by 45 and 126%, respectively, and the second CO₂ increment enhanced these two parameters by 49 and 69%.

Leishman *et al.* (1999) grew four weedy C₃ plants common to European grasslands (*Cardamine hirsute*, *Spergula arvensis*, *Senecio vulgaris*, and *Poa annua*) from seed to senescence in glasshouses maintained at atmospheric CO₂ concentrations of 350 and 550 ppm at two light intensities: full light and 67% of full light. The extra 200 ppm of CO₂ did not significantly impact vegetative growth in three of the species. For *Spergula arvensis*, it increased maximum leaf length by an average of 15%, regardless of light treatment, and total dry weight by 20 and 68% at full and reduced light levels, respectively. It significantly enhanced reproductive success in only one of the species, increasing the number of seeds in *Poa annua* by 50 and 26% at full and reduced light levels, respectively.

Nagashima *et al.* (2003) established even-aged stands of the summer annual *Chenopodium album* (a weed commonly found in open habitats, such as abandoned fields and flood plains) at ambient and twice-ambient atmospheric CO₂ concentrations and low and high levels of soil nutrient availability in open-top chambers in the experimental garden of Tohoku University, Sendai, Japan. They monitored the growth of individual plants every week until flowering. At the conclusion of the experiment, they could detect no significant effect of elevated CO₂ on aboveground biomass in the low nutrient regime; in

the high nutrient regime, the extra CO₂ increased aboveground biomass by 50%. The CO₂-induced enhancement of growth in the high nutrient regime gradually waned and ultimately disappeared altogether in smaller subordinate individuals but continued in larger dominants throughout the experiment.

Ziska and Bunce (1999) grew four C₄ plants in controlled-environment chambers maintained continuously at atmospheric CO₂ concentrations of 350 and 700 ppm or at a nocturnal CO₂ concentration of 700 ppm and 350 ppm during the day for approximately three weeks. They found continuous CO₂ enrichment caused a significant increase in photosynthesis (+13%) and total dry mass (+21%) in only one of the four species, *Amaranthus retroflexus*. Nocturnal CO₂ enrichment provided no significant effects in this species, indicating the CO₂-induced increase in biomass was not facilitated by a reduction in dark respiration rate. Plants exposed to continuous CO₂ enrichment did not increase their biomass due to improved internal water balance, as leaf water potentials were not significantly different among plants of any CO₂ treatment.

Ziska *et al.* (1999) grew broad-leaved C₃ (*Chenopodium album*) and C₄ (*Amaranthus retroflexus*) weeds in glasshouses maintained at atmospheric CO₂ concentrations of 360 and 720 ppm. Both young and mature plants of each species were sprayed with one-tenth and full-strength solutions of the chemical glyphosate ("Roundup"). The elevated CO₂ significantly increased the photosynthetic rate and total dry weight (by 51%) of the unsprayed C₃ weed, regardless of maturity stage, but it had no effect on these parameters in the case of the C₄ weed. Spraying both young and mature *A. retroflexus* plants with full-strength herbicide resulted in their death, regardless of atmospheric CO₂ concentration; spraying *C. album* plants with full-strength glyphosate severely reduced, but did not eliminate, growth in the elevated-CO₂ air, whereas chemically treated plants died in ambient CO₂ air. Consequently, farmers who use glyphosate to control *A. retroflexus* should not have to modify their current chemical practices in the future, but better control of *C. album* may require application of glyphosate earlier in the season when the weeds are smaller or, if applied later, at higher concentrations, as elevated CO₂ slightly increases the glyphosate tolerance of this particular C₃ weed.

These studies suggest although atmospheric CO₂ enrichment tends to increase the growth of many weeds, it may not do so by as great a percentage as for non-weeds. (See, for example, the results of the

many non-weed plants listed in Tables 1.1.1 and 1.1.2 in Appendices 3 and 4.)

References

Gibeaut, D.M., Cramer, G.R., and Seemann, J.R. 2001. Growth, cell walls, and UDP-glucose dehydrogenase activity of *Arabidopsis thaliana* grown in elevated carbon dioxide. *Journal of Plant Physiology* **158**: 569–576.

Leishman, M.R., Sanbrooke, K.J., and Woodfin, R.M. 1999. The effects of elevated CO₂ and light environment on growth and reproductive performance of four annual species. *New Phytologist* **144**: 455–462.

Lewis, J.D., Wang, X.Z., Griffin, K.L., and Tissue, D.T. 2002. Effects of age and ontogeny on photosynthetic responses of a determinate annual plant to elevated CO₂ concentrations. *Plant, Cell and Environment* **25**: 359–368.

Nagashima, H., Yamano, T., Hikosaka, K., and Hirose, T. 2003. Effects of elevated CO₂ on the size structure in even-aged monospecific stands of *Chenopodium album*. *Global Change Biology* **9**: 619–629.

Ziska, L. 2002. Influence of rising atmospheric CO₂ since 1900 on early growth and photosynthetic response of a noxious invasive weed, Canada thistle (*Cirsium arvense*). *Functional Plant Biology* **29**: 1387–1392.

Ziska, L.H. and Bunce, J.A. 1999. Effect of elevated carbon dioxide concentration at night on the growth and gas exchange of selected C₄ species. *Australian Journal of Plant Physiology* **26**: 71–77.

Ziska, L.H., Teasdale, J.R., and Bunce, J.A. 1999. Future atmospheric carbon dioxide may increase tolerance to glyphosate. *Weed Science* **47**: 608–615.

3.16.2 Parasitic

- Rising atmospheric CO₂ concentrations appear to reduce the negative effects of parasitic weed infection so infected host plants continue to exhibit positive (but somewhat reduced) growth responses to elevated CO₂.

Parasitic plants obtain energy, water, and nutrients from their host plants and cause widespread reductions in harvestable yields. This brief section examines how increasing atmospheric CO₂ concentrations may impact the growth of parasitic weeds and the relationships that exist between them and their host plants.

Dale and Press (1999) infected white clover

(*Trifolium repens*) plants with *Orobancha minor*, a parasitic weed that primarily infects leguminous crops in the United Kingdom and the Middle East, and exposed them to atmospheric CO₂ concentrations of either 360 or 550 ppm for 75 days in controlled-environment growth cabinets. The elevated CO₂ had no effect on the total biomass of parasite per host plant, nor did it affect the number of parasites per host plant or the time to parasitic attachment to host roots. While infected host plants growing in ambient air produced 47% less biomass than uninfected plants growing in ambient air, infected plants growing at 550 ppm CO₂ exhibited final dry weights only 20% less than those of uninfected plants growing in the CO₂-enriched air, indicating a significant CO₂-induced partial alleviation of parasite-induced biomass reductions in the white clover host plants.

Watling and Press (1997) infected several C₄ sorghum plants with *Striga hermonthica* and *Striga asiatica* (parasitic C₃ weeds of the semi-arid tropics that infest many grain crops) and grew them, along with uninfected control plants, for approximately two months in controlled-environment cabinets maintained at atmospheric CO₂ concentrations of 350 and 700 ppm. In the absence of parasite infection, the extra 350 ppm of CO₂ increased sorghum biomass by approximately 36%. When infected with *S. hermonthica*, the sorghum plants grown at ambient and elevated CO₂ concentrations produced only 32 and 43% of the biomass displayed by their respective uninfected controls. Infection with *S. asiatica* was somewhat less stressful and led to host biomass production of about half that of uninfected controls in both ambient and CO₂-enriched air. Therefore, the doubling of the air's CO₂ content employed in this study increased sorghum biomass by 79% and 35% in the C₄ sorghum plants infected with *S. hermonthica* and *S. asiatica*, respectively.

Watling and Press (2000) grew upland rice (*Oryza sativa* L.) in pots in controlled-environment chambers maintained at 350 and 700 ppm CO₂ in either the presence or absence of the root parasite *S. hermonthica* for 80 days after sowing, after which they harvested and weighed the plants. In ambient air, the presence of the parasite reduced the biomass of the rice to only 35% of what it was in the absence of the parasite. In air enriched with CO₂ the presence of the parasite reduced the biomass of infected plants to 73% of what it was in the absence of the parasite.

These few observations suggest rising atmospheric CO₂ concentrations generally tend to reduce the negative effects of parasitic weed infection so

Plants Under Stress

infected host plants continue to exhibit positive growth responses to elevated CO₂. It is likely host plants infected by parasitic weeds will fare better under higher atmospheric CO₂ conditions than they do currently.

References

- Dale, H. and Press, M.C. 1999. Elevated atmospheric CO₂ influences the interaction between the parasitic angiosperm *Orobanche minor* and its host *Trifolium repens*. *New Phytologist* **140**: 65–73.
- Watling, J.R. and Press, M.C. 1997. How is the relationship between the C₄ cereal *Sorghum bicolor* and the C₃ root hemi-parasites *Striga hermonthica* and *Striga asiatica* affected by elevated CO₂? *Plant, Cell and Environment* **20**: 1292–1300.
- Watling, J.R. and Press, M.C. 2000. Infection with the parasitic angiosperm *Striga hermonthica* influences the response of the C₃ cereal *Oryza sativa* to elevated CO₂. *Global Change Biology* **6**: 919–930.

4

Earth's Vegetative Future

Key Findings

Introduction

4.1 Agricultural and Food Production

4.1.1 The Past

4.1.2 The Future

4.2 Biospheric Productivity: The Greening of the Earth

4.2.1 Global Terrestrial

4.2.2 Continental Terrestrial

4.2.3 Rising Temperatures and Biospheric Productivity

4.3 Biodiversity

4.4 Extinction

4.4.1 Migrating Plants

4.4.2 Stationary Plants

4.5 Evolution

4.5.1 A Major Opportunity

4.5.2 Carbon Dioxide Induced

4.5.3 Temperature Induced

4.5.4 Drought Induced

Key Findings

The key findings of this chapter are listed below.

- Rising atmospheric CO₂ and warming temperatures, both of which IPCC claims constitute a significant threat to the biosphere, benefited agriculture in the ancient past and in the twentieth century.
- Empirical studies suggest a future warming of the climate coupled with rising atmospheric CO₂ levels will boost global agricultural production and help meet the food needs of the planet's growing population.
- When model-based studies fully account for the growth-enhancing and water-conserving benefits of atmospheric CO₂ enrichment, they project significant gains for future agricultural production.
- The vigor of the terrestrial biosphere has been increasing with time, revealing a great greening of the planet that extends across the globe.
- Satellite-based analyses of net terrestrial primary productivity (NPP) reveal an increase of around 6–13% since the 1980s.
- There is no empirical evidence to support the model-based claim that future carbon uptake will

Climate Change Reconsidered II: Biological Impacts

diminish on a global scale due to rising temperatures.

- Earth's land surfaces were a net *source* of CO₂-carbon to the atmosphere until about 1940. From 1940 onward, the terrestrial biosphere has become, in the mean, an increasingly greater *sink* for CO₂-carbon.
- Over the past 50 years, global carbon uptake has doubled from 2.4 ± 0.8 billion tons in 1960 to 5.0 ± 0.9 billion tons in 2010.
- The observed greening of the Earth has occurred in spite of the many real and imagined assaults on the planet's vegetation over this time period, including fires, disease, outbreaks of pests, deforestation, and climatic changes (primarily in temperature and precipitation).
- The atmosphere's rising CO₂ content—which IPCC considers to be the chief culprit behind its concerns about the future of the biosphere—is most likely the primary cause of the observed greening trends.
- In the future, plants should be able to adjust their physiology to accommodate a warming of the magnitude and rate of rise typically predicted by climate models to accompany the projected future increase in atmospheric CO₂ content.
- The rise in the air's CO₂ concentration and its anti-transpiration effect, which improves plant water-use efficiency, are enhancing and will continue to enhance the vegetative productivity of Africa.
- The rise of the air's CO₂ concentration and temperature to their highest values of the past century enhanced the terrestrial vegetative productivity of all parts of Asia, including deserts, forests, grasslands, and the Tibetan Plateau.
- Evergreen vegetation, woody plants, and other plant life have increased across Australia over the past 200 years as a result of CO₂ enrichment.
- Over the last two decades of the twentieth century, Europe as a whole became greener and much of it is seeing an increase in woodlands due to the recent rise in atmospheric CO₂, which has tended to offset the detrimental effects of climate change in the region.
- Opposite the forecasts promulgated by the models used by IPCC, land-based plants of the Arctic and near-Arctic regions of North America are thriving, thanks in large part to the ongoing rise in the atmosphere's CO₂ concentration and global warming.
- Late twentieth-century increases in air temperature and atmospheric CO₂ concentration did not negatively affect plant communities in the eastern United States. Rather, the temperature and CO₂ increases significantly enhanced local and regional productivity, and there is little reason to think such enhancements will not continue throughout the foreseeable future.
- The late twentieth-century rise in temperature and atmospheric CO₂ concentrations improved the productivity of plant communities in the central region of the United States, notwithstanding model-based concerns to the contrary.
- The late twentieth-century rise in temperature and atmospheric CO₂ improved the productivity of plant communities in the western region of the United States, notwithstanding model-based projections of unprecedented ecological disaster due to rising temperatures and drought.
- Warmer temperatures and higher CO₂ concentrations are resulting in net primary productivity increasing across tropical South America, overcoming the effects of deforestation, forest fires, and incursions by human civilization into natural areas.
- It is likely the greening of the planet will continue in the future, even if the largest temperature increases predicted by the models occur, because the optimum temperature for plant growth and development typically rises with increasing levels of atmospheric CO₂. This response, coupled with expected increases in plant photosynthetic rates from the rise in the air's CO₂ concentration, is more than enough to compensate for any temperature-induced plant stress caused by global warming.
- Real-world observations reveal plants have many ways of adjusting to changes in climate in addition to their ability to spread from places of rising warmth to cooler habitats, and these observations suggest the planet's current assemblage of plants

is likely to be around a good deal longer than many theoretical models have predicted.

- A major cause of biodiversity reductions is not rising atmospheric CO₂ concentrations, but instead the direct encroachment of man upon the world of nature. Anthropogenic global warming, to whatever extent it exists, is helping plants overcome these assaults and thrive despite the growing human presence.
- As good as things currently are for world agriculture, and as much better as they are expected to become as the atmospheric CO₂ content continues to rise, there may be additional substantial room for both natural selection and bioengineering to remove the constraints of low CO₂ adaptation in several important agricultural crops and thereby create novel genotypes able to exploit high CO₂ conditions to their—and our—advantage.
- The ongoing rise in atmospheric CO₂ content is likely exerting significant selection pressure on Earth's naturally occurring terrestrial plants, which should improve their performance in the face of various environmental stressors via the process of microevolution. Plants may be much better prepared than most scientists once thought to meet whatever climatic challenges, including global warming, the future may pose for them.
- Evidence continues to accumulate for substantial heritable variation of ecologically important plant traits, including root allocation, drought tolerance, and nutrient plasticity, which suggests rapid evolution based on epigenetic variation alone should be possible.

Introduction

A remarkable global phenomenon occurred throughout much of the twentieth century that the authors of IPCC's reports pretend never occurred despite hundreds of scholarly studies documenting its extent, causes, and consequences. The phenomenon is a gradual yet dramatic increase in biospheric productivity, or more simply, the greening of the Earth. According to IPCC's assumptions, theories, and models, this should not be occurring, indeed *cannot* be occurring. And yet, as this chapter will document, the evidence is overwhelming.

The aerial fertilization effect caused by the rise in

CO₂ following the last deglaciation, combined with its transpiration-reducing effect that in turn led to a large increase in the water use efficiencies of the world's major C₄ founder crops, was the global trigger that made human agriculture possible. By dramatically increasing the yields of the first crops, that natural rise in CO₂ made modern civilization possible. Far from being a crisis, it was a miracle.

Fast-forward to the modern era and we are witnessing a rise in CO₂ levels similar to what occurred some 22,000 to 7,000 years ago. Once again, agricultural production is increasing throughout the world and across all types of landscapes, including plants and areas where improvements in human cultivation techniques cannot explain the improvement. Could global warming be good? In China, home to a fifth of all of humanity, Liu *et al.* (2004) report "all of China would benefit from climate change in most scenarios." Julien *et al.* (2006) say of the last two decades of the twentieth century, "Europe as a whole has a tendency to greening," and much of it is "seeing an increase in its wood land proportion." Extensive research has found the benefits of global warming on agriculture are occurring globally, across Asia, North America, and South America.

Nor is there evidence this greening is soon to end. Ballantyne *et al.* (2012) conclude, "although present predictions indicate diminished C uptake by the land and oceans in the coming century, with potentially serious consequences for the global climate, as of 2010 there is no empirical evidence that C uptake has started to diminish on the global scale." Their results clearly indicate just the opposite appears to be the case, with global carbon uptake doubling over the past half-century. Their research refutes the hypothesis of Canadell *et al.* (2007) and Raupach *et al.* (2008), who claimed to have detected a decreasing trend in the efficiency of the planet's carbon sinks, and it vindicates the many studies revealing an increasing greening of planet Earth.

IPCC feigns ignorance of this reality. Its authors seem still to be in the thrall of two authors who, two decades ago, wrote CO₂-induced changes in global climate were expected to occur "too fast for evolutionary processes such as natural selection to keep pace," and this phenomenon "could substantially enhance the probability of extinction of numerous species" (Root and Schneider (1993)). This famous but unsubstantiated declaration has pervaded the publications of IPCC ever since ... but it never has been proven correct. It is more likely to be incorrect.

This chapter begins, in Section 4.1, with a

discussion of how the rise in CO₂ levels boosted food production globally in the past and how models that include the fertilizing effects of CO₂ suggest a future warming of the climate coupled with rising CO₂ levels will boost future global agricultural production, helping to meet the food needs of the planet's growing population. Section 4.2 surveys the extensive literature on the greening of the Earth, first presenting global studies and then studies focusing on specific continents, and finally studies that ask whether rising temperatures could check or offset the greening trend.

Section 4.3 reviews evidence on the impact of the rise in CO₂ levels on biodiversity and finds that impact to be positive. Similarly, Section 4.4. looks at the impact of the rise in CO₂ levels on plant extinctions and finds CO₂ makes extinctions less likely to occur. Finally, Section 4.5 asks whether plants can in fact evolve fast enough to adapt to a world with higher levels of CO₂, higher temperatures, and more drought. The evidence is clear that many plant species can make significant adaptations to changes in their environment in just a few generations.

References

Ballantyne, A.P., Alden, C.B., Miller, J.B., Tans, P.P., and White, J.W. 2012. Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature* **488**: 70–72.

Canadell, J.G., LeQuere, C., Raupach, M.R., Field, C.B., Buitenhuis, E.T., Ciais, P., Conway, T.J., Gillett, N.P., Houghton, R.A., and Marland, G. 2007. Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 18,866–18,870.

Julien, Y., Sobrino, J.A., and Verhoef, W. 2006. Changes in land surface temperatures and NDVI values over Europe between 1982 and 1999. *Remote Sensing of Environment* **103**: 43–55.

Liu, H., Li, X., Fischer, G., and Sun, L. 2004. Study on the impacts of climate change on China's agriculture. *Climatic Change* **65**: 125–148.

Raupach, M.R., Canadell, J.G., and LeQuere, C. 2008. Anthropogenic and biophysical contributions to increasing atmospheric CO₂ growth rate and airborne fraction. *Biogeosciences* **5**: 1601–1613.

Root, T.L. and Schneider, S.H. 1993. Can large-scale climatic models be linked with multiscale ecological studies? *Conservation Biology* **7**: 256–270.

4.1 Agricultural and Food Production

According to IPCC, over the past century or so the atmosphere's temperature and CO₂ concentration have risen at rates (and to levels) not seen for millennia in the case of temperature and millions of years in the case of CO₂. Section 4.1.1 examines how the modern increase in temperature and CO₂ affected agriculture and food production in the past, and Section 4.1.2 provides an appraisal of how they might affect them in the future.

4.1.1 The Past

- Rising atmospheric CO₂ and warming temperatures, both of which IPCC claims constitute a significant threat to the biosphere, benefited agriculture in the ancient past and in the twentieth century.

According to Cunniff *et al.* (2008), “early agriculture was characterized by sets of primary domesticates or ‘founder crops’ that were adopted in several independent centers of origin,” all at about the same time, and “this synchronicity suggests the involvement of a global trigger.” Further noting Sage (1995) saw a causal link between this development and the rise in atmospheric CO₂ concentration that followed deglaciation (a jump from about 180 to 270 ppm), they hypothesized the aerial fertilization effect caused by the rise in CO₂ combined with its transpiration-reducing effect led to a large increase in the water use efficiencies of the world's major C₄ founder crops, and that this development was the global trigger that launched the agricultural enterprise.

To test this hypothesis, Cunniff *et al.* designed “a controlled environment experiment using five modern day representatives of wild C₄ crop progenitors, all ‘founder crops’ from a variety of independent centers.” The five C₄ crops employed in their study were *Setaria viridis*, *Panicum miliaceum* var. *ruderalis*, *Pennisetum violaceum*, *Sorghum arundinaceum*, and *Zea mays* subsp. *parviglumis*. They were grown individually in small pots filled with a 1:1 mix of washed sand and vermiculite for 40–50 days in growth chambers maintained at atmospheric CO₂ concentrations of either 180, 280, or 380 ppm, characteristic of glacial, post-glacial, and modern times, respectively.

Cunniff *et al.* report the “increase in CO₂ from glacial to postglacial levels [180 to 280 ppm] caused a significant gain in vegetative biomass of up to 40%,” together with “a reduction in the transpiration rate via

decreases in stomatal conductance of ~35%,” which led to “a 70% increase in water use efficiency, and a much greater productivity potential in water-limited conditions.” The five researchers write, “these key physiological changes could have greatly enhanced the productivity of wild crop progenitors after deglaciation ... improving the productivity and survival of these wild C₄ crop progenitors in early agricultural systems.” They further note “the lowered water requirements of C₄ crop progenitors under increased CO₂ would have been particularly beneficial in the arid climatic regions where these plants were domesticated.”

Expanding on their work two years later, Cunliff *et al.* (2010) conducted a second set of experiments designed to further study the physiological and yield responses to glacial and post-glacial atmospheric CO₂ concentrations of modern representatives of the wild crop progenitors, but this time they included an analysis of C₃ and C₄ cereals. Once again, their experimental work was conducted in the laboratory in controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 180 or 280 ppm. Cunliff *et al.* report “both the C₃ and C₄ species responded positively to rising CO₂ from the glacial to post-glacial level,” with vegetative biomass near-doubling and yield rising by 50% in the C₃ species, consistent with the findings of Polley *et al.* (1992) and Dippery *et al.* (1995), and with a 10–15% yield enhancement under well-watered conditions in the C₄ species, consistent with the findings of Polley *et al.* (1996), Ziska and Bunce (1997), and Ward *et al.* (1999). In the case of the C₄ species, which typically are found in semi-arid environments, they discovered the transpiration-reducing effect of atmospheric CO₂ enrichment had a considerably larger positive impact on plant growth and yield. They write, “this stronger response of photosynthesis to soil drying in the C₄ species could represent an important route for rising CO₂ to stimulate biomass accumulation in a semi-arid environment,” citing Cunliff (2009).

Cunliff *et al.* state the data described in their paper “provide experimental support for Sage’s CO₂ limitation hypothesis, showing that atmospheric conditions of the last glacial period would have placed direct and indirect limitations on the productivity of crop progenitors.” Although they also note the hypothesis does not explain why the domestication of crops occurred, they opine “it does offer evidence-based explanations of why agriculture did not begin earlier.” It is logical to conclude civilizations of the past, which could not have existed without agriculture, were largely made possible by

the increase in the atmospheric CO₂ content that accompanied deglaciation, and that people of today are likewise indebted to this phenomenon as well as to the additional 100 ppm of CO₂ the atmosphere has subsequently acquired.

A number of studies reveal the important role of temperature in agricultural production. Following the centuries-long cold period of the Little Ice Age (sixteenth through nineteenth centuries), global agriculture production has benefited from the warmer climate of the twentieth and twenty-first centuries.

Shen *et al.* (2005), for example, derived and analyzed long-term (1901–2002) temporal trends in the agroclimate of Alberta, Canada, reporting “an earlier last spring frost, a later first fall frost, and a longer frost-free period are obvious all over the province.” They also say May–August precipitation in Alberta increased 14% from 1901 to 2002, and annual precipitation exhibited a similar increasing trend, with most of the increase coming in the form of low-intensity events. They note “the area with sufficient corn heat units for corn production, calculated according to the 1973–2002 normal, had extended to the north by about 200–300 km, when compared with the 1913–32 normal, and by about 50–100 km, when compared with the 1943–72 normal.”

These changes, Shen *et al.* write, “imply that Alberta agriculture has benefited from the last century’s climate change” and “the potential exists to grow crops and raise livestock in more regions of Alberta than was possible in the past.” They also state the increase in the length of the frost-free period “can greatly reduce the frost risks to crops and bring economic benefits to Alberta agricultural producers.” In addition, they note the northward extension of the corn heat unit boundary sufficient for corn production “implies that Alberta farmers now have a larger variety of crops to choose from than were available previously.” Shen *et al.* say “there is no hesitation for us to conclude that the warming climate and increased precipitation benefit agriculture in Alberta.”

Qian *et al.* (2010) derived a set of agroclimatic indices representing Canadian climatic conditions, which they analyzed for trends sure to prove useful for agricultural production planning for many years to come. They used a homogenized temperature dataset consisting of daily maximum and minimum air temperatures obtained from 210 meteorological stations distributed across Canada that cover the period 1895–2007, along with an adjusted precipitation dataset developed at the Climate Research Division of Environment Canada. They found “a significant lengthening of the growing season due to a sig-

nificantly earlier start and a significantly later end of the growing season,” adding, “significant positive trends are also observed for effective growing degree-days and crop heat units at most locations across the country.” Qian *et al.* report “the occurrence of extremely low temperatures had become less frequent during the non-growing season, implying a more favorable climate for overwinter survival,” and “the total numbers of cool days, frost days, and killing-frost days within a growing season had a decreasing trend,” so “crops may also be less vulnerable to cold stress and injury during the growing season.” Their work revealed “extreme daily precipitation amounts and 10-day precipitation totals during the growing season have been increasing” and “significant trends associated with increased availability of water during the growing season are identified.”

Clearly, the global warming that brought an end to the debilitating cold of the Little Ice Age and ushered the planet into the Current Warm Period is proving to be a benefit to Canada.

Hicke and Lobell (2004) calculated cropland net primary production (NPP) in the central part of the United States (South Dakota, Nebraska, Kansas, Missouri, Iowa, Minnesota, Wisconsin, and Illinois) using U.S. Department of Agriculture information together with crop-specific parameters that convert agronomic data into carbon fluxes for the period 1972–2001. Total cropland area exhibited no temporal trend over the study period, but “both NPP (flux per unit area) and P (spatially aggregated flux) increased during the study period (46 and 51%, respectively).”

These results indicate agricultural productivity in the central United States increased, and dramatically so, over the last three decades of the twentieth century, contrary to frequent claims that rising air temperatures and CO₂ concentrations will have negative effects on agriculture. Possible drivers of this increased agricultural productivity, according to Hicke and Lobell, include “improved cultivars, better fertilizer and pest management, more favorable climate, shifts to productive crop types, and economic influences (Duvick and Cassman, 1999; Evans, 1997; Lobell and Asner, 2003).”

Moonen *et al.* (2002) studied agriculturally important data collected from 1878 to 1999 on the outskirts of Pisa, Italy. Meteorological parameters routinely measured over this period were daily maximum, minimum, and mean air temperature plus daily rainfall. Agrometeorological parameters included the date of first autumn frost, date of last spring frost, length of growing season, number of

frost days, lengths of dry spells, potential evapotranspiration, reference evapotranspiration, soil moisture surplus, theoretical irrigation requirement, number of days with soil moisture surplus, and number of days with soil moisture deficit.

Moonen *et al.*’s analysis found “extremely cold temperature events have decreased and extremely warm temperature events have remained unchanged.” They suggest these observations may be attributed to the increase in cloud cover that would be expected to occur in a warming world, since more clouds would reduce midday heating and thereby offset much, if not all, of the impetus for global warming during the hottest part of the day. At night, the increased cloud cover would enhance the atmosphere’s greenhouse effect, thereby adding to the long-term warming trend. Moonen *et al.* conclude, “no negative effects can be expected on crop production from this point of view.” They found a real “silver lining” in the latter of these cloud feedback phenomena: “the number of frost days per year had decreased significantly resulting in a decrease in risk of crop damage.” Hence, they say the time of planting spring crops could be safely advanced by many days, noting the length of the growing season increased by fully 47 days during the period they studied.

With respect to rainfall, Moonen *et al.* found a somewhat analogous situation. On an annual basis, the incidence of extremely high rainfall events did not appear to have changed, but there was an increase in the incidence of very low rainfall events. The one exception to this rule on a seasonal basis was a decrease in high rainfall events in the spring, which might be expected to increase drought risk at that time of year. However, when the maximum length of dry spells was assessed on a seasonal basis, the only significant change observed was a lengthening of this parameter in the autumn. Autumn is the wettest season of the year in Pisa, Italy; the researchers conclude “no increased drought risk is to be expected.”

The bottom line with respect to water in agriculture is the balance between what is received via rainfall and what is lost via evapotranspiration, as this difference is what determines the soil moisture balance. Although there was a downward trend in yearly rainfall at Pisa over the past 122 years (due to the decrease of high rainfall events in the spring), there also was a nearly offsetting downward trend in evapotranspiration (possibly induced by enhanced daytime cloud cover), so there were “no significant changes in soil water surplus or deficit on an annual basis.” The scientists noted a significant decrease in

the number of surplus soil moisture days in the autumn, but because autumn is the wettest season of the year, they write, “this indicates a reduced flooding risk in autumn, which could have positive effects on workability of the soil and imply a reduction of erosion.”

Thus Moonen *et al.* conclude, concomitant with the warming of the Northern Hemisphere over the past 122 years, “extreme events in Pisa have not changed in a way that is likely to negatively affect crop production.” More often than not, the changes demonstrated to have occurred seem to have had positive impacts on agriculture. Moonen *et al.* say “there is no doubt regarding the reality of the observed changes.”

Fengjin and Lianchun (2011) write, “the damage from extreme low temperature events during the warm season in Northeast China is one of the major disasters that affect agriculture in China,” noting “rice, sorghum, corn, soybeans, and other major crops are all vulnerable to low-temperature damage.” They computed temporal trends in the frequency of occurrence of extreme minimum temperatures during Northeast China’s warm season (May to September) during the years 1956–2005, concurrently calculating trends in the region’s annual average near-surface air temperature, after which they compared the former dependent trend with the latter independent trend.

The two Beijing Climate Center researchers found for the 1956–2005 period, the overall rate of increase in the annual average temperature was 0.32°C per decade. But from 1970 to 2005 it was 0.49°C per decade, and “from 1990, the increasing trend in the annual average temperature has become much more significant.” They further report, “the average number of extreme minimum temperature days during the warm season in the 1950s was 15.8 days; in the 1960s, the average was 16.5 days; in the 1970s, the average increased to 17.3 days, and this was similar in the 1980s.” In the 1990s, the average number of extreme minimum temperature days “decreased sharply to 13.3 days,” and since 2000 the number of extreme minimum temperature days has been “decreasing constantly with an average of 11.4 days.”

As warming accelerated across Northeast China over the latter part of the past half-century, there was a concomitant decrease in the number of extreme minimum temperature events during that region’s warm season. Fengjin and Lianchun state a “decreased frequency of extreme low temperatures over the past few decades has also been reported in other regions, e.g., Australia and New Zealand

(Salinger *et al.*, 2000; Stone *et al.*, 1996).” The two Chinese scientists say the decrease in extreme minimum temperature events in response to the warmer temperatures of the past few decades has enabled farmers in Northeast China to harvest greater amounts of rice, sorghum, corn, soybeans, and other major crops than would otherwise have been possible.

Chen *et al.* (2011) report corn acreage in Northeast China—specifically Heilongjiang, Jilin, and Liaoning provinces—“accounts for 26.3% of the corn area in the country and accounts for about 29.4% of Chinese total corn grain production.” They note the corn production of this region “plays a significant role in ensuring Chinese food security,” and “knowledge of the potential effects of climate change on corn production in Northeast China will be highly valuable, not only for China but also for the world.” Chen *et al.* “performed a multiple regression analysis to study the relationship between corn growth and the key climatic factors of temperature and precipitation during the crop growing season and during specific months in Northeast China from 1965 to 2008,” to learn “which variables of climate change and which month in the crop growing season were associated with yield variability over this 44-year period.”

The six scientists determined the major climatic factor affecting corn yield in Northeast China is daily minimum temperature, particularly in the months of May and September. They found a warming of 1.0°C in the mean daily minimum temperature of either of these months may enhance corn yield by 303 kg/ha (May) or 284 kg/ha (September). They report growth duration—defined as the period from sowing to harvest (days to maturity)—rose by six days in Liaoning province and by seven days in Jilin and Heilongjiang provinces during the years 1950–2008, which encompassed the period of 1965–2008, when daily minimum temperature rose at a rate of 0.44°C per decade. They conclude, “in order to fully exploit the positive effects of global warming on corn production, new varieties should be adapted to the longer growing season.” This adjustment could be described as a good example of man and nature working together to ensure maximum food security for a significant portion of humanity.

Magrin *et al.* (2005) evaluated twentieth-century changes in climate and the yields of the chief crops (soybean, wheat, maize, and sunflower) of nine areas of contrasting environment in Argentina’s Pampas region, which accounts for more than 90% of the country’s grain production. After determining low-frequency upward trends in yield due to improvements in crop genetics and management techniques,

as well as the aerial fertilization effect of the historical increase in the air's CO₂ concentration, they used annual yield anomalies and concomitant climatic anomalies to develop relations describing the effects of precipitation, temperature, and solar radiation on crop yields, to determine the effects of long-term changes in these climatic parameters on Argentina's agriculture.

Although noting "technological improvements account for most of the observed changes in crop yields during the second part of the 20th century"—which totaled 110% for maize, 56% for wheat, and 102% for sunflower—Magrin *et al.* report changes in climate between the periods 1950–1970 and 1970–1999 led to yield increases of 38% in soybean, 18% in maize, 13% in wheat, and 12% in sunflower.

These studies suggest rising atmospheric CO₂ concentrations and warmer temperatures—both of which IPCC claims to constitute significant threats to the biosphere, having reached levels IPCC describes as unprecedented over the past one to two millennia—were far from problematic for agriculture.

References

- Chen, C., Lei, C., Deng, A., Qian, C., Hoogmoed, W., and Zhang, W. 2011. Will higher minimum temperatures increase corn production in northeast China? An analysis of historical data over 1965–2008. *Agricultural and Forest Meteorology* **151**: 1580–1588.
- Cunniff, J. 2009. The Roles of Atmospheric Carbon Dioxide and Plant Ecological Traits in the Origin of Agriculture. PhD Thesis, University of Sheffield, United Kingdom.
- Cunniff, J., Charles, M., Jones, G., and Osborne, C.P. 2010. Was low atmospheric CO₂ a limiting factor in the origin of agriculture? *Environmental Archaeology* **15**: 113–123.
- Cunniff, J., Osborne, C.P., Ripley, B.S., Charles, M., and Jones, G. 2008. Response of wild C₄ crop progenitors to subambient CO₂ highlights a possible role in the origin of agriculture. *Global Change Biology* **14**: 576–587.
- Dipperry, J.K., Tissue, D.T., Thomas, R.B., and Strain, B.R. 1995. Effects of low and elevated CO₂ on C₃ and C₄ annuals. I. Growth and biomass allocation. *Oecologia* **101**: 13–20.
- Duvick, D.N. and Cassman, K.G. 1999. Post-green revolution trends in yield potential of temperate maize in the north-central United States. *Crop Science* **39**: 1622–1630.
- Evans, L.T. 1997. Adapting and improving crops: The endless task. *Philosophical Transactions of the Royal Society of London, Series B* **352**: 901–906.
- Fengjin, X. and Lianchun, S. 2011. Analysis of extreme low-temperature events during the warm season in Northeast China. *Natural Hazards* **58**: 1333–1344.
- Hicke, J.A. and Lobell, D.B. 2004. Spatiotemporal patterns of cropland area and net primary production in the central United States estimated from USDA agricultural information. *Geophysical Research Letters* **31**: 10.1029/2004GL 020927.
- Lobell, D.B. and Asner, G.P. 2003. Climate and management contributions to recent trends in US agricultural yields. *Science* **299**: 1032.
- Magrin, G.O., Travasso, M.I., and Rodriguez, G.R. 2005. Changes in climate and crop production during the 20th century in Argentina. *Climatic Change* **72**: 229–249.
- Moonen, A.C., Ercoli, L., Mariotti, M., and Masoni, A. 2002. Climate change in Italy indicated by agrometeorological indices over 122 years. *Agricultural and Forest Meteorology* **111**: 13–27.
- Polley, H.W., Johnson, H.B., and Mayeux, H.S. 1992. Growth and gas-exchange of oats (*Avena sativa*) and wild mustard (*Brassica kaber*) at sub-ambient CO₂ concentrations. *International Journal of Plant Sciences* **153**: 453–461.
- Polley, H.W., Johnson, H.B., Mayeux, H.S., Brown, D.A., and White, J.W.C. 1996. Leaf and plant water use efficiency of C₄ species grown at glacial to elevated CO₂ concentrations. *International Journal of Plant Sciences* **157**: 164–170.
- Qian, B., Zhang, X., Chen, K., Feng, Y., and O'Brien, T. 2010. Observed long-term trends for agroclimatic conditions in Canada. *Journal of Applied Meteorology and Climatology* **49**: 604–618.
- Sage, R.F. 1995. Was low atmospheric CO₂ during the Pleistocene a limiting factor for the origin of agriculture? *Global Change Biology* **1**: 93–106.
- Salinger, M.J., Stigter, C.J., and Das, H.P. 2000. Agrometeorological adaptation strategies to increasing climate variability and climate change. *Agricultural and Forest Meteorology* **103**: 167–184.
- Shen, S.S.P., Yin, H., Cannon, K., Howard, A., Chetner, S., and Karl, T.R. 2005. Temporal and spatial changes of the agroclimate in Alberta, Canada, from 1901 to 2002. *Journal of Applied Meteorology* **44**: 1090–1105.
- Stone, R., Nicholls, N., and Hammer, G. 1996. Frost in NE Australia: trends and influence phases of Southern Oscillation. *Journal of Climate* **9**: 1896–1909.
- Ward, J.K., Tissue, D.T., Thomas, R.B., and Strain, B.R.

1999. Comparative responses of model C₃ and C₄ plants to drought in low and elevated CO₂. *Global Change Biology* 5: 857–867.

Ziska, L.H. and Bunce, J.A. 1997. Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C₄ crops and weeds. *Photosynthesis Research* 54: 199–208.

4.1.2 The Future

Several researchers have expressed concerns about a looming food production crisis on the horizon, suggesting just a few decades from now the ever-growing human population of the planet will need a near-doubling of present-day agricultural production. One example is the brief Perspective article published in *Science*, where Running (2012) resurrected shades of Meadows *et al.*'s 1972 treatise on *The Limits to Growth*.

Noting “terrestrial plant production is the foundation of the biospheric carbon cycle” and that “water and atmospheric CO₂ are transformed into plant carbohydrate matter with the help of solar energy,” Running states this plant matter “sustains the global food web and becomes the source of food, fiber and fuel for humanity.” A problem Running sees, however, is that for more than 30 years, global net primary production (NPP) has “stayed near 53.6 Pg per year, with only ~1 Pg of inter-annual variability,” citing two studies of which he was a coauthor (Nemani *et al.*, 2003; Zhao and Running, 2010). He thus speculates, “if global NPP is fixed by planetary constraints, then no substantial increase in plant growth may be possible.”

If true, this would indeed have catastrophic consequences, for it is almost universally agreed, as Running writes, “the projected 40% increase in human population by 2050 CE, combined with goals to substantially improve standards of living for the poorest 5 billion people on Earth, implies at least a doubling of future resource demand by 2050.” The most important of these resources is food.

But is a doubling of food production by mid-century realistic? Agriculture already consumes 38% of the world's land surface, and Running notes “many analyses now conclude that freshwater use for irrigation has already reached a planetary boundary.” Furthermore, with “massive river pollution and ocean anaerobic dead zones,” he states, “if anything, future increases in NPP must be achieved with less, not more, irrigation and fertilizer use.” Others have noted additional challenges, such as Tilman *et al.* (2009)

noting “land previously allocated to food production is transformed to bioenergy production, raising food prices for the people who can least afford it.”

Has the planet reached a limit to its growth? In a 2012 paper published in *Nature*, titled “Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years,” Ballantyne *et al.* (2012) suggest it has not. The five U.S. scientists state their mass balance analysis shows “net global carbon uptake has increased significantly by about 0.05 billion tonnes of carbon per year and that global carbon uptake doubled, from 2.4 ± 0.8 to 5.0 ± 0.9 billion tonnes per year, between 1960 and 2010.” They conclude, “there is no empirical evidence that carbon uptake has started to diminish on the global scale.” In fact, as their results indicate, just the opposite appears to be the case, with global carbon uptake actually *doubling* over the past half-century.

There are many reasons why this doubling has occurred: breeding of better crop varieties that are higher-yielding, more competitive with weeds, less tasty to insect pests, more nutritious, and more drought-resistant, as well as smarter ways of farming, improved technologies, and the worldwide aerial fertilization and transpiration-reducing effects of the historical and still-ongoing rise in the atmosphere's CO₂ content. The latter two phenomena benefit agriculture and nature simultaneously.

Also concerned about adequately meeting the food needs of a growing world population, Parry and Hawkesford (2010) note “food production needs to increase 50% by 2030 and double by 2050 to meet projected demands.” They say while the demand for food is increasing, production is progressively being limited by “non-food uses of crops and cropland,” such as the production of biofuels. In their UK homeland, for example, they note, “by 2015 more than a quarter of wheat grain may be destined for bioenergy production,” which is both sad and puzzling, as they also point out “currently, at least one billion people are chronically malnourished and the situation is deteriorating,” with more people “hungrier now than at the start of the millennium.”

The two researchers turn their discussion to photosynthesis, the all-important process by which plants “convert light energy into chemical energy, which is used in the assimilation of atmospheric CO₂ and the formation of sugars that fuel growth and yield.” These phenomena make this natural and life-sustaining process “a major target for improving crop productivity both via conventional breeding and biotechnology,” they write.

Next to a plant's need for carbon dioxide is its

need for water, the availability of which, in the words of Parry and Hawkesford, “is the major constraint on world crop productivity.” They state, “since more than 80% of the [world’s] available water is used for agricultural production, there is little opportunity to use additional water for crop production,” because as populations increase, “the demand to use water for other activities also increases.” Hence they conclude, “a real and immediate challenge for agriculture is to increase crop production with less available water.”

They provide an example of a success story: the Australian wheat variety Drysdale, which gained fame “because it uses water more efficiently.” This valued characteristic was achieved “by slightly restricting stomatal aperture and thereby the loss of water from the leaves.” They note this ability “reduces photosynthetic performance slightly under ideal conditions,” but it enables plants to “have access to water later in the growing season thereby increasing total photosynthesis over the life of the crop.”

Of course, Drysdale is but one variety of one crop, and the ideal goal would be to get nearly all varieties of all crops to use water more efficiently. That goal in fact can be reached without doing anything new, because allowing atmospheric CO₂ concentrations to rise will cause the vast majority of plants to reduce the apertures of their stomata and thereby lower the rate at which water vapor escapes from them into the air. The result is even better than that produced by the breeding of Drysdale, because the extra CO₂ in the air more than overcomes the photosynthetic reduction that results from the partial closure of plant stomatal apertures, allowing even more yield to be produced per unit of water transpired in the process.

Human ingenuity can make the situation better still, by breeding and selecting crop varieties that perform better under higher atmospheric CO₂ concentrations than the varieties people currently rely upon, and by employing various technological means of altering them. Humanity can succeed even though “the United Nations Millennium Development Goal of substantially reducing the world’s hungry by 2015 will not be met,” as Parry and Hawkesford conclude. This truly seems to be the path to take, as they write “at least one billion people are chronically malnourished and the situation is deteriorating,” with more people “hungrier now than at the start of the millennium.”

Ainsworth *et al.* (2008) argue for breeding major crop varieties upon which the world depends for food to best take advantage of the ongoing rise in the atmospheric CO₂ content. The international consor-

tium of 32 scientists from 12 countries notes, “the growing world population, increasing demands for grains for animal feeds, land loss to urban expansion and demand for bioenergy production are exerting more and more pressure on global agricultural productivity.” They state, “a major challenge for plant biologists, agronomists and breeders will be to provide germplasm and seed material that maximize future crop production,” particularly in the context of rising atmospheric CO₂ concentrations that provide “a unique opportunity to increase the productivity of C₃ crops.” They say “only a fraction of available germplasm of crops has been tested for CO₂ responsiveness,” and “further research is needed to elucidate the mechanisms of yield response to CO₂, to assess the genetic diversity available for improving responsiveness and to devise efficient schemes for selection for adaptation to rising ambient CO₂, whether based on conventional plant breeding or systems biology approaches for selecting and engineering improved genetics.”

The first step in meeting these objectives, according to the researchers, “is to create facilities for field screening the yield response to elevated CO₂ across a wide range of germplasm,” and doing so under “conditions and management that reflect dominant agronomic practices and provide as natural an environment as possible.” They recommend free air CO₂ enrichment (FACE) experimentation, which these scientists say meets many of these criteria and presents a minimally obtrusive interaction with the natural environment.

Although FACE systems are often considered expensive to construct and operate, Ainsworth *et al.* note “the net cost is compensated for by economies of scale, and the cost per unit ground area is considerably less than alternative systems.” This is very important, as they explain, because “the new research requires investigating large numbers of genotypes,” and “to investigate the association of CO₂ responsiveness with a single quantitative trait locus mapping population, approximately 150 inbred lines would need to be investigated.”

The world-renowned group of scientists concludes, “because it may take 10–15 years to move from discovery of new advantaged genetics to commercial cultivars of annual grain crops, developing a robust strategy and supporting the planned work with the best possible facilities should be an urgent priority.”

Zhu *et al.* (2010) embrace an alternative strategy for boosting agricultural production. They say meeting the global increase in agricultural demand

Earth's Vegetative Future

during this century “is predicted to require a doubling of global production,” but “the world has limited capacity to sustainably expand cropland,” and this capacity is actually “shrinking in many developed countries.” The three researchers contend, “meeting future increases in demand will have to come from a near doubling of productivity on a land area basis.” They suggest “a large contribution will have to come from improved photosynthetic conversion efficiency,” for which they estimate “at least a 50% improvement will be required to double global production.”

The researchers focus on photosynthetic conversion efficiency because experimental evidence has found increases in the atmosphere's CO₂ concentration boost the photosynthetic rates of nearly all plants, and those rate increases generally lead to equivalent increases in plant productivity on a land-area basis. They examined the prospects for boosting photosynthetic conversion efficiency in an entirely different way: genetically, without increasing the atmosphere's CO₂ content.

The three scientists write, “Improving photosynthetic conversion efficiency will require a full suite of tools including breeding, gene transfer, and synthetic biology in bringing about the designed alteration to photosynthesis.” For some of these “near-term” endeavors, they write, “implementation is limited by technical issues that can be overcome by sufficient investment.” But a number of “mid-term” goals could take 20 years to achieve, and “even when these improvements are achieved, it may take an additional 10–20 years to bring such innovations to farms in commercial cultivars at adequate scale.” And they write of still longer-term goals for which “too little of the science has been undertaken to identify what needs to be altered to effect an increase in yield.” They acknowledge some of what they envision may not even be possible, such as developing a form of rubisco that exhibits a significant decrease in oxygenation activity, or designing C₃ crops to utilize the C₄ form of photosynthetic metabolism. The focus of Ainsworth *et al.* (2008) appears to be a far better path to pursue: conducting research to “elucidate the mechanisms of yield response to CO₂, to assess the genetic diversity available for improving responsiveness and to devise efficient schemes for selection for adaptation to rising ambient CO₂, whether based on conventional plant breeding or systems biology approaches for selecting and engineering improved genetics.”

Godfray *et al.* (2010) note, “more than one in seven people today still do not have access to sufficient protein and energy from their diet and even

more suffer some form of micronutrient malnourishment,” citing the FAO (2009). They write, although “increases in production will have an important part to play” in correcting this problem and keeping it from worsening in the future, mankind “will be constrained by the finite resources provided by the Earth's lands, oceans and atmosphere.” This set of difficulties they describe at the end of their review as a “perfect storm.”

The first question they ask in regard to how mankind might successfully navigate this highly restricted terrain is: “How can more food be produced sustainably?” They say the primary solution to food shortages of the past had been “to bring more land into agriculture and to exploit new fish stocks,” but they quickly note there is precious little remaining of either of these resources. They conclude, “the most likely scenario is that more food will need to be produced from the same or less land,” because “we must avoid the temptation to sacrifice further the Earth's already hugely depleted biodiversity for easy gains in food production, not only because biodiversity provides many of the public goods upon which mankind relies, but also because we do not have the right to deprive future generations of its economic and cultural benefits.”

The key to meeting these diverse requirements simultaneously is in Godfray *et al.*'s statement, “greater water and nutrient use efficiency, as well as tolerance of abiotic stress, are likely to become of increasing importance.” As discussed previously, rising carbon dioxide can bring about all of these changes in mankind's crops. Rising concentrations of atmospheric CO₂ increase the photosynthetic prowess of essentially all plants, while generally reducing the rate at which they transfer water from the soil to the air. In addition, an increase of CO₂ in the atmosphere tends to enhance the efficiency with which plants utilize nutrients in constructing their tissues and producing the edible portions that essentially all of Earth's animals and humans depend on.

Each of the important benefits noted above has been discussed in great detail in the preceding chapters of this volume. In the material that follows, we limit our discussion to studies that directly imply general trends regarding these global benefits. Section 4.1.2.1 examines the findings of several empirical studies from which trends in future agricultural production can be inferred, and Section 4.1.2.2 presents a review of several model-based studies that shed additional light on the subject.

References

Ainsworth, E.A., Beier, C., Calfapietra, C., Ceulemans, R., Durand-Tardif, M., Farquhar, G.D., Godbold, D.L., Hendrey, G.R., Hickler, T., Kaduk, J., Karnosky, D.F., Kimball, B.A., Korner, C., Koornneef, M., LaFarge, T., Leakey, A.D.B., Lewin, K.F., Long, S.P., Manderscheid, R., McNeil, D.L., Mies, T.A., Miglietta, F., Morgan, J.A., Nagy, J., Norby, R.J., Norton, R.M., Percy, K.E., Rogers, A., Soussana, J.-F., Stitt, M., Weigel, H.-J., and White, J.W. 2008. Next generation of elevated [CO₂] experiments with crops: a critical investment for feeding the future world. *Plant, Cell and Environment* **31**: 1317–1324.

Ballantyne, A.P., Alden, C.B., Miller, J.B., Tans, P.P., and White, J.W. 2012. Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature* **488**: 70–72.

FAO. 2009. *State of Food Insecurity in the World 2009*. Food and Agriculture Organization, Rome, Italy.

Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M., and Toulmin, C. 2010. Food security: The challenge of feeding 9 billion people. *Science* **327**: 812–818.

Meadows, D.H., Meadows, D.L., Randers, J., and Behrens III, W.W. 1972. *The Limits to Growth*. Universe Books, New York, New York, USA.

Nemani, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneni, R.B., and Running, S.W. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* **300**: 1560–1563.

Parry, M.A.J. and Hawkesford, M.J. 2010. Food security: increasing yield and improving resource use efficiency. *Proceedings of the Nutrition Society* **69**: 592–600.

Running, S.W. 2012. A measurable planetary boundary for the biosphere. *Science* **337**: 1458–1459.

Tilman, D., Socolow, R., Foley, J.A., Hill, J., Larson, E., Lynd, L., Pacala, S., Reilly, J., Searchinger, T., Somerville, C., and Williams, R. 2009. Beneficial biofuels: The food, energy, and environment trilemma. *Science* **325**: 270–271.

Zhao, M. and Running, S.W. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science* **329**: 940–943.

Zhu, X.-G., Long, S.P., and Ort, D.R. 2010. Improving photosynthetic efficiency for greater yield. *Annual Review of Plant Biology* **61**: 235–261.

4.1.2.1 Empirical Studies

- Empirical studies suggest a future warming of the climate coupled with rising atmospheric CO₂ levels will boost global agricultural production and help meet the food needs of the planet's growing population.

As discussed in the preceding chapters of this volume, numerous studies attest to the growth-enhancing, water-conserving, and stress-alleviating benefits of CO₂ enrichment for plants. In the present subsection, therefore, we limit our discussion to studies from which we can infer general trends in future agricultural production.

According to Tian *et al.* (2012), “more than 20% of the world's food consumers depend on wheat (*Triticum aestivum* L.), which is produced on an area of over 200 million hectares worldwide (Ortiz *et al.*, 2008).” They note “winter wheat area accounts for more than 80% of this total,” and “it is typically grown in the seasons of winter and spring where warming is mainly anticipated.” China, the writers note, is the world's largest producer of winter wheat, and more than 70% of the crop is sown in the country's eastern provinces on the Yangtze Delta Plain.

Tian *et al.* “conducted a five-year field warming experiment since 2004 with a facility of Free Air Temperature Increase (FATI) in Nanjing, Jiangsu province,” in which their objectives were “to investigate the actual responses of winter wheat phenophase, biomass production and grain yield to anticipated warming [~1.5°C] under field conditions” where “there were no water and nitrogen limitations for winter wheat growth, which is common in East China.” They studied *Triticum aestivum* L. cv Yangmai 11, a local cultivar having a “high yield potential.”

The 1.5°C increase in temperature significantly advanced crop phenophases, leading to a reduction in the length of the entire growth period of about 10 days, with the result that grain yields rose due to “the mitigation of low temperature limitation during the pre-anthesis phase and to the avoidance of hot-dry stress during the post-anthesis phase.” The researchers found the areas of flag leaves and total green leaves at anthesis, as well as the 1,000-grain weight of the plants, were 36.0, 19.2, and 5.9% higher in the warmed plots than in the unaltered control, respectively. The net effect of these warmth-induced changes was a mean grain yield increase of 16.3%, and they therefore conclude “anticipated warming

may facilitate winter wheat production in East China.”

Ortiz *et al.* (2008) reviewed some of the approaches for ameliorating the oft-predicted negative impacts climate change may have on wheat production in some of the most important wheat growing areas of the world. They write, “to adapt and mitigate the climate change effects on wheat supplies for the poor, germplasm scientists and agronomists are developing heat-tolerant wheat germplasm, as well as cultivars better adapted to conservation agriculture,” noting these encouraging results include “identifying sources of alleles for heat tolerance and their introgression into breeding populations through conventional methods and biotechnology.” They report “wheat geneticists and physiologists are also assessing wild relatives of wheat as potential sources of genes with inhibitory effects on soil nitrification.” This activity could lead to significantly reduced emissions of nitrous oxide from agricultural soils and thereby shrink the impetus for global warming provided by this powerful trace greenhouse gas, which molecule-for-molecule is about 300 times more radiatively active than CO₂. Ortiz *et al.* conclude important technology and knowledge will ultimately flow to farmers and enable them “to face the risks associated with climate change.”

Bunce (2008) grew adequately fertilized plants of four varieties of the common garden bean (*Phaseolus vulgaris*)—Matterhorn (a great northern bean), Jaguar (a black bean), Red Hawk (a kidney bean), and Brown Beauty (a snap bean)—from seed to maturity under standard field conditions at Beltsville, Maryland (USA) in open-top chambers. They made photosynthetic measurements of mature upper-canopy leaves in full sunlight at midday during the pod-filling stages of four growing seasons and determined final seed yields and other plant characteristics at harvest. They found an extra 180 ppm of CO₂ in the CO₂-enriched chambers (a concentration increase of close to 50% during daylight hours) resulted in a mean long-term stimulation of midday net photosynthesis of approximately 18% in the Matterhorn and Jaguar bean varieties, and an increase of twice that much (36%) in the Red Hawk and Brown Beauty cultivars. In terms of dry mass seed yield, the Matterhorn variety experienced a CO₂-induced increase of about 39%, followed by Red Hawk at 21%, Brown Beauty at 18%, and Jaguar with a 10% decline in seed yield. As Bunce reports, “the highest yielding variety at ambient CO₂ [Jaguar] was out-yielded by a different variety at elevated CO₂ [Matterhorn].”

These observations make it clear there is

significant variability in seed yield response to atmospheric CO₂ enrichment among the four bean varieties tested by Bunce. In addition, it is equally clear there was no *a priori* way of knowing which of the four cultivars would respond best to an increase in atmospheric CO₂ concentration, or that one would actually respond negatively. Bunce’s experiment demonstrates the great need to perform a host of such studies on the planet’s most important crop plants, to identify which of their many varieties should be selected for additional crop breeding work. That is the only way to take full advantage of the significant increase in the atmosphere’s CO₂ concentration that will occur over the next several decades.

In a standard paddy-culture FACE experiment conducted at Yangzhou, Jiangsu, China, during the years 2004–2006, Yang *et al.* (2009) grew a two-line inter-subspecific hybrid rice variety (Liangyoupeijiu) at ambient and elevated atmospheric CO₂ concentrations of 376 and 568 ppm, respectively, at two levels of field nitrogen (N) application—low N (12.5 g N m⁻²) and high N (25 g N m⁻²)—while measuring numerous aspects of crop growth, development, and final yield. The eight Chinese scientists found the 51% increase in atmospheric CO₂ concentration increased the final grain yield of the low N rice crop by 28% and that of the high N rice crop by 32%. As a result, and in light of the findings of two prior rice FACE experiments (Kim *et al.*, 2003; Yang *et al.*, 2006), they conclude “hybrid rice appears to profit much more from CO₂ enrichment than inbred rice cultivars (c. +13%).” Yang *et al.* describe Liangyoupeijiu as “one of the most popular ‘super’ hybrid rice varieties in China (Peng *et al.*, 2004).”

Shimono *et al.* (2007) say lodging—the environmental beating down of a crop—“can occur under heavy rains and strong winds,” and this phenomenon “decreases canopy photosynthesis due to self-shading (Setter *et al.*, 1997) and disturbs the translocation of carbon and nutrients to the rice grains (Hitaka and Kobayashi, 1961), resulting in lower yield and poor grain quality.” They note Setter *et al.* (1997) found a moderate degree of lodging reduced canopy height by 35% and decreased yield by about 20%, whereas severe lodging reduced canopy height by 75% and decreased yield by up to 50%.

Shimono *et al.* designed a free-air CO₂-enrichment experiment to determine what effect the ongoing rise in the atmosphere’s CO₂ content might have on lodging in rice plants, growing the cultivar Akitakomachi in paddy fields under three nitrogen (N) fertilization regimes—low N (6 g N m⁻²), medium N (9 g N m⁻²), and high N (15 g N m⁻²)—at two