

season-long 24-hour mean CO₂ concentrations—375 ppm (ambient) and 562 ppm (enriched)—measuring the degree of naturally occurring lodging at the time of grain maturity on a scale of 0–5, based on the bending angles of the stems at 18° intervals, where 0 = 0° from the vertical, 1 = 1°–18°, 2 = 19°–36°, 3 = 37°–54°, 4 = 55°–72°, and 5 = 73°–90°.

The six scientists report lodging was significantly higher under high N than under medium and low N. The lodging experienced in the high N treatment “was alleviated by elevated CO₂,” because the lowest internodes of the rice stems “became significantly shorter and thicker under elevated CO₂,” which likely “strengthened the rice culms against the increased lodging that occurred under high N.” They note the reduced lodging experienced under elevated CO₂ in the high N treatment increased the grain-ripening percentage of the rice by 4.5% per one-unit decrease in lodging score.

Shimono *et al.* note there is concern that in order “to increase rice yield under projected future CO₂ levels, N fertilization must be increased to meet increased plant demand for this nutrient as a result of increased growth rates,” but greater N fertilization might enhance lodging, thereby defeating the purpose of the fertilization. Their study found “elevated CO₂ could significantly decrease lodging under high N fertilization, thereby increasing the ripening percentage and grain yield,” in what amounts to another CO₂-induced success story for what the researchers called “the most important crop for feeding the world’s population.”

Lou *et al.* (2008) note there is a pressing need to identify genotypes that produce maximum grain yields under projected future atmospheric CO₂ levels. They grew four different rice cultivars—Dular (a traditional indica variety), IR72 (an improved indica variety), Koshihikari (a temperate japonica variety), and IR65598 (a new variety not yet released to farmers at that time)—in Japan in growth chambers in submerged pots filled with a fertilized soil at two atmospheric CO₂ concentrations: ambient (~370 ppm) and elevated (~570 ppm). They found the extra 200 ppm of CO₂ reduced the ultimate grain yield of Dular (by 0.7%) and increased it for IR72 (by 8.0%), Koshihikari (by 13.4%), and IR65598 (by 17.7%).

Roy *et al.* (2012) write “an average annual increase in grain production of 44 million metric tons is required to meet the food demands of the world by 2050,” citing Tester and Langridge (2010), and they note “the predicted 2.0°C increase in air temperature by the end of 2050 (IPCC, 2007) might lead to a 20–40% decrease in cereal yields,” citing Lele (2010). To

assess this situation from an experiment-based perspective, the five researchers from the Central Rice Research Institute of India conducted a three-year open-top-chamber field study to observe the effects of elevated atmospheric CO₂ concentration (550 vs. ambient 390 ppm), as well as elevated temperature (T, 2°C above ambient temperature), on dry matter production, carbon (C), and nitrogen (N) concentrations and their allocation in a tropical rice cultivar (cv. *Naveen*).

In the elevated CO₂/normal temperature treatment, their experiment revealed: dry matter accumulation in the aboveground portion of the rice plants was enhanced by 17.7% at maturity; root biomass, leaf area index, and net carbon assimilation rates increased by 28, 19, and 40%, respectively; grain yield was significantly higher (22.6%); the net carbon yield increased by 23.3%; and nitrogen allocation increased significantly in leaf (13%), stem (14%), and panicle (17%) at maturity.

In the elevated CO₂/elevated temperature treatment, the found: dry matter accumulation in the aboveground portion of the rice plants was enhanced by 18.1% at maturity; root biomass, leaf area index, and net carbon assimilation rates also increased significantly; grain yield was significantly higher (19.6%); the net carbon yield increased by 24.2%; and nitrogen allocation increased significantly in leaf (13%), stem (14%), and panicle (17%) at maturity.

Jin *et al.* (2009) conducted a CO₂ enrichment study in three pairs of greenhouses placed over a uniform soil surface, in which they planted celery (*Apium graveolens* L.), leaf lettuce (*Lactuca virosa* L.), stem lettuce (*Lactuca saiva* L.), oily sowthistle (*Sonchus oleraceus* L.), and Chinese cabbage (*Brassica chinensis* L.). In response to a slightly more-than-doubling of atmospheric CO₂ content, “the average percentage of yield increases of all three sites were 270%, 257%, 87%, 140% and 227% for celery, leaf lettuce, stem lettuce, oily sowthistle, and Chinese cabbage, respectively.” The extra CO₂ also increased the concentration of vitamin C in all five species, “by 13%, 39%, 25%, 72%, and 37% for celery, leaf lettuce, stem lettuce, oily sowthistle, and Chinese cabbage, respectively.”

Vanaja *et al.* (2010) write, “food grain requirements of India (both human and cattle) are estimated at 300 Mt in 2020,” citing Sinha *et al.* (1998), and they note “grain legumes are one of the mainstays of the drylands, as these crops provide much needed nutritional security in the form of proteins to the predominant vegetarian populations of India and also the world.” They further state legumes—of which

pigeon peas are an important example—"have the potential to maximize the benefit of elevated CO₂ by matching [CO₂]-stimulated photosynthesis with increased N₂ fixation," citing Rogers *et al.* (2009).

Vanaja *et al.* grew pigeon peas (*Cajanus cajan* L. Millsp.) from seed to maturity out-of-doors at Hyderabad (India) in open-top chambers maintained at atmospheric CO₂ concentrations of either 370 or 700 ppm (ambient or enriched, respectively), after which they harvested them and measured a number of pertinent productivity parameters. The team of nine Indian scientists from the country's Central Research Institute for Dryland Agriculture report "total biomass recorded an improvement of 91.3%, grain yield 150.1% and fodder yield 67.1%." They write, "the major contributing components for improved grain yield under elevated CO₂ were number of pods, number of seeds and test weight," which exhibited increases of 97.9%, 119.5%, and 7.2%, respectively. In addition, they found "a significant positive increase of harvest index at elevated CO₂ with an increment of 30.7% over ambient values," which they attribute to the crop's "improved pod set and seed yield under enhanced CO₂ concentration." These findings, Vanaja *et al.* conclude, illustrate the importance of pigeon peas for "sustained food with nutritional security under a climate change scenario."

Rosenthal *et al.* (2012) write, "given the projections that future food production will need to double to meet the global demand by 2050 (Lobell *et al.*, 2008; Godfray *et al.*, 2010; Tilman *et al.*, 2011), there is an urgent need to assess the impact of climate drivers on crops of food insecure regions." They note, "more than 900 million people are undernourished and nearly 90% live in Sub-Saharan Africa, Asia, and the Pacific," citing the United Nations Food and Agriculture Organization (FAO, 2010). The eight researchers also write, "in Sub-Saharan Africa, the starchy root tuber crop cassava accounts for almost two-thirds of the direct human caloric intake," and in areas where drought is recurrent, "cassava is harvested when other crops fail (FAO, 2005)," adding, cassava "provides food security during armed conflicts when above-ground crops are destroyed, as the cassava tuber remains viable below ground for up to three years (Cock, 1982; Lebot, 2009)."

Rosenthal *et al.* report a recent greenhouse study on cassava found decreased yields at elevated CO₂, and the smaller yields were accompanied by increases in leaf, but not tuber, cyanide content (Gleadow *et al.*, 2009). This finding alarmed them because, they write, "cassava leaves are eaten for their protein, and a higher leaf cyanide content suggests increased

toxicity at elevated CO₂." But since this study was conducted in a greenhouse, they opted to conduct a study to determine whether increases in cassava biomass or leaf toxicity would occur in plants grown under natural field conditions, employing free-air CO₂ enrichment (FACE) technology at the SoyFACE facility located at the Experimental Research Station of the University of Illinois in Urbana-Champaign (USA), where the air of four plots was enriched with CO₂ to approximately 200 ppm above what was measured in four ambient-treatment plots.

The U.S. and Australian researchers report, after three-and-a-half months of growth at elevated CO₂, the above-ground biomass of cassava was 30% greater and cassava tuber dry mass was more than 100% greater than in plants grown in ambient air. This result, they write, "surpasses all other C₃ crops and thus exceeds expectations." In contrast to the greenhouse study they cited, they find "no evidence" of increased leaf or total cyanide concentrations in the plants grown in the elevated CO₂ plots.

Vanuytrecht *et al.* (2012) acquired peer-reviewed publications reporting the results of free-air CO₂-enrichment (FACE) studies via searches of the ISI Web of Science citation database (Thomson) and the ScienceDirect citation database (Elsevier BV). They conducted a meta-analysis of 529 independent observations of various plant growth responses to elevated CO₂ obtained from 53 papers containing relevant data in graphical or numerical format pertaining to wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), rice (*Oryza sativa* L.), soybean (*Glycine max* L.), potato (*Solanum tuberosum* L.), sugar beet (*Beta vulgaris* L.), cotton (*Gossypium hirsutum* L.), maize (*Zea mays* L.), and sorghum (*Sorghum bicolor* L.), as well as the two major pasture species of perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.).

Considered *en masse*, Vanuytrecht *et al.* report an approximate 200 ppm increase in the air's CO₂ concentration (the mean enhancement employed in the studies they analyzed) led to water productivity improvements of 23% in terms of aboveground biomass production per unit of water lost to evapotranspiration, and 27% in terms of aboveground yield produced per unit of water lost to evapotranspiration. These two productivity increases would roughly correspond to enhancements of 34% and 40% for a 300 ppm increase in the air's CO₂ concentration.

Although "the FACE technique avoids the potential limitations of (semi-) closed systems by studying the influence of elevated CO₂ on crop growth in the field without chamber enclosure," the

team of Belgian researchers writes, other studies have demonstrated a significant problem caused by the rapid (sub-minute) fluctuations of CO₂ concentration about a target mean common to most FACE experiments, as described by Bunce (2011, 2012). The latter found total shoot biomass of vegetative cotton plants in a typical FACE study averaged 30% less than in a constantly elevated CO₂ treatment at 27 days after planting, and wheat grain yields were 12% less in a fluctuating CO₂ treatment compared with a constant elevated CO₂ concentration treatment.

The results of the empirical studies described above suggest a future warming of the climate, coupled with rising atmospheric CO₂ levels, will boost global agricultural production and help to meet the food needs of the planet's growing population.

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4.1.2.2 Model-based Studies

- 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.

Bootsma *et al.* (2005) derived relationships between agroclimatic indices and average grain yields of corn, soybeans, and barley obtained from field trials conducted in the eastern part of Canada and used them to estimate the impacts of projected climate change scenarios on the yields of these commodities for the years 2040–2069. Based on a range of heat units projected by multiple climate model simulations, they report average yields achievable in field trials could increase by 40–115% for corn and 21–50% for soybeans by 2040–2069, “not including the direct effect of increased atmospheric CO₂ concentrations.” Adding the expected CO₂ increase into the mix, along with gains in yield anticipated to be achieved through breeding and improved technology, these numbers rose to 114–186% for corn and 117–157% for soybeans.

Initial yields of barley, in contrast, were projected to decline, by as much as 25% in areas with significant water deficits, but after reviewing the scientific literature on the subject, the Canadian researchers conclude the direct effect of increased CO₂ alone “would more than offset the yield reductions anticipated due to effects of rising temperature and changes in water deficit.” All things considered, they conclude, “barley yields would increase by an average of about 15% under this scenario.” Bootsma *et al.* predict a “switch to high-energy and high-protein-content crops (corn and soybeans) better adapted to the warmer climate,” but say “there will likely still be a considerable area of land seeded to barley and other small grain cereals, as these are very desirable in rotation with potatoes.”

Liu *et al.* (2004) made detailed calculations of the economic impact of predicted climate changes for the year 2050 (a mean countrywide temperature increase of 3.0°C and a mean precipitation increase of 3.9%) on agriculture in China, using the methodology of Mendelsohn *et al.* (1994) and agricultural, climate, social, economic, and edaphic data for 1,275 agricultural counties for the period 1985–1991. In the mean, Liu *et al.* report “all of China would benefit from climate change in most scenarios.” In addition, they write, “the effects of CO₂ fertilization should be included, for some studies indicate that this may produce a significant increase in yield,” an increase that is well-established (see Chapter 1, this volume) and was not included in their analysis. Liu *et al.* note “China’s agriculture has to feed more than one-fifth of the world’s population, and, historically, China has been famine prone,” noting, “as recently as the late

1950s and early 1960s a great famine claimed about thirty million lives (Ashton *et al.*, 1984; Cambridge History of China, 1987)."

Chavas *et al.* (2009) also showed the importance of including the effects of CO₂ fertilization in projecting agricultural trends, studying potential climate change impacts on the productivity of five major crops (canola, corn, potato, rice, and winter wheat) of eastern China (30 to 42°N, 108 to 123°E). They conducted full-domain simulations of the EPIC agro-ecosystem model for the baseline period 1961–1990 and the future period 2071–2100 under IPCC's A2 scenario for projected atmospheric CO₂ concentrations and accompanying climate change. They found, "without the enhanced CO₂-fertilization effect, potential productivity declines in all cases ranging from 2.5 to 12%." When the CO₂-fertilization effect was included, "aggregate potential productivity (i.e. if the crop is grown everywhere) increases 6.5% for rice, 8.3% for canola, 18.6% for corn, 22.9% for potato, and 24.9% for winter wheat." In addition, "similar results are reported at the national scale in the work of Lin *et al.* (2005) using alternative RCM output and the CERES crop simulation model."

Thus, despite the supposedly deleterious climate changes predicted to occur over the rest of the twenty-first century, when the seven scientists factored into the yield model the aerial fertilization effect of the projected increase in atmospheric CO₂, they found the net productivities of all five crops rose over the entire study region.

Noting "rice is an essential component of the diet in more than half the world's population" and "the most socially and economically important crop in China," where it "contributes 43.7% of total national grain production," Xiong *et al.* (2009) assessed the effect of greenhouse gas-induced climate change and the direct fertilization effect of CO₂ on rice yields and production in China by coupling "the regional climate model PRECIS (Providing Regional Climates for Impacts Studies) with the CERES (Crop Environment Resources Synthesis) rice crop model to simulate current (1961–1990) and future (2011–2100) rice yields and production under [IPCC's] A2 and B2 climate change scenarios."

They found "single rice cropping may expand further north in China, and double rice cropping may move to the northern portion of the Yangtze River basin." In addition, "the national mean rice production is estimated to increase by 2.7 to 19.2% considering the combined effects of climate change, CO₂ and shifting rice-producing areas." Consequently, even considering the inflated temperature

increases predicted by IPCC, the estimated net effect of global warming and concomitant growth in anthropogenic CO₂ emissions results in a significant increase in rice production in the world's most populous country, where it is the people's most important food source.

Tao *et al.* (2013) introduce their work by writing "future climate change is projected to be one of the major challenges for regional agricultural production in broad regions of the world," noting Tao *et al.* (2009a,b) and Tao and Zhang (2010) developed "a new process-based Model to capture the Crop-Weather relationship over a Large Area (MCWLA) and a new super-ensemble-based probabilistic projection (Super EPPS) to account for the uncertainties not only from greenhouse gas emission scenarios and climate change scenarios but also from biophysical processes in crop models, and to assess the impacts of climate change (variability) on regional crop productivity and water use in a probabilistic framework." These model projections "have been demonstrated," they continue, "in addressing the probabilistic responses and adaptations of maize production to climate change in the North China Plain (NCP)."

Tao and Zhang state the crop model MCWLA-Wheat was first developed "by adapting the process-based general crop model, MCWLA, to winter wheat," after which "Bayesian probability inversion and a Markov chain Monte Carlo (MCMC) technique were applied to the MCWLA-Wheat to analyze uncertainties in parameter estimations, and to optimize parameters." Ensemble hindcasts show "the MCWLA-Wheat could capture the inter-annual variability of detrended historical yield series fairly well, especially over a large area." Based on the MCWLA-Wheat, they developed a Super EPPS and applied it to project the probabilistic responses of wheat productivity and water use in the NCP to future climate change. The scientists used 10 climate scenarios "consisting of the combinations of five global climate models and two greenhouse gases emission scenarios (A1F1 and B1), the corresponding atmospheric CO₂ concentration range, and multiple sets of crop model parameters representing the biophysical uncertainties from crop models."

The Chinese researchers found a high probability that future climate change would increase winter wheat yields in the NCP during the 2020s, 2050s, and 2080s, with (and without) CO₂ fertilization effects and relative to 1961–1990 levels, by, on average, 37.3% (18.6%), 67.8% (23.1%), and 87.2% (34.4%), respectively, over 80% of the study area.

These findings are encouraging in light of the analysis of Schmidhuber and Tubiello (2007), who suggest global food production may need to rise by as much as 70% by the year 2050 in order to adequately feed the nine billion people (compared to today's seven billion) they project to be inhabiting the planet at that midcentury point.

Trnka *et al.* (2004) used the crop growth model CERES-Barley version 2.1 (Otter-Nacke *et al.*, 1991) to assess the direct biological effect of a doubling of the air's CO₂ concentration (from 350 to 700 ppm) on the growth and yield of spring barley in the Czech Republic, along with the indirect effect on growth and yield produced by the climate changes predicted to accompany such a CO₂ increase, as simulated by several GCMs, including ECHAM4, HadCM2, NCAR-DOE, and seven other GCMs available from IPCC. They report the indirect effect on spring barley yield caused by changed weather conditions was mostly negative, ranging from -19% to +5% for the several climate scenarios applied to three different production regions of the Czech Republic.

CO₂ enrichment made a positive difference in these results. Trnka *et al.* write, "the magnitude of the direct [and positive] effect of doubled CO₂ on the stressed yields for the three test sites is 35–55% in the present climate and 25–65% in the 2 x CO₂ climates," and "the stressed yields would increase in 2 x CO₂ conditions by 13–52% when both direct [biological] and indirect [climatic] effects were considered." In addition, "the decrease of the mean yields due to the indirect [climatic] effect of doubled CO₂ may be reduced, and it might be even turned to increase, if the spring barley is planted 45–60 days sooner." They conclude, "application of the earlier planting date would result thus in an additional 15–22% increase of the yields in 2 x CO₂ conditions." They conclude, "the positive direct effect of doubled CO₂ dominates over the negative effect of changed weather conditions," and they note the results they obtained "might be applied to vast regions of Central Europe with similar environmental characteristics."

Kvalvik *et al.* (2011) state the consequences of predicted climate change "are not straightforward, but dependent on the interaction between different weather and biological elements, as well as political, economic and social conditions." In their interdisciplinary study of this complex situation, the six Norwegian scientists "assessed biological and agronomic effects of climate change, and their interaction with political, economic and social factors to identify farmers' vulnerability and adaptive capacity to climate change," based on "downscaled climate

change scenarios and interviews with local farmers in the three northernmost counties in Northern Norway (latitude 65.5° to 70°N)."

The scientists found "the farmers themselves are willing to use the opportunities afforded by a more favorable climate," and "a warmer climate is generally regarded as favorable by the farmers in our study region." However, they report their study of farmers in northern Norway shows they are "vulnerable to a changing climate, not because of the direct effect of changing growing conditions, but because these changes are an added factor to an already tenuous situation created by Norwegian agricultural policy and the socio-economic development in general," which "poses a greater challenge to farming and is likely to reduce the farmers' adaptive capacity."

Kvalvik *et al.* conclude farmers in northern Norway "are highly adaptive, to both changing growing conditions and changing agricultural policies." They note "changes in policy are currently a greater challenge to farmers than climate change," and "such changes are therefore a more salient driver of vulnerability," implying the Norwegian government's presumptive cure for the disease of global warming (which is described in some detail in their paper) is probably no cure at all, and possibly worse than the disease itself.

Cullen *et al.* (2012) introduce their study by noting "climate change projections for southern Australia indicate the region is likely to become warmer and drier," noting "there is considerable variation in the projections from different climate models and emission pathways." They point out "there is some uncertainty about how rapidly warming will occur" and "projections for rainfall change vary widely." Given the large uncertainty in climate change projections from global circulation models, Cullen *et al.* conclude an alternative approach would be "to explore the sensitivity of agricultural systems to a range of likely future temperature, carbon dioxide and rainfall combinations, thereby creating a three-dimensional surface of response."

The three Australian researchers report the simulated changes in pasture production and the approach adopted in their study highlight when and where possible adaptation options may be required, adding this approach "clearly demonstrates the resistance of pasture production over a range of climate changes." Cullen *et al.* conclude that for south-eastern Australia, "annual pasture production is resistant to climatic changes of up to 2°C warming," thanks to the collective wisdom of farmers, who

Climate Change Reconsidered II: Biological Impacts

learned from experience how to cope with various degrees of temperature and precipitation change, and of scientists who had studied the subject in considerable detail.

Marin *et al.* (2013) evaluated the effects of climate change on sugarcane yield, water use efficiency, and irrigation needs in southern Brazil, based on downscaled outputs of two general circulation models (PRECIS and CSIRO) and a sugarcane growth model (DSSAT/CANEGRO) calibrated for the main cultivar currently grown in Brazil. They used data from five field experiments conducted under several soil and climate conditions, analyzing the sensitivities of simulated stalk fresh mass (SFM) to air temperature, CO₂ concentration, and rainfall, to identify increases in simulated SFM and water use efficiency (WUE) for all scenarios investigated.

On average, this analysis revealed, “for the current sugarcane area in the State of Sao Paulo, SFM would increase 24% and WUE 34% for rain-fed sugarcane.” The authors write, “considering the current technological improvement rate, projected yields for 2050 ranged from 96 to 129 tons per hectare, which are respectively 15 and 59% higher than the current state average yield.” They say their simulations suggest “the WUE increase due to higher CO₂ seems to be the main cause for the positive simulated yield response.”

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.

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4.2 Biospheric Productivity: The Greening of the Earth

Since 1980, some parts of the world registered three of the warmest decades in the instrumental temperature record, intense and persistent El Niño events, large-scale deforestation, “unprecedented” forest fires, and the eruption of several volcanoes. Concurrently, the atmosphere's CO₂ content increased by 16% and the human population grew by 55%. How badly is the biosphere suffering in response to these much-feared events? Is it even suffering at all?

As reviewed in the subsections below, several research groups have explored those questions. This section begins with a discussion of what has been learned about the terrestrial biosphere as a whole, followed by a regional analysis exploring terrestrial productivity trends on continental and subcontinental scales.

4.2.1 Global Terrestrial

- The vigor of Earth's 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 6–13% since the 1980s. There is no empirical evidence to support the model-based claim that future carbon uptake will diminish on a global scale due to rising temperatures.

Reichenau and Esser (2003) investigated the individual influences of the El Niño-Southern Oscillation (ENSO), volcanic eruptions, and the North Atlantic Oscillation (NAO) on the 1958–1994 time series of anomalous CO₂ fluxes using the High Resolution Biosphere Model of Esser *et al.* (1994) and real-world CO₂ measurements. Although the two researchers could conclude nothing about the NAO, other than to say “the influence of the NAO remain[s] unclear,” they determined periods of anomalous rising atmospheric CO₂ concentrations coincided with El Niño periods, and times of anomalous declining atmospheric CO₂ concentrations coincided with periods of significant volcanism.

They write, “the globally averaged effect of [the

El Niño] circulation pattern on the terrestrial biosphere is a net release of carbon,” in agreement with the results of earlier investigations of the subject (Bacastow, 1976; Bacastow *et al.*, 1980), which in turn “confirms earlier findings that the terrestrial biosphere is mainly responsible for atmospheric CO₂ variations on the ENSO timescale (Keeling *et al.*, 1995; Lee *et al.*, 1998; Feely *et al.*, 1999; Gerard *et al.*, 1999; Rayner and Law, 1999; Battle *et al.*, 2000; Bousquet *et al.*, 2000; Houghton, 2000; Knorr, 2000, LeQuere *et al.*, 2000; Langenfelds *et al.*, 2002).” At the other end of the spectrum, Reichenau and Esser report “volcanic eruptions with considerable aerosol production may create disturbances of the (biospheric) carbon cycle by increasing the photosynthetic carbon uptake due to the enhanced diffuse fraction of the incoming [solar] radiation.” This accords with the findings of Roderick *et al.* (2001), Cohan *et al.* (2002), Law *et al.* (2002), and Gu *et al.* (2002, 2003).

The many published studies of anomalous CO₂ fluxes between Earth's surface and its atmosphere indicate warm El Niño conditions tend to reduce biospheric productivity, whereas cool volcanic conditions tend to enhance that productivity. At first glance, this appears to support claims of “cool is good” and “warm is bad” for the planet's plants. But there is much more to the story.

For one thing, the productivity-enhancing effect of volcanic eruptions arises not from their cooling influence, but from their increasing the amount of diffuse solar radiation received at Earth's surface, which allows for an enhanced penetration of solar radiation deeper into plant canopies, which reduces within-canopy shade and boosts rates of canopy net photosynthesis. As for the productivity-reducing effect of El Niños, it could be more a consequence of changes in global precipitation patterns than a direct effect of the temperature increases. Indermuhle *et al.* (1999), for example, demonstrated the pattern of biospheric productivity over the last 7,000 years of the Holocene was essentially that of a slow monotonic decline from the peak growth conditions of the interglacial's Climatic Optimum, and this productivity decline, they write, was “due to a change from the warmer and wetter mid-Holocene climate to colder and drier conditions.”

Additional evidence of the benefits of long-term warming on plants comes from the study of Lin *et al.* (2010), who conducted a meta-analysis of data from 127 individual studies, reporting for the totality of terrestrial plants included in their analysis, “warming significantly increased biomass by 12.3%” and there

was a “significantly greater stimulation of woody (+26.7%) than herbaceous species (+5.2%).” They also state the warming effects on plant biomass production “did not change with mean annual precipitation or experimental duration,” and “other treatments, including CO₂ enrichment, nitrogen addition, drought and water addition, did not alter warming responses of plant biomass.” Thus the Chinese researchers conclude, “results in this and previous meta-analyses (Arft *et al.*, 1999; Rustad *et al.*, 2001; Dormann and Woodin, 2002; Walker *et al.*, 2006) have revealed that warming generally increases terrestrial plant biomass, indicating enhanced terrestrial carbon uptake via plant growth and net primary productivity.”

These studies indicate long-term global warming tends to increase biospheric productivity. Deviations from this basic relationship evident in variations of CO₂ fluxes between Earth’s surface and atmosphere are likely to be short-lived and anomalous.

Langenfelds *et al.* (1999) analyzed O₂/N₂ measurements of the contents of a suite of tanks filled with background air collected at Cape Grim, Tasmania between April 1978 and January 1997. The rates of carbon storage in the world’s oceans and the terrestrial biosphere they derived from these data indicate the terrestrial biosphere was essentially in balance with respect to surface fluxes of carbon throughout this 19-year interval. However, other studies have established tropical deforestation produced a huge net loss of carbon during each of those years. Langenfelds *et al.* necessarily acknowledge the existence of a terrestrial carbon sink of like magnitude. They suggest this “compensating growth of the [terrestrial] biosphere” is due to “re-forestation, higher rates of net production in response to climatic trends, fertilisation by elevated levels of atmospheric CO₂ or nitrogen deposition or a combination of these factors.” Thus, the biosphere appears to be re-sequestering the carbon man takes out of it.

In a broad review of the scientific literature, Idso and Idso (2011) described a number of biological consequences of the “fertilization of elevated levels of atmospheric CO₂.” The best-known of these impacts is probably CO₂’s aerial fertilization effect, which works on plants that utilize all three of the major biochemical pathways of photosynthesis (C₃, C₄, and CAM). In the case of herbaceous plants, this phenomenon typically boosts their productivities by about a third in response to a 300-ppm increase in atmospheric CO₂ content, and it enhances the growth of woody plants by 50% or more, as demonstrated in

literally thousands of laboratory and field experiments (Idso and Singer, 2009) (see Chapter 1, this volume).

Plant water use efficiency, which may be defined as the amount of organic matter produced per unit of water transpired to the atmosphere, is directly enhanced by the aerial fertilization effect of atmospheric CO₂ enrichment and its anti-transpirant effect, which is produced by CO₂-induced decreases in the number density and degree of openness of leaf stomatal apertures that occur at higher atmospheric CO₂ concentrations (see Chapter 2). CO₂-induced percentage increases as large as, or even larger than, those exhibited by plant productivity are commonplace.

An important ramification of this CO₂-induced increase in plant water use efficiency is that it enables plants to grow and reproduce in areas previously too dry for them. The consequent increases in ground cover in these regions reduce the adverse effects of wind- and water-induced soil erosion. This creates a tendency to reverse desertification and make vast tracts of previously unproductive land able to support more abundant animal life, both above- and below-ground.

In addition to helping vegetation overcome the stress of limited water supplies, elevated levels of atmospheric CO₂ help plants better cope with other environmental stresses, such as low soil fertility, low light intensity, high soil and water salinity, high air temperature, various oxidative stresses, and the stress of herbivory (see Chapter 3). When confronted with the specter of global warming, for example, many experiments have revealed concomitant enrichment of the air with CO₂ tends to increase the temperature at which plants function at their optimum, often making them even better suited to the warmer environment than they were to the cooler environment to which they were originally adapted. Under the most stressful of such conditions, extra CO₂ can be the deciding factor in determining whether a plant lives or dies.

These benefits of atmospheric CO₂ enrichment apply to both agricultural and natural ecosystems. As Wittwer (1995) has noted, “the rising level of atmospheric CO₂ could be the one global natural resource that is progressively increasing food production and total biological output in a world of otherwise diminishing natural resources of land, water, energy, minerals, and fertilizer.” This phenomenon is thus a means, he says, “of inadvertently increasing the productivity of farming systems and other photosynthetically active ecosystems,” and “the effects know no boundaries and both developing and developed countries are, and will

be, sharing equally.”

In light of these observations and the rising CO₂ content of Earth's atmosphere, especially since 1950, one would expect to see some evidence of a greening of the Earth (Idso, 1986). As indicated in the papers described below, a growing number of researchers have joined Langenfelds *et al.* in acknowledging these stimulatory effects on Earth's biosphere.

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 begins with the study of 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 (USA), discovering large increases in growth rate between 1859 and 1983, rates that exceeded what might have been expected from climatic trends but were consistent with the global trend of atmospheric CO₂. A further development was provided by a study of ring-width measurements of Douglas fir trees in British Columbia, Canada, which also revealed a marked increase in growth in the trees' latter decades (Parker, 1987), leading 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 began to rise at an unusual rate about 1920, increasing by approximately 30% by the mid-1980s—and he too 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 increase in productivity.

Hari *et al.* (1984) and Hari and Arovaara (1988) reported stands of Scots pines in northern Finland were found to have experienced growth increases ranging from 15 to 43% between 1950 and 1983. The researchers state “CO₂ seems to be the only environmental factor that has been changing systematically during this century in the remote area under study.”

Graybill and Idso (1993) found 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 (USA) showed an unprecedented upward growth trend 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 climatic variables played a significant role in enhancing the trees' growth rates, strongly implicating the historical rise in atmospheric CO₂ content as the factor responsible for their ever-increasing productivity over the prior century and a half.

Phillips and Gentry (1994) provided perhaps the most striking evidence for the significant twentieth-century growth enhancement of Earth's forests by the historical increase in the air's CO₂ concentration. 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 from around the world in order to test the hypothesis global forest productivity was increasing *in situ*. They found the turnover rates of these highly productive forests had indeed been continually rising since at least 1960, with an apparent pan-tropical acceleration since 1980 (see Figure 4.2.1.1). They note “the accelerating increase in turnover coincides with an accelerating buildup of CO₂,” and as Pimm and Sugden (1994)

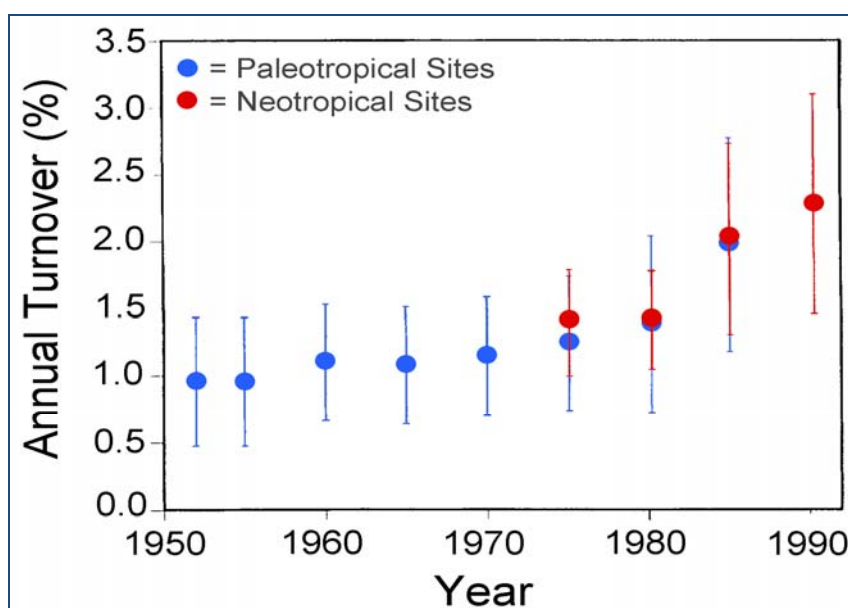


Figure 4.2.1.1. Average annual turnover rates (a surrogate for net productivity) for various tropical forests around the world since 1950. Adapted from Phillips and Gentry (1994).

note 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, a team of 11 researchers headed by Phillips (Phillips *et al.*, 1998) reported another impressive finding. Working with data on tree basal area (a surrogate for tropical forest biomass) for the years 1958–1996, which they obtained from several hundred plots of mature tropical trees around the world, they report average forest biomass for the tropics as a whole increased substantially. They calculate the increase amounted to approximately 40% of the missing terrestrial carbon sink of the 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, and they identify the aerial fertilization effect of the ongoing rise in the atmospheric CO₂ content as one of the factors responsible for this phenomenon. Other contemporary studies support their findings (Grace *et al.*, 1995; Malhi *et al.*, 1998), verifying that neotropical forests were indeed accumulating ever-more carbon, and Phillips *et al.* (2002) state this phenomenon was occurring “possibly in response to the increasing atmospheric concentrations of carbon dioxide (Prentice *et al.*, 2001; Malhi and Grace, 2000).”

The conclusions of Phillips and company were repeatedly challenged (Sheil, 1995; Sheil and May, 1996; Condit, 1997; Clark, 2002; Clark *et al.*, 2003). In response to those challenges, Phillips and 17 other researchers (Lewis *et al.*, 2004c), including one who had earlier criticized his and his colleagues’ conclusions, published a new analysis that vindicated Phillips *et al.*’s earlier thoughts on the subject.

One of the primary criticisms of Phillips *et al.*’s work was their meta-analyses included sites with a wide range of tree census intervals (two–38 years), which critics claimed could be confounding or “perhaps even driving conclusions from comparative studies,” as Lewis *et al.* (2004c) write. In Lewis *et al.*’s detailed study of this potential problem, which they conclude was indeed real, they state a re-analysis of Phillips *et al.*’s published results “shows that the pan-tropical increase in stem turnover rates over the late 20th 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.* (2004c) additionally note “Sheil’s (1995) original critique of the evidence for increasing turnover over the late twentieth 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, they continue, “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.*, 2004; Lewis *et al.*, 2004a; Phillips *et al.*, 2004).”

In a review of these global forest studies and many others (which led to their citing 186 scientific journal articles), Boisvenue and Running (2006) examined reams of “documented evidence of the impacts of climate change trends on forest productivity since the middle of the 20th century.” They write, “globally, based on both satellite and ground-based data, climatic changes seemed to have a generally positive impact on forest productivity when water was not limiting,” which was most of the time, because they report “less than 7% of forests are in strongly water-limited systems.” Thus there has been what Boisvenue and Running call a significant “greening of the biosphere” in recent years, the world’s forests in particular.

In another review of the scientific literature on this issue of global biospheric productivity, Lewis *et al.* (2009a) evaluated tropical forest inventory data, plant physiology experiments, ecosystem flux observations, Earth observations, atmospheric measurements, and dynamic global vegetation models. The five researchers report both theory and experiments suggest that over the past several decades “plant photosynthesis should have increased in response to increasing CO₂ concentrations, causing increased plant growth and forest biomass.” They find “long-term plot data collectively indicate an increase in carbon storage, as well as significant increases in tree growth, mortality, recruitment, and forest dynamism.” They also say satellite measurements “indicate increases in productivity and forest dynamism,” and five Dynamic Global Vegetation Models, incorporating plant physiology, competition, and dynamics, predict “increasing gross primary productivity, net primary productivity, and carbon storage when forced using late-twentieth century

Earth's Vegetative Future

climate and atmospheric CO₂ concentration data.” They write, “the predicted increases in carbon storage via the differing methods are all of similar magnitude (0.2% to 0.5% per year).”

Another indication these CO₂- and temperature-induced biological benefits are indeed occurring in the real world of nature comes from the decline in the air’s diurnal temperature range (DTR), evident in many parts of the world (Easterling *et al.*, 1997). Collatz *et al.* (2000) employed a simple land surface subroutine in a general circulation model of the atmosphere that included parameterizations of canopy physiological responses to various environmental changes, and by running the model with and without the vegetation subroutine, they were able to determine the degree of influence the planet’s plant life may have on near-surface air temperature in a world of rising temperature and atmospheric CO₂ concentration.

They found realistic changes in the amount and physiological activity of Earth’s plant life can produce changes in DTR of the order observed in the real world. The researchers state their results “suggest that reported increases in vegetation cover in the Northern Hemisphere during the 1980s [Myneni *et al.*, 1997] could have contributed to the lowered DTR.” Thus, whereas some scientists have viewed the declining diurnal temperature range near the surface of Earth as a “fingerprint” of deleterious CO₂-induced global warming, evidence suggests the declining DTR may instead be an indication of beneficial CO₂-induced “global greening.”

Alexandrov and Oikawa (2002) constructed a model of biospheric productivity based on empirical observations. Applied to the period 1980–1990, it suggests the total terrestrial carbon sink induced by the aerial fertilization effect of the contemporaneous increase in atmospheric CO₂ was approximately 1.3 Pg C yr⁻¹. This result compares well with estimates of up to 1.1 Pg C yr⁻¹ derived from independent empirical observations of same-period anthropogenic CO₂ emissions, changes in land use, CO₂ uptake by the world’s oceans, and increases in the air’s CO₂ concentration.

Gurney and Eckles (2011) reported similar findings nearly a decade later. They state, “projections of atmospheric CO₂ concentrations and the resulting climate change rely to a significant degree on projections about future land and ocean uptake,” citing Friedlingstein *et al.* (2006) and Sitch *et al.* (2008). To investigate how CO₂ uptake by Earth’s terrestrial surfaces has varied over the past three decades, they examined the results of atmospheric CO₂ inversions—constrained by observed atmospheric CO₂ concentrations (Tans *et al.*, 1990) and simulated atmospheric transport—to estimate trends in air-to-land carbon fluxes, as per Enting (2002). They did so, they write, “at spatial scales down to the continents using the results of the TransCom 3 international atmospheric CO₂ inversion inter-comparison (Gurney *et al.*, 2002, 2008),” which involved 13 participating modeling groups. Their analyses indicate the global land carbon sink is intensifying (see Figure 4.2.1.2) at a rate of 0.057 PgC/year/year, resulting in 1.65 PgC of additional uptake over the period examined (1980–2008). This finding, they write, “is consistent with related findings in recent years,” citing Cao *et al.* (2002), Cao *et al.* (2005), LeQuere *et al.* (2009), and Piao *et al.* (2009).

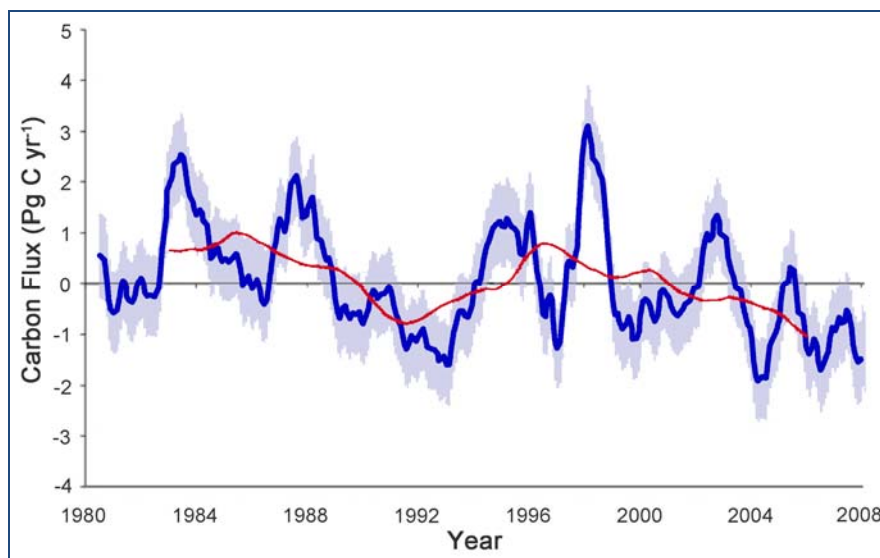


Figure 4.2.1.2. Global terrestrial biosphere net carbon exchange (positive from land to air, negative from air to land) during the years 1980–2008 (blue line), as calculated by Gurney and Eckles (2011). Also shown is the five-yr running mean (red line) and total 1σ flux uncertainty (light blue shading).

Other studies have produced additional evidence for a worldwide increase in vegetative productivity dating back to the inception of the Industrial Revolution. Joos and Bruno (1998), for example, used

ice core data and direct observations of atmospheric CO₂ and ¹³C to reconstruct the histories of terrestrial and oceanic uptake of anthropogenic carbon over the past two centuries. They discovered the biosphere typically acted as a source of CO₂ during the nineteenth century and the first decades of the twentieth century, but it subsequently “turned into a sink.” Lloyd (1999) calculated that from 1730 to the early 1980s the increase in temperate deciduous forest net primary productivity (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 Lloyd’s model, the NPP stimulation was 40%, more than the sum of the individual contributions of the extra CO₂ and nitrogen.

Tans (2009) employed measurements of atmospheric and oceanic carbon contents, along with reasonably constrained estimates of global anthropogenic CO₂ emissions, to calculate the residual fluxes of carbon (in the form of CO₂) from the terrestrial biosphere to the atmosphere (+) or from the atmosphere to the terrestrial biosphere (-), obtaining the results depicted in Figure 4.2.1.3.

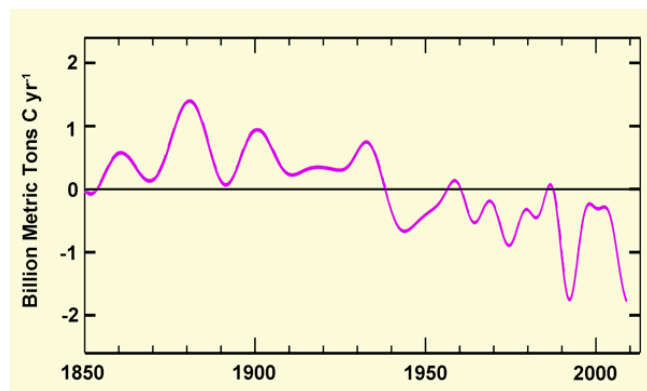


Figure 4.2.1.3. Five-year smoothed rates of carbon transfer from land to air (+) or from air to land (-) vs. time. Adapted from Tans (2009).

As the figure illustrates, Earth’s land surfaces were a net *source* of CO₂-carbon to the atmosphere until about 1940, primarily because of the felling of forests and the plowing of grasslands to make way for expanded agricultural activities. From 1940 onward, however, the terrestrial biosphere has become, in the mean, an increasingly greater *sink* for CO₂-carbon, and it has done so despite increasing temperatures, massive global deforestation, and rising atmospheric

CO₂, more than compensating for any negative effects these phenomena have on the global biosphere.

Such findings, which do “not depend on models” but “only on the observed atmospheric increase and estimates of fossil fuel emissions,” led Tans to conclude “suggestions that the carbon cycle is becoming less effective in removing CO₂ from the atmosphere (e.g., LeQuere *et al.*, 2007; Canadell *et al.*, 2007) can perhaps be true locally, but they do not apply globally, not over the 50-year atmospheric record, and not in recent years.” Tans continues, “to the contrary,” and “despite global fossil fuel emissions increasing from 6.57 GtC in 1999 to 8.23 in 2006, the five-year smoothed global atmospheric growth rate has not increased during that time, which requires more effective uptake [of CO₂] either by the ocean or by the terrestrial biosphere, or both, to satisfy atmospheric observations.” The results portrayed in Figure 4.2.1.3, adapted from Tans’ paper, clearly indicate this “more effective uptake” of CO₂-carbon has occurred primarily over land.

Many researchers also have examined trends in biospheric productivity using satellite data. Nemani *et al.* (2003), for example, discovered the terrestrial biosphere is growing ever more robust (see Figure 4.2.1.4). Globally, the group of eight scientists found terrestrial net primary production (NPP) increased by 6.17%, or 3.42 PgC, over the 18 years between 1982 and 1999. In addition, they observed net positive responses over all latitude bands studied: 4.2% (47.5–22.5°S), 7.4% (22.5°S–22.5°N), 3.7% (22.5–47.5°N), and 6.6% (47.5–90.0°N).

Nemani *et al.* mention a number of likely contributing factors to these significant NPP increases: nitrogen deposition and forest regrowth in northern mid and high latitudes; wetter rainfall regimes in water-limited regions of Australia, Africa, and the Indian subcontinent; increased solar radiation reception over radiation-limited parts of Western Europe and the equatorial tropics; warming in many parts of the world; and the aerial fertilization effect of rising atmospheric CO₂ concentrations.

Regarding the latter factor, Nemani *et al.* remark, “an increase in NPP of only 0.2% per 1-ppm increase in CO₂ could explain all of the estimated global NPP increase of 6.17% over 18 years and is within the range of experimental evidence.” However, they report NPP increased by more than 1% per year in Amazonia alone, noting “this result cannot be explained solely by CO₂ fertilization.”

Although Nemani *et al.*’s conclusion may be correct, the aerial fertilization effect of atmospheric CO₂ enrichment is most pronounced at higher tem-

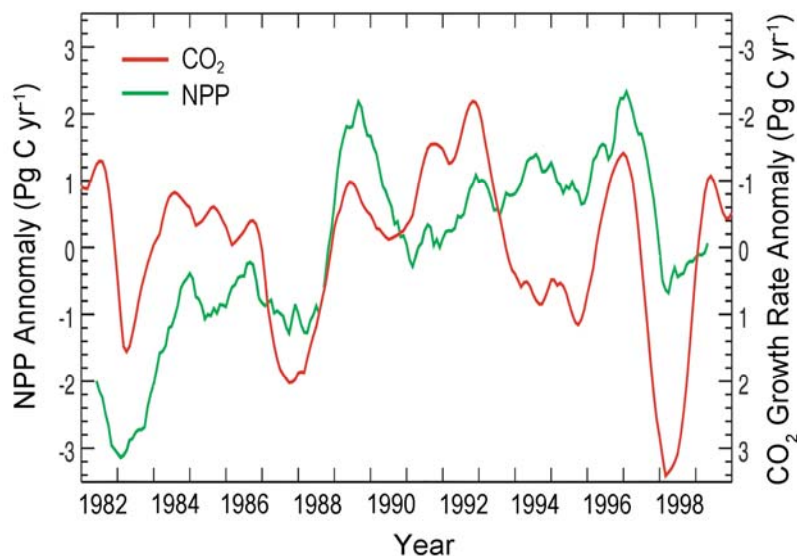


Figure 4.2.1.4. Interannual variations in global Net Primary Productivity (NPP) in relation to atmospheric CO₂ growth rate during the years 1982 to 1999. Adapted from Nemani *et al.* (2003).

peratures, rising from next to nothing at a mean temperature of 10°C to a 0.33% NPP increase per 1-ppm increase in CO₂ at a mean temperature of 36°C for a mixture of plants comprised predominantly of herbaceous species (Idso and Idso, 1994). For woody plants, this number could likely be two (Idso, 1999) or even three (Saxe *et al.*, 1998; Idso and Kimball, 2001; Leavitt *et al.*, 2003) times larger, yielding a 0.7% to 1% NPP increase per 1-ppm increase in CO₂, which would indeed represent the lion's share of the growth stimulation Nemani *et al.* observed in tropical Amazonia.

Chen *et al.* (2004) utilized the monthly satellite-derived normalized difference vegetation index (NDVI) dataset of 1987–1997 obtained from the advanced very high resolution radiometer (AVHRR) to calculate an 11-year history of global (75°N to 55°S) terrestrial NPP, deriving three results based on the three “NPP coefficient sets” of Whittaker and Likens (1975), Atjay *et al.* (1979), and Olson *et al.* (1983). Calculating from the beginning and end points of the graphical presentations of Chen *et al.*'s results, global terrestrial NPP increased by approximately 6.6% between 1987 and 1997 when the Atjay *et al.* coefficients were used, 9.9% when the Olson *et al.* coefficients were used, and 13.8% when the Whittaker and Likens coefficients were used, for a mean NPP increase of about 10% over the 11-year period.

Cao *et al.* (2004) derived net primary production

(NPP) values at 8-km and 10-day resolutions for the years 1981–2000 using variables based almost entirely on satellite observations, as described in the Global Production Efficiency Model (GLO-PEM). The model consists, they write, “of linked components that describe the processes of canopy radiation absorption, utilization, autotrophic respiration, and the regulation of these processes by environmental factors (Prince and Goward, 1995; Goetz *et al.*, 2000).” Over the last two decades of the twentieth century, “there was an increasing trend toward enhanced terrestrial NPP,” which they say was “caused mainly by increases in atmospheric carbon dioxide and precipitation.

Cao *et al.* (2005) used the CEVSA (Carbon Exchanges in the Vegetation-Soil-Atmosphere system) model (Cao and Woodward, 1998; Cao *et al.*, 2002), forced by observed variations in climate

and atmospheric CO₂, to quantify changes in NPP, soil heterotrophic respiration (HR), and net ecosystem production (NEP) from 1981 to 1998. As an independent check on the NPP estimate of CEVSA, they also estimated 10-day NPP for 1981–2000 with the GLO-PEM model that uses data almost entirely from remote sensing, including both the normalized difference vegetation index and meteorological variables (Prince and Goward, 1995; Cao *et al.*, 2004).

Cao *et al.* found “global terrestrial temperature increased by 0.21°C from the 1980s to the 1990s, and this alone increased HR more than NPP and hence reduced global annual NEP.” They write, “combined changes in temperature and precipitation increased global NEP significantly,” and “increases in atmospheric CO₂ produced further increases in NPP and NEP.” They also note “the CO₂ fertilization effect [was] particularly strong in the tropics, compensating for the negative effect of warming on NPP.”

They write, “the response of photosynthetic biochemical reactions to increases in atmospheric CO₂ is greater in warmer conditions, so the CO₂ fertilization effect will increase with warming in cool regions and be high in warm environments.” They found global NEP increased “from 0.25 Pg C yr⁻¹ in the 1980s to 1.36 Pg C yr⁻¹ in the 1990s.”

Commenting on their findings, Cao *et al.* note “the NEP that was induced by CO₂ fertilization and

climatic variation accounted for 30% of the total terrestrial carbon sink implied by the atmospheric carbon budget (Schimel *et al.*, 2001), and the fraction changed from 13% in the 1980s to 49% in the 1990s,” which indicates the growing importance of the CO₂ fertilization effect. Moreover, “the increase in the terrestrial carbon sink from the 1980s to the 1990s was a continuation of the trend since the middle of the twentieth century, rather than merely a consequence of short-term climate variability,” suggesting as long as the atmosphere’s CO₂ content continues to rise, so too will its stimulation of the terrestrial biosphere likely increase.

Using a newly developed satellite-based vegetation index (Version 3 Pathfinder NDVI) in conjunction with a gridded global climate dataset (global monthly mean temperature and precipitation at 0.5° resolution from New *et al.*, 2000), Xiao and Moody (2005) analyzed trends in global vegetative activity from 1982 to 1998. The greening trends exhibited substantial latitudinal and longitudinal variability, with the most intense greening of the globe located in high northern latitudes, portions of the tropics, southeastern North America, and eastern China. Temperature correlated strongly with greening trends in Europe, eastern Eurasia, and tropical Africa. Precipitation, in contrast, was not a significant driver of increases in greenness, except for isolated and spatially fragmented regions. Some decreases in greenness also were observed, mainly in the Southern Hemisphere in southern Africa, southern South America, and central Australia, and these trends were associated with concomitant increases in temperature and decreases in precipitation. Large regions of the globe showed no trend in greenness over the 17-year period, and large areas underwent strong greening that showed no association with trends of either temperature or precipitation. These greening trends, the scientists conclude, must have resulted from other factors, such as “CO₂ fertilization, reforestation, forest regrowth, woody plant proliferation and trends in agricultural practices.”

Young and Harris (2005) investigated, for the majority of Earth’s land surface, a near 20-year time series (1982–1999) of NDVI data, based on measurements obtained from the advanced very high resolution radiometer (AVHRR) carried aboard U.S. National Oceanic and Atmospheric Administration satellites. They employed two datasets derived from the sensor: the Pathfinder AVHRR Land (PAL) dataset and the Global Inventory Modeling and Mapping Studies (GIMMS) dataset.

Based on their analysis of the PAL data, the two

researchers report “globally more than 30% of land pixels increased in annual average NDVI greater than 4% and more than 16% persistently increased greater than 4%,” while “during the same period less than 2% of land pixels declined in NDVI and less than 1% persistently declined.” Regarding the GIMMS dataset, they report “even more areas were found to be persistently increasing (greater than 20%) and persistently decreasing (more than 3%).” All told, they report “between 1982 and 1999 the general trend of vegetation change throughout the world has been one of increasing photosynthesis.”

As for what has been responsible for the worldwide increase in photosynthesis, the researchers mention global warming and “associated precipitation change and increases in atmospheric carbon dioxide,” citing Myneni *et al.* (1997) and Ichii *et al.* (2002). In addition, they write, “many of the areas of decreasing NDVI are the result of human activity,” primarily deforestation (Skole and Tucker, 1993; Steininger *et al.*, 2001) and urbanization Seto *et al.* (2000).

Piao *et al.* (2006a) note “enhanced terrestrial vegetation growth in the middle and high latitudes of the Northern Hemisphere over the past two decades has been well documented (Zhou *et al.*, 2001; Nemani *et al.*, 2003),” but “the mechanisms for this phenomenon are still under debate.” Using a leaf area index dataset for the years 1981–2000, created from satellite-derived observations of the normalized difference vegetation index parameter for land areas above 25°N latitude, the authors investigated “spatial patterns of mechanisms controlling current enhanced vegetation growth in the Northern Hemisphere,” focusing on “how recent changes in precipitation, temperature [and] atmospheric CO₂ concentration have influenced vegetation growth.”

Over the final two decades of the twentieth century, the researchers found, the mean rate of increase in growing-season leaf area index was 0.0041/year. They report 13% of that increase was provided by increases in precipitation, 31% by increases in temperature, and 49% by the increase in the atmosphere’s CO₂ concentration.

Liu *et al.* (2010) looked for, and computed changes in, leaf area index (LAI) data derived from satellite observations for six latitude bands (50–90°N, 30–50°N, 10–30°N, 10°N–10°S, 10–30°S, and 30–63°S) that included all of Earth’s continents but Antarctica. They report LAI “prominently increased” during the period July 1981 through December 2006 throughout Europe, Siberia, the Indian Peninsula, America and south Canada, the south region of the Sahara, the southwest corner of Australia, and the

Earth's Vegetative Future

Kgalagadi Basin, while it declined in southeast Asia, southeastern China, central Africa, central and southern South America, and arctic areas in North America. Despite the latter negative results, they found all six of the latitudinal bands they analyzed showed positive trends. Consequently, for the globe as a whole (the conglomerate of the six latitude bands they analyzed), they note, “LAI has increased at a rate of 0.0013 per year during July 1981–December 2006,” while for the middle and high northern latitudes (north of 30°N), the linear LAI trend was 0.0032 per year.

Some researchers have expressed doubts the positive trends in global biospheric productivity are real or sustainable in a CO₂-induced globally warmed world of the future. Gloor *et al.* (2010) note the ratio of CO₂ accumulating in the atmosphere to the CO₂ flux into the atmosphere due to human activities—known as the airborne fraction (AF)—is central to predicting changes in Earth’s surface temperature due to greenhouse gas-induced warming. This ratio has remained remarkably constant over the past five decades. However, they report Canadell *et al.* (2007) and Raupach *et al.* (2008) claim to have detected a long-term increasing trend in the airborne fraction, which they interpret as being indicative of “a decreasing trend in the efficiency of the ocean and land carbon sinks.”

Gloor *et al.* report Knorr (2009) has challenged Canadell *et al.* and Raupach *et al.* regarding their detection of a positive AF trend, “arguing that given the noise in the data, the trend is not detectable.” They then challenge the second claim of Canadell *et al.* and Raupach *et al.*—their contention a positive AF trend indicates a decreasing planetary carbon sink efficiency—by investigating “the question of what controls trends and decadal scale variations in CO₂ airborne fraction using simple linear models describing the evolution of an atmospheric perturbation in CO₂.”

The three researchers first determined there is no one-to-one association between positive trends in CO₂ flux (due to fossil fuel emissions and changes in land use) to the atmosphere and negative trends in Earth’s carbon sink efficiency. Second, they report in order to detect trends in sink efficiencies from the time of fossil fuel-derived CO₂ emissions and temporal changes in land use, “it is necessary to disentangle the spin-up time and fossil fuel growth rate variation signatures in the airborne fraction from signatures due to other causes.” They make the pertinent

calculations for fossil-fuel and land-use changes and state they “do indeed find a positive trend in the residuals,” but they argue this trend “is not statistically significant after correcting for known events such as the temporal distribution of the extrinsic forcings and likely omissions in the emissions (particularly from land-use change).” They note their analysis suggests “trends in airborne fraction are not a very good diagnostic to detect changes in carbon sink efficiency because variations in the signal are complex and the signal-to-noise ratio is small.”

In describing another doubt about the recent greening of the Earth, Zhao and Running (2010) state “previous studies have shown that climate constraints were relaxing with increasing temperature and solar radiation, allowing an upward trend in NPP [net primary production] from 1982–1999,” but over the past decade (2000–2009), satellite data “suggest a reduction in the global NPP.” This finding caused some alarm in the scientific community. Zhao and Running demonstrate there is likely no cause for concern.

The graphical representation of this trend (Figure 4.2.1.5) illustrates that apart from the starting point of the initial year (2000) of their study, there is only one other year (2004) in which the global NPP was greater than it was at the end of the study (2009). Since global NPP was on the rise in 1982–1999, the more recent data would more accurately be described as a leveling off of that prior upward trend. Zhao and Running report the leveling off of global NPP over the past decade was induced by drought, and climate models have long predicted more frequent and more intense droughts would accompany global warming.

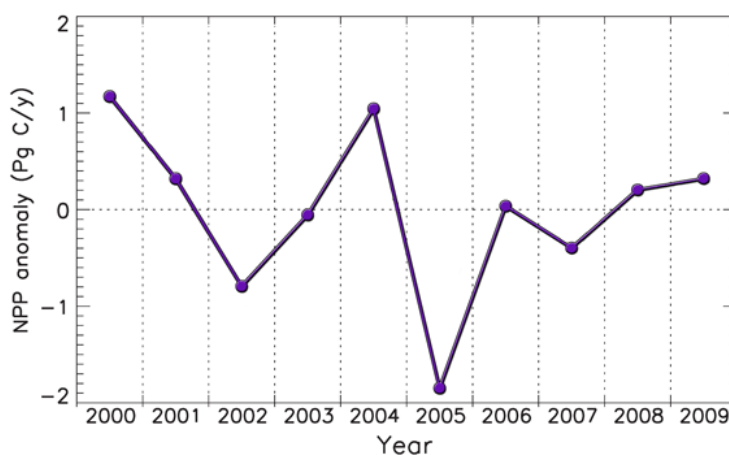


Figure 4.2.1.5. Interannual variations from the mean of global NPP over the past ten years. Adapted from Zhao and Running (2010).

The two researchers write, “NPP in the tropics explains 93% of variations in the global NPP,” and “tropical rainforests explain 61% of global NPP variations.” These findings are especially important because of the work of Coelho and Goddard (2009), who studied El Niño-induced tropical droughts as portrayed in climate models.

Coelho and Goddard write, “the majority of drought-related hazards and the attendant economic losses and mortality risks reside in the tropics,” citing Dilley *et al.* (2005); They further note “changes in climate variability, including more frequent and damaging extreme events such as drought, is one of many anticipated impacts of climate change.” More specifically (and germane to the subject at hand), they write, “El Niño brings widespread drought (i.e., precipitation deficit) to the tropics,” and “stronger or more frequent El Niño events in the future” would “exacerbate drought risk in highly vulnerable tropical areas.”

The two researchers evaluated “the patterns, magnitude, and spatial extent of El Niño-induced tropical droughts during a control period in the twentieth century in climate simulations, which have realistic evolution of greenhouse gases,” after which they examined “the projected changes in the characteristics of El Niño and in the strength of the identified patterns of El Niño-induced tropical drought in the twenty-first century.” That information allowed them to examine patterns of mean precipitation changes in order to “assess whether those changes exacerbate or ameliorate the risk of El Niño-induced drought conditions in the twenty-first century.”

In the first instance, Coelho and Goddard say the models they studied “exhibit realistic patterns, magnitude, and spatial extent of El Niño-induced drought patterns in the twentieth century,” and “the teleconnections are not projected to change in the twenty-first century.” They add, “a possible slight reduction in the spatial extent of droughts is indicated over the tropics as a whole.” They also report “all model groups investigated show similar changes in mean precipitation for the end of the twenty-first century, with increased precipitation projected between 10°S and 10°N.”

De Jong *et al.* (2012) employed “detection of trend changes in normalized difference vegetation index (NDVI) satellite data between 1982 and 2008,”

based on “time series of 648 fortnightly images [that] were analyzed using a trend breaks analysis procedure,” for 14 classes of land cover (biomes). The four researchers found short-term greening and browning trends in portions of the studied period for almost 15% of Earth’s land surface, but for the entire time period, “net greening was detected in all biomes,” and “the net global figure—considered over the full length of the time series—showed greening since the 1980s.”

Ballantyne *et al.* (2012) used “global-scale atmospheric CO₂ measurements, CO₂ emission inventories and their full range of uncertainties to calculate changes in global CO₂ sources and sinks during the past fifty years.” The five U.S. scientists say 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” (see Figure 4.2.1.6).

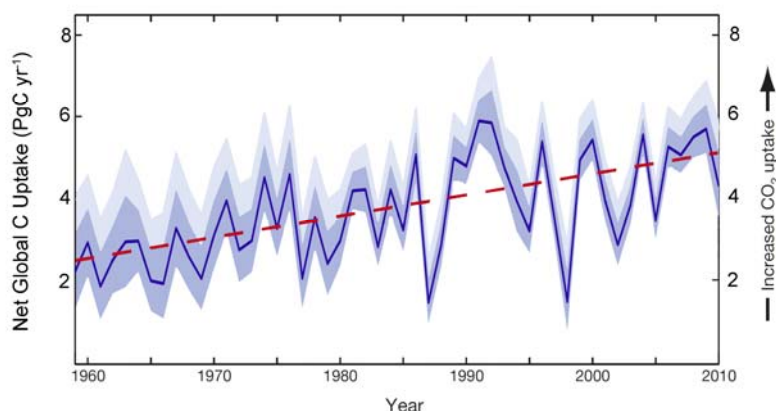


Figure 4.2.1.6. Annual global net carbon (C) uptake by Earth’s lands and oceans (solid blue line) for 1959–2010, adapted from Ballantyne *et al.* (2012). The linear trend (dashed red line) and 1 σ (dark shaded bands) and 2 σ (light shaded bands) uncertainties are also shown.

They 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. This most recent effort refutes the hypothesis of Canadell *et al.* (2007) and Raupach *et al.* (2008), who claimed to have detected a decreasing trend in

Earth's Vegetative Future

the efficiency of the planet's carbon sinks, and it vindicates the many studies described above revealing an increasing greening of planet Earth.

The above-described research demonstrates the terrestrial biomass of the globe has been rising, and it appears to be doing so at a remarkable rate. It is also clear recent increases in atmospheric CO₂ and temperature have positively affected those trends, likely responsible for the lion's share of the observed increase. This remarkable increase in biospheric productivity and observed greening of the Earth has occurred in spite of several real assaults on the globe's vegetation, such as deforestation and other land-use changes.

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Climate Change Reconsidered II: Biological Impacts

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Earth's Vegetative Future

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Earth's Vegetative Future

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4.2.2 Continental Terrestrial

The following subsections analyze terrestrial productivity trends on continental and subcontinental scales, detailing what researchers have reported for Africa, Asia, Australia, Europe, North America, and South America.

4.2.2.1 Africa

- The ongoing 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.

According to a 2002 *New Scientist* article by Fred Pearce, “Africa’s deserts are in ‘spectacular’ retreat,”

as vegetation is reclaiming great tracts of barren land across the entire southern edge of the Sahara. He notes, “the southern Saharan desert is in retreat, making farming viable again in what were some of the most arid parts of Africa.” He writes, “Burkina Faso, one of the West African countries devastated by drought and advancing deserts 20 years ago, is growing so much greener that families who fled to wetter coastal regions are starting to go home.”

“Vegetation,” Pearce writes, “is ousting sand across a swathe of land stretching from Mauritania on the shores of the Atlantic to Eritrea 6000 kilometers away on the Red Sea coast.” In addition to being widespread geographically, the greening was widespread in time, occurring since at least the mid-1980s.

Quoting Chris Reij of the Free University of Amsterdam, Pearce writes, “aerial photographs taken in June show ‘quite spectacular regeneration of vegetation’ in northern Burkina Faso.” The data indicate the presence of more trees for firewood and more grassland for livestock. In addition, a survey Reij was collating showed, according to Pearce, “a 70 percent increase in yields of local cereals such as sorghum and millet in one province in recent years.”

Kjeld Rasmussen of the University of Copenhagen studied the same area, reporting that since the 1980s there has been a “steady reduction in bare ground” with “vegetation cover, including bushes and trees, on the increase on the dunes.”

Pearce also reports on the work of a team of geographers from Britain, Sweden, and Denmark who spent much of the summer of 2001 analyzing archived satellite images of the Sahel. Citing Andrew Warren of University College London as a source of information on this study, he says the results show “that ‘vegetation seems to have increased significantly’ in the past 15 years, with major regrowth in southern Mauritania, northern Burkina Faso, north-western Niger, central Chad, much of Sudan and parts of Eritrea.”

In a study of a series of satellite images of the Central and Western Sahel taken from 1980 to 1995, Nicholson *et al.* (1998) found no evidence of any overall expansion of deserts and no drop in the rainfall use efficiency of native vegetation. Prince *et al.* (1998) further observed, in a satellite study of the Sahel from 1982 to 1990, a steady rise in rainfall use efficiency, suggesting plant productivity and coverage of the desert increased during this period.

Eklundh and Olsson (2003) provide further evidence. They analyzed normalized difference vegetation index (NDVI) data obtained from the U.S. National Oceanic and Atmospheric Administration’s

satellite-borne advanced very high resolution radiometer (AVHRR) whenever it passed over the African Sahel for the years 1982–2000. They write, “strong positive change in NDVI occurred in about 22% of the area, and weak positive change in 60% of the area,” and “weak negative change occurred in 17% of the area, and strong negative change in 0.6% of the area.” In addition, “integrated NDVI has increased by about 80% in the areas with strong positive change,” whereas in areas with weak negative change, “integrated NDVI has decreased on average by 13%.” The primary story these data tell, therefore, is of strong positive trends in NDVI for large areas of the African Sahel over the last two decades of the twentieth century, and Eklundh and Olsson conclude the “increased vegetation, as suggested by the observed NDVI trend, could be part of the proposed tropical sink of carbon.”

Many more scientists subsequently confirmed the recent stunning increase in African vegetation. In 2005, Africa was featured in a special issue of the *Journal of Arid Environments*, “The ‘Greening’ of the Sahel.” In that issue, Anyamba and Tucker (2005) describe their development of an NDVI history of the region for the years 1981–2003. Comparing this history with the precipitation history of the Sahel developed by Nicholson (2005), they report, “the persistence and spatial coherence of drought conditions during the 1980s is well represented by the NDVI anomaly patterns and corresponds with the documented rainfall anomalies across the region during this time period.” In addition, “the prevalence of greener than normal conditions during the 1990s to 2003 follows a similar increase in rainfall over the region during the last decade.”

In another analysis of NDVI and rainfall data in the same issue of the *Journal of Arid Environments*, Olsson *et al.* (2005) report finding “a consistent trend of increasing vegetation greenness in much of the region,” which they describe as “remarkable.” They say increasing rainfall “is certainly one reason” for the greening phenomenon but “does not fully explain” the increase in greenness.

The three Swedish scientists note, “only eight out of 40 rainfall observations showed a statistically significant increase between 1982–1990 and 1991–1999.” In addition, “further analysis of this relationship does not indicate an overall relationship between rainfall increase and vegetation trend.” Olsson *et al.* suggest “another potential explanation could be improved land management, which has been shown to cause similar changes in vegetation response elsewhere (Runnstrom, 2003).” However, in more

detailed analyses of Burkina Faso and Mali, where production of millet rose by 55% and 35%, respectively, since 1980, they could find “no clear relationship” between agricultural productivity and NDVI, which argues against the land management explanation.

Olsson *et al.* then suggest the greening of the Sahel could be caused by increasing rural-to-urban migration. In this scenario, widespread increases in vegetation occur as a result of “reduced area under cultivation,” due to a shortage of rural laborers, and/or “increasing inputs on cropland,” such as seeds, machinery, and fertilizers made possible by an increase in money sent home to rural households by family members working in cities. Olsson *et al.* note, “more empirical research is needed to verify this [hypothesis].”

Ichii *et al.* (2005) “simulated and analyzed 1982–1999 Amazonian, African, and Asian carbon fluxes using the Biome-BGC prognostic carbon cycle model driven by National Centers for Environmental Prediction reanalysis daily climate data,” after which they “calculated trends in gross primary productivity (GPP) and net primary productivity (NPP).” They found solar radiation variability to be the primary factor responsible for interannual variations in GPP, followed by temperature and precipitation variability. As to GPP trends, the authors report, “recent changes in atmospheric CO₂ and climate promoted terrestrial GPP increases with a significant linear trend in all three tropical regions.” In the African region, the rate of GPP increase was about 0.3 PgC year⁻¹ per decade. In identifying the major cause of the increased growth, Ichii *et al.* favored carbon dioxide, reporting “CO₂ fertilization effects strongly increased recent NPP trends in regional totals.”

Herrmann *et al.* (2005) investigated the “temporal and spatial patterns of vegetation greenness and rainfall variability in the African Sahel and their interrelationships based on analyses of Normalized Difference Vegetation Index (NDVI) time series for the years 1982–2003 and gridded satellite rainfall estimates.” The three researchers determined “the overall trend in monthly maximum NDVI [was] positive over a large portion of the Sahel region, reaching up to 50% increase in the average NDVI in parts of Mali, Mauritania and Chad” (see Figure 4.2.2.1.1). In addition, they report, “rainfall emerges as the dominant causative factor in the dynamics of vegetation greenness in the Sahel at an 8 km spatial resolution,” but “the presence of spatially coherent and significant long-term trends in the residuals suggests that there might be another, weaker,

Climate Change Reconsidered II: Biological Impacts

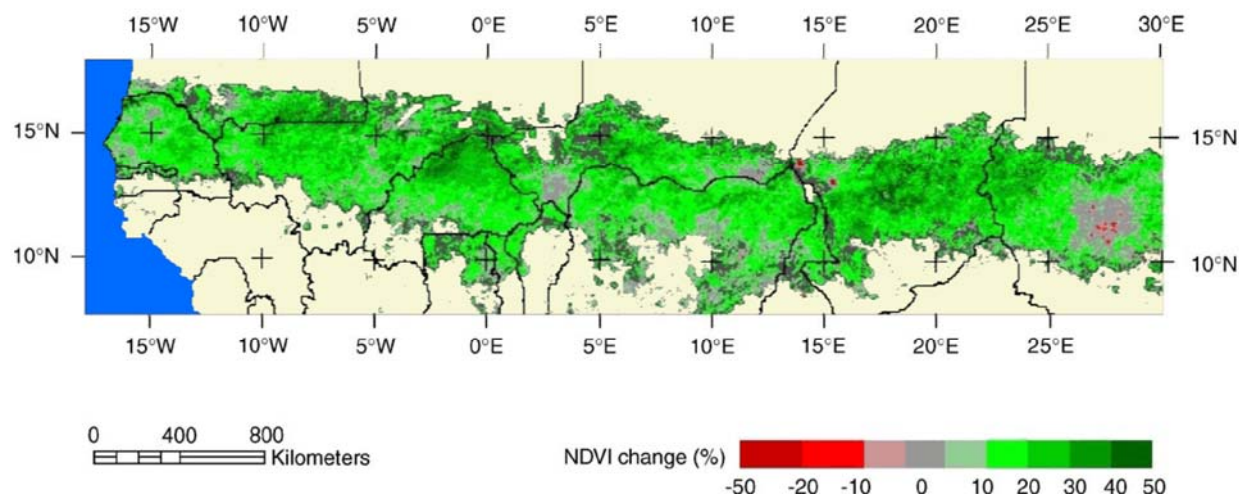


Figure 4.2.2.1.1. Percent change in vegetation greenness throughout the African Sahel during the years 1982–2003 based on monthly AVHRR NDVI time series data. Percentages indicate changes in average NDVI between 1982 and 2003. Adapted from Herrmann *et al.* (2005).

causative factor,” as the “recovery of vegetation greenness [was] beyond what would be expected from the recovery of rainfall conditions alone.”

Herrmann *et al.* state their study “confirms previous regional-scale findings for the years 1982–1999 by Eklundh and Olsson (2003) and Olsson *et al.* (2005), who observed widespread positive trends of both time-integrated NDVI and NDVI amplitudes, and Anyamba and Tucker (2005), who [observed] increases in growing season NDVI across most parts of the region.” They conclude, “a greening of the Sahel expressed in positive trends in NDVI indicates a net increase in biomass production during the period 1982–2003, which challenges the notion of irreversible desertification in the Sahel.”

Midgley and Seydack (2006) note “present and predicted future impacts of global environmental change on intact forests are both alarming and contentious,” and “some local models have predicted the demise of South Africa’s only significant extent of indigenous forest, the Knysna forest, by 2050,” as reported by Midgley *et al.* (2001). To see how bad things had become by the end of the twentieth century, the authors measured and analyzed the growth of all trees greater than 10 cm in diameter at breast height in 108 0.04-ha plots distributed throughout an unharvested nature reserve in the Knysna forest for the years 1991–2001.

Following a protocol that provided what they say is “probably an under-estimate,” the two researchers state, “net basal area and aboveground biomass increased over the 10-year study period by 2% and

there was a 1.2% increase in stem numbers, distributed almost equally amongst all size-classes.” Because of the nature of the Knysna forest, Midgley and Seydack say “over relatively short periods such as our decade, the aboveground biomass of this forest is more sensitive to negative/stressful conditions that would increase mortality, than to factors which may increase growth.” Nevertheless, they found “biomass increased.” And because “precipitation over the period 1991–2001 was some 5% less than the long-term average,” they conclude the observed increase in growth rate “may have been the effect of the increase in global atmospheric carbon dioxide.”

Seaquist *et al.* (2006) provided important new details about the “greening up” of the African Sahel. Using a satellite data-driven light-use efficiency model to assess changes in absolute amounts of net primary production (NPP), expressed as carbon content, and its interannual variability in the African Sahel for the years 1982–1999, Seaquist *et al.* report they found an extensive, albeit discontinuous, east-west band of NPP increase ($>10 \text{ g C m}^{-2} \text{ year}^{-1}$). The band extends up to about 17°N and includes several hotspots ($>20 \text{ g C m}^{-2} \text{ year}^{-1}$) in central Senegal, south-western Mali, southern Chad, southern Sudan, and the Ivory Coast and southern Benin. For the Sahel in its entirety, the researchers calculate the mean rate of change per pixel was $8.4 \text{ g C m}^{-2} \text{ year}^{-1}$, yielding a total mean rate of change of $51.0 \text{ Mt C year}^{-1}$ and an absolute net gain in NPP over the 18-year period of 918.0 Mt C . In addition, they report, “this increase is associated with a decrease in the inter-annual

variability of NPP for the 1990s compared to the 1980s,” such that “overall, the increase in NPP through time appears to be associated with an increase in the stability of this ecosystem,” with the changes in carbon capture and increase in stability being driven primarily by rainfall “followed by atmospheric CO₂.”

Lewis *et al.* (2009a) 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 on more than 70,000 individual trees in 10 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,” which equates to “a carbon sink of 1.3 Pg C year⁻¹ across all tropical forests during recent decades.” That can account for roughly half of the so-called 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.”

Ciais *et al.* (2009) modeled the terrestrial carbon balance of Africa over the past century (1901–2002) using a spatially resolved process-based vegetation model (ORCHIDEE), which is forced by changing climate, human-induced changes in land use, and a parameterization of natural fires. They found the African net terrestrial carbon (C) balance increased “from a net CO₂ source to the atmosphere of 0.14 Pg C per year in the 1980s to a net sink of 0.15 Pg C per year in the 1990s.” In addition, the land use flux due to deforestation was “a source of 0.13 Pg C per year,” and “this implies that climatic trends (mainly increasing precipitation) and CO₂ increase (the fertilization effect), are causing a sink of 0.28 Pg C per year which

offsets the land-use source.”

The five researchers write, “the trend of gross primary production is closely matching the trend in satellite observed NDVI.” They state their simulated trend in gross primary production “is also consistent with an increased vegetation activity over [the] Sahel reported by Eklundh and Olsson (2003) and Olsson *et al.* (2005).” At the continental scale, they say the gross primary production trend can be largely (70%) explained by the CO₂ fertilization effect.

Doherty *et al.* (2010) modeled future changes in land biogeochemistry and biogeography in the region bounded by 12.5°N, 12.5°S, 25°E, and 42.5°E, representing most of East Africa (Kenya, Tanzania, Uganda, Rwanda, Burundi, Ethiopia, and Somalia) and portions of Central Africa (the Democratic Republic of Congo and Southern Sudan). They used 18 future climate projections derived from nine general circulation models that figured prominently in IPCC’s *Fourth Assessment Report*, employing the projections as input to the Lund-Potsdam-Jena dynamic global vegetation model that simulates changes in vegetation and ecosystem carbon cycling under future climate conditions, based on what they describe as “a coupled photosynthesis-hydrological scheme [that] computes gross primary productivity, plant respiration, and evapotranspiration on a daily time step based on the current climate, atmospheric CO₂ concentration, vegetation structure and phenological state, and soil water content.”

Doherty *et al.* report “all simulations showed future increases in tropical woody vegetation over the region at the expense of grasslands,” noting “regional increases in net primary productivity (18–36%) and total carbon storage (3–13%) by 2080–2099 compared with the present-day were common to all simulations,” and “seven out of nine simulations continued to show an annual net land carbon sink in the final decades of the 21st century because vegetation biomass continued to increase.” They write, “overall, our model results suggest that East Africa, a populous and economically poor region, is likely to experience some ecosystem service benefits through increased precipitation, river runoff and fresh water availability,” and “resulting enhancements in net primary productivity may lead to improved crop yields in some areas.” They note their results “stand in partial contradiction of other studies that suggest possible negative consequences for agriculture, biodiversity and other ecosystem services caused by temperature increases.”

Scheiter and Higgins (2009) write, “recent IPCC projections suggest that Africa will be subject to

particularly severe changes in atmospheric conditions” in the future, and these changes could have equally severe repercussions for its flora and fauna. How the continent’s “grassland-savanna-forest complex will respond to these changes has rarely been investigated,” they note, and “most studies on global carbon cycles use vegetation models that do not adequately account for the complexity of the interactions that shape the distribution of tropical grasslands, savannas and forests.”

The two scientists developed a new vegetation model—the adaptive dynamic global vegetation model (aDGVM)—that employs established sub-models for photosynthesis, respiration, canopy scaling, competition for water, competition for light, reproduction, and mortality. Their model also contains novel elements: dynamic carbon allocation and phenology functions, as well as a fire model that estimates fire intensity as a function of fuel biomass, fuel moisture, and wind speed, and which simulates topkill (stem mortality) as a function of individual tree size and fire intensity. All of these phenomena are related to the individual plant’s physiological state and the environmental conditions surrounding it.

Simulations to the year 2100 with this model suggest “grasslands will spread into the Sahara and into the horn of Africa, such that the total area covered by deserts or bare soil decreases by 5.7%.” In addition, “it is predicted that 34.6% of today’s grasslands are transformed into savannas,” and “45.3% of today’s savannas are transformed into deciduous woodlands.” As a result, “the total biomass stored in each of the biomes increases, with high relative changes in grasslands and savannas (by 256% and 241%, respectively),” with a 102% increase in tree biomass.

Heubes *et al.* (2011) modeled the future spatial distribution of desert, grassland, savanna, and deciduous and evergreen forests in West Africa using six bioclimatic models. None of the models accounted for the photosynthetic-enhancing and transpiration-reducing effects of projected increases in atmospheric CO₂ concentration, as they were based solely on the climatic projections of 17 general circulation models of the atmosphere for emissions scenario A2a, as described in the *Fourth Assessment Report* of IPCC (2007). These projections were downscaled to 0.1 degree of latitude and longitude as described by Ramirez and Jarvis (2008).

Heubes *et al.* report finding “a climate-driven greening trend,” with “northward spread of grassland into the Sahara and the replacement of savannas by deciduous forest.” These results, they write, “are

concordant with results from Cramer *et al.* (2001), Scholze *et al.* (2006) and Scheiter and Higgins (2009),” although they add the latter investigators “attributed the greening to increased CO₂ levels.” They say the models they used “indicate climatic change alone can yield this pattern,” where “the expected ‘greening’ of the Sahara is primarily driven by increasing precipitation,” as they note Hickler *et al.* (2005) also suggested.

Using satellite images that reflect the region’s current vegetation state, Heubes *et al.* additionally modeled “real” as opposed to “potential” vegetation, which enabled them to “clearly show,” as they describe it, “effects of human activity negatively affecting tree cover, as also demonstrated by other case studies, e.g. in Senegal (Vincke *et al.*, 2010) and Mali (Ruelland *et al.*, 2010).” They report, in West Africa, “agricultural expansion, sometimes facilitated by other human activities such as wood extraction, has been identified as major drivers of forest loss and degradation,” citing Norris *et al.* (2010).

“Considering climate change alone,” Heubes *et al.* write, “the model results of potential vegetation (biomes) show a ‘greening’ trend by 2050,” although “the modeled effects of human impact suggest future forest degradation.”

The research presented here indicates the ongoing 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.

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4.2.2.2 Asia

- 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.

Many scientists have examined terrestrial productivity trends in Asia, with a vast majority of those studies focusing on locations in China. The material below is arranged into two sub-headings: *China* and *All Other Asian Countries*. In addition, given the sheer number of studies conducted in China, that subsection is further divided into five sub-regions: *Country-wide*, *Deserts*, *Forests*, *Grasslands*, and the *Tibetan Plateau*.

4.2.2.2.1 China

4.2.2.2.1.1 Country-wide

Liu *et al.* (2004) derived detailed estimates of the economic impact of predicted climate change on agriculture in China. They used county-level agricultural, climate, social, economic, and edaphic data for 1,275 agriculture-dominated counties for the years 1985–1991, together with the outputs of three general circulation models of the atmosphere based on five scenarios of anthropogenic CO₂-induced climate change that yielded a mean countrywide temperature increase of 3.0°C and a mean precipitation increase of 3.9% for the 50-year period ending in AD 2050. They determined “all of China would benefit from climate change in most scenarios.” They also note, “the effects of CO₂ fertilization should be included, for some studies indicate that this may produce a significant increase in yield.”

Fang *et al.* (2003) also looked at the whole of China, finding its terrestrial NPP increased by 18.7%

between 1982 and 1999. Referring to this result as “an unexpected aspect of biosphere dynamics,” they say this increase “is much greater than would be expected to result from the fertilization effect of elevated CO₂, and also greater than expected from climate, based on broad geographic patterns.” They may be wrong in that assessment. From 1982 to 1999 the atmosphere's CO₂ concentration rose by approximately 27.4 ppm, which could be expected to have increased the NPP of the forest types found in China by about 7.3% (see <http://www.co2science.org/articles/V5/N38/EDIT.php> for an explanation of this calculation).

And this increase is only part of the total NPP increase one could expect, for Fang *et al.* note “much of the trend in NPP appeared to reflect a change towards an earlier growing season,” which was driven by the 1.1°C increase in temperature they found in their region of study between 1982 and 1999. White *et al.* (1999) analyzed 88 years of data (1900–1987) from 12 locations in the eastern U.S. deciduous forest that stretches from Charleston, South Carolina to Burlington, Vermont, finding a 1°C increase in mean annual air temperature increases the length of the forest's growing season by approximately five days. They further report a one-day extension in growing season increased the mean forest NPP of the 12 sites they studied by an average of 1.6%.

Applying White *et al.*'s results to Fang *et al.*'s findings suggests there could easily be an additional increase in the NPP of China's forests due to the warming-induced growing season expansion experienced there from 1982 to 1999: 1.6%/day x 5 days = 8.0%, bringing the total CO₂-induced plus warming-induced increase in NPP for China to 15.3%.

Moreover, as noted previously in this chapter, there is a well-documented positive synergy between increasing air temperature and CO₂ concentration (Idso and Idso, 1994), so the 1°C increase in temperature experienced in China between 1982 and 1999 could easily boost the initial CO₂-induced 7.3% NPP enhancement to 10.7%. That, when combined with the 8.0% enhancement caused by the warming-induced increase in growing season length, would produce the 18.7% increase in NPP Fang *et al.* detected in the satellite data.

Piao *et al.* (2005a) found “terrestrial NPP in China increased at a rate of 0.015 Pg C yr⁻¹ over the period 1982–1999, corresponding to a total increase of 18.5%, or 1.03% annually.” They also report, “during the past 2 decades the amplitude of the seasonal curve of NPP has increased and the annual

Earth's Vegetative Future

peak NPP has advanced,” which “may indirectly explain the enhanced amplitude and advanced timing of the seasonal cycle of atmospheric CO₂ concentration (Keeling *et al.*, 1996).” They further suggest the enhanced amplitude of the seasonal CO₂ cycle “was probably due to the rise in atmospheric CO₂ concentration, elevated temperature, and increased atmospheric N and P deposition,” and they attribute the advanced timing of the seasonal cycle to “advanced spring onset and extended autumn growth owing to climate warming.”

Citing 20 scientific papers, Piao *et al.* conclude “results from observed atmospheric CO₂ and O₂ concentrations, inventory data, remote sensing data, and carbon process models have all suggested that terrestrial vegetation NPP of the Northern Hemisphere has increased over the past 2 decades and, as a result, the northern terrestrial ecosystems have become important sinks for atmospheric CO₂.”

Zhu *et al.* (2007a) analyzed 18 years (1982–1999) of climatic data and satellite observations of normalized difference vegetation index (NDVI) throughout China, calculating terrestrial vegetative net primary productivity (NPP) using the revised light-use efficiency model of Zhu *et al.* (2006) and Zhu *et al.* (2007b). They find “climatic changes in China have eased some critical climatic constraints on plant growth.” They note, for example, “water availability most strongly limits vegetation growth over 28% of the whole country surface, whereas temperature limits growth over 43% and radiation over 29%,” but “from 1982 to 1999, modeled NPP increased by 1.42% per year in water-limited regions of Northwest China, 1.46% per year in temperature-limited regions of Northeast China and Tibet Plateau, and 0.99% per year in radiation-limited regions of South China and East China.” Summed over the 18-year period, total Chinese terrestrial vegetation NPP increased by 24.2%. They report “interannual variations of NPP in Chinese terrestrial vegetation are positively correlated with global increases in atmospheric CO₂ growth rate, indicating that NPP in Chinese terrestrial vegetation will increase with the global increases in atmospheric CO₂ growth rate.”

Peng *et al.* (2011) report, “using satellite-derived normalized difference vegetation index (NDVI) datasets, previous studies have found that vegetation growth significantly increased in most areas of China during the period 1982–99 and that the increased vegetation growth was significantly correlated with increased temperature (e.g., Zhou *et al.*, 2001; Piao *et al.*, 2003).” In addition, “the increased temperature boosted vegetation growth through an increase in

growing season length and enhanced photosynthesis (e.g., Zhou *et al.*, 2001; Slayback *et al.*, 2003; Piao *et al.*, 2006b).”

Peng *et al.* used NOAA/AVHRR NDVI composites at a spatial resolution of 0.083° and 15-day intervals produced by the Global Inventory Modeling and Mapping Studies (GIMMS) program, Tucker *et al.* (2005), to explore vegetation activity over China for the years 1982–2010. They note “the GIMMS NDVI datasets have been corrected to minimize the effects of volcanic eruptions, solar angle and sensor errors and shifts,” as described by Zhou *et al.* (2001) and Slayback *et al.* (2003), and state these datasets also have proved to be “one of the best products to depict the temporal change of vegetation growth,” as Beck *et al.* (2011) demonstrated.

At the national scale and for the average growing season (April–October) a linear regression model predicts a significant increasing NDVI trend of 0.0007/year from 1982 to 2010, with an R² value of 0.40 and P < 0.001 (see Figure 4.2.2.1.1.1). They also found increasing trends for all three subsets of the growing season: April–May, June–August, and September–October.

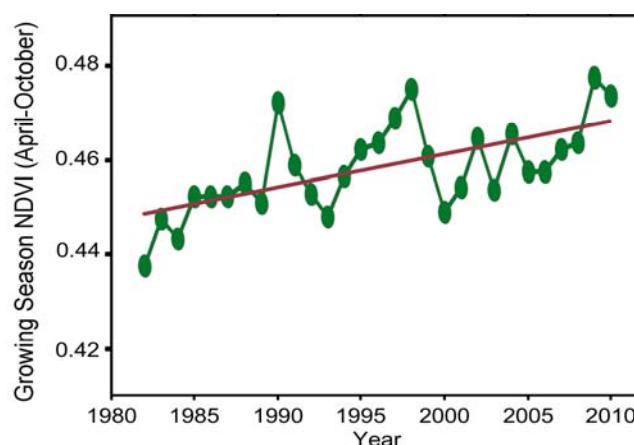


Figure 4.2.2.1.1.1. Interannual variations in growing season (April–October) NDVI for China during the years 1982–2010. The linear trend in the data, as mentioned in the text, is also shown. Adapted from Peng *et al.* (2011).

Mao *et al.* (2009) used a modified version of the Sheffield Dynamic Global Vegetation Model described by Woodward and Lomas (2004) to study changes in the structure, composition, and carbon storage of vegetation and soils throughout China in response to changes in climate and atmospheric CO₂ concentration between 1901 and 2000. They report their modeling exercise indicates “during the past

Climate Change Reconsidered II: Biological Impacts

100 years a combination of increasing CO₂ with historical temperature and precipitation variability in continental China have caused the total vegetation carbon storage to increase by 2.04 Pg C, with 2.07 Pg C gained in the vegetation biomass but 0.03 Pg C lost from the organic soil carbon matter.” They also found “the increasing CO₂ concentration in the 20th century is primarily responsible for the increase of the total potential vegetation carbon.”

Mu *et al.* (2008) used “a well-documented daily ecosystem process model Biome-BGC (Running and Hunt, 1993; White *et al.*, 2000; Thornton *et al.*, 2002) to differentiate the effects of changing climate and increasing CO₂ on the carbon cycle for terrestrial China for two time periods, 1961–2000 (present conditions), and future (2071–2110) conditions with projected climate change under doubled CO₂.” The five researchers write, “during 1961–2000 at the national scale, changes in climate reduced carbon storage in China’s ecosystems, but increasing CO₂ compensated for these adverse effects of climate change, resulting in an overall increase in the carbon storage of China’s ecosystems.” They continue, “under the future scenario (2071–2110), with a doubling [of] CO₂, China will experience higher precipitation and temperature,” but “the concomitant doubling of CO₂ will continue to counteract the negative effects of climate change on carbon uptake in the future, leading to an increase in carbon storage relative to current levels.”

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4.2.2.2.1.2 Deserts

Brogaard *et al.* (2005) examined the dry northern and northwestern regions of China, including the Inner Mongolia Autonomous Region (IMAR), which had been thought to have experienced declining vegetative productivity over the past few decades due to “increasing livestock numbers, expansion of cultivated land on erosive soils and the gathering of fuel wood and herb digging.” These practices were believed to have been driven by rising living standards that, in combination with a growing population, increased the pressure on these marginal lands. Brogaard *et al.* note the total number of livestock in the IMAR increased from approximately 46 million head in 1980 to about 71 million in 1997.

To better assess the seriousness of this “ongoing land degradation process,” as they describe it, the researchers adapted a satellite-driven parametric model, originally developed for Sahelian conditions, to the central Asian steppe region of the IMAR by

including “additional stress factors and growth efficiency computations.” The applied model, they write, “uses satellite sensor-acquired reflectance in combination with climate data to generate monthly estimates of gross primary production.” They found, “despite a rapid increase in grazing animals on the steppes of the IMAR for the 1982–1999 period,” their model estimates did “not indicate declining biological production.”

Clearly, some strong positive influence compensated for the increased human and animal pressures on the lands of the IMAR over the period of Brogaard *et al.*'s study. They mention the possibility of increasing productivity on the agricultural lands of the IMAR, but crops are grown on “only a small proportion of the total land area.” They also mention “an increase in precipitation, as well as afforestation projects.” Two things they do not mention are the aerial fertilization and transpiration-reducing effects of the increase in the air's CO₂ concentration over the study period. Applied together, these positive influences, and possibly others that remain unknown, are demonstrably sufficient to keep plant productivity from declining in the face of greatly increasing animal and human pressures.

Yang *et al.* (2011) studied *Caragana microphylla* plantations established five to 40 years ago in the semi-arid Loess Plateau of northwestern Shanxi, China in efforts to combat desertification, which in the 1960s had claimed 48.5% of the region's surface area. These perennial leguminous and sand-binding shrubs have well-developed stems with many clustered branches and large root systems capable of adapting to poor nutrient conditions, and they were positioned in groups to act as sand barriers and windbreaks.

The establishment and development of the *C. microphylla* shrubs, in the words of the five Chinese scientists, “improved soil texture, enhanced soil organic matter (SOM), total nitrogen (TN), and cation exchange capacity (CEC).” In addition, “SOM, TN, and CEC were significantly higher at the center than at the outside of the shrub canopies and were higher at the 0–5 cm depth than at the 5–10 cm depth.” They report “the differences in SOM, TN, and CEC from the center to the outside of shrub canopies were greater under 30- and 40-year-old shrubs than under 10- and 5-year-old shrubs.” They found the spatio-temporal heterogeneity of the soil properties “facilitated the development of herbaceous species diversity and the restoration of the [region's] natural ecosystem,” which had been lost to desertification.

Peng *et al.* (2010) used snow-depth measure-

ments collected at 279 meteorological stations across China, plus co-located satellite-derived normalized difference vegetation index (NDVI) data, to investigate spatio-temporal changes in snow depth for the years 1980–2006 and the effects of those changes on vegetative growth the following spring and summer. The five researchers report, “over the past three decades, winter snow depth overall increased in northern China, particularly in the most arid and semiarid regions of western China where desert and grassland are mainly distributed.” In those areas they found positive correlations between mean winter snow depth and spring NDVI data. They also note Piao *et al.* (2005b) determined the net primary productivity of the same desert and grasslands during 1982–1999 “increased by 1.6% per year and 1.1% per year, respectively,” and “desertification has been reversed in some areas of western China since the 1980s,” citing Runnstrom (2000), Wu (2001), Zhang *et al.* (2003), and Piao *et al.* (2005b).

Peng *et al.* state the “increase in vegetation coverage in arid and semiarid regions of China, possibly driven by winter snow, will likely restore soil and enhance its anti-wind-erosion ability, reducing the possibility of released dust and mitigating sand-dust storms,” noting the frequency of sand-dust storms has indeed “declined in China since the early 1980s (Qian *et al.*, 2002; Zhao *et al.*, 2004).”

Piao *et al.* (2005b) used a time series of NDVI data from 1982 to 1999, together with precipitation and temperature data, to investigate variations of desert area in China by “identifying the climatic boundaries of arid area and semiarid area, and changes in NDVI in these areas.” They discovered “average rainy season NDVI in arid and semiarid regions both increased significantly during the period 1982–1999.” They report the NDVI increased for 72.3% of total arid regions and for 88.2% of total semiarid regions, such that the area of arid regions decreased by 6.9% and the area of semiarid regions decreased by 7.9% (see Figure 4.2.2.2.1.2.1). They also report, by analyzing Thematic Mapper satellite images, “Zhang *et al.* (2003) documented that the process of desertification in the Yulin area, Shannxi Province showed a decreased trend between 1987 and 1999,” and “according to the national monitoring data on desertification in western China (Shi, 2003), the annual desertification rate decreased from 1.2% in the 1950s to -0.2% at present.”

Further noting “variations in the vegetation coverage of these regions partly affect the frequency of sand-dust storm occurrence (Zou and Zhai, 2004),” Piao *et al.* conclude “increased vegetation coverage in these areas will likely fix soil, enhance its anti-wind-erosion ability, reduce the possibility of released dust, and consequently cause a mitigation of sand-dust storms.” They report, “recent studies have suggested

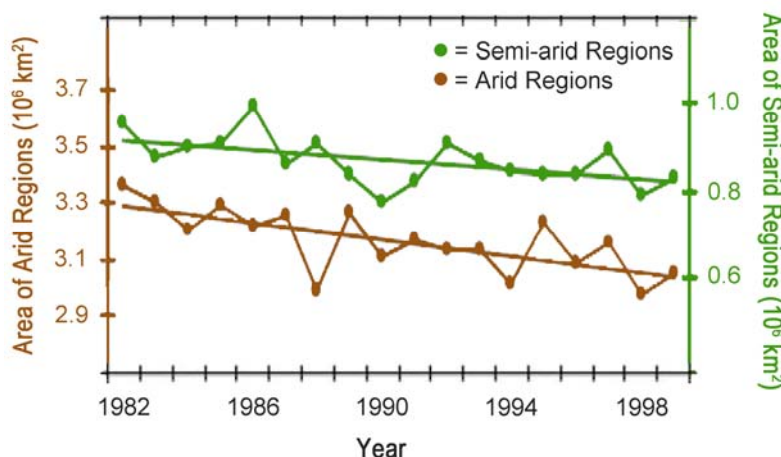


Figure 4.2.2.2.1.2.1. Interannual variation in area of arid (brown line) and semiarid region (green line) in China during the years 1982 to 1999. Adapted from Piao *et al.* (2005b).

that the frequencies of strong and extremely strong sand-dust storms in northern China have significantly declined from the early 1980s to the end of the 1990s (Qian *et al.*, 2002; Zhao *et al.*, 2004).”

Zhao *et al.* (2011) note “many studies based on analyses of satellite images have detected a greening trend at global (Myneni *et al.*, 1997; Nemani *et al.*, 2003; Potter *et al.*, 2007; Zhou *et al.*, 2001) and regional scales (Donohue *et al.*, 2009; Fang *et al.*, 2004; Herrmann *et al.*, 2005),” and they point out “the response of vegetation to climatic changes widely differed by biome (Fang *et al.*, 2005; Piao *et al.*, 2006c) and bioregion (Verbyla, 2008).” Focusing on the grassland-oasis-desert complex of northwest China, the four Chinese researchers “investigated spatio-temporal changes in vegetation growth and their responses to a changing climate by biome and bioregion, using satellite-sensed Normalized Difference Vegetation Index (NDVI) data from 1982 to 2003, along with corresponding climate data.”

Over the 22 years of their study, during which annual mean temperature increased by 0.06°C/year, “about 30% of the total vegetated area showed an annual increase of 0.7% in growing season NDVI,” they write. This trend “occurred in all biomes and all

bioregions except Sawuer, a sub-region of the study area with no significant climate change.” They report the NDVI increase was remarkable during 1982–1988, then tended to be slight, and finally declined a bit from 1998 to 2003. This pattern largely resembles the concomitant pattern of global air temperature change, which could have been responsible for the shifts in regional precipitation that appeared to be driving the observed shifts in NDVI. Zhao *et al.* note “previous analyses of satellite-measured vegetation growth suggested a greening trend of vegetation in the central United States (Wang *et al.*, 2001, 2003) and the Sahel (Anyamba and Tucker, 2005; Herrmann *et al.*, 2005) due to the effects of increasing precipitation at seasonal or annual scales.”

The findings presented above indicate the vegetation in China's deserts has fared well in response to what has been called the most dramatic global warming and CO₂ rise of the past two millennia.

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4.2.2.2.1.3 Forests

Ren *et al.* (2011) note, “in recent decades, there has been increased concern that elevated tropospheric ozone (O₃) and climate change have [negatively] influenced the ability of China’s ecosystems to provide people with essential goods and services.” They investigated “the potential effects of elevated O₃ along with climate change/variability on NPP [net primary production] and NCE [net carbon exchange] in China’s forest ecosystems for the period 1961–2005 using a process-based dynamic land ecosystem model (DLEM, Tian *et al.*, 2005, 2010a,b),” while also considering “other environmental factors such as land-cover/land-use change (LCLUC), increasing [atmospheric] CO₂ and nitrogen deposition.”

Ren *et al.* report O₃ pollution had consistent negative effects on forest production, reducing total NPP by 0.2 to 1.6% from the 1960s to 2000–2005; without O₃ pollution, carbon uptake rates would have increased by 3.5% in the 1960s and 12.6% in the six years of 2000–2005. Climate change had both negative and positive effects on NPP and NCE, and it was thus the major factor controlling the interannual variability of these two productivity parameters.

LCLUC also had negative impacts on NPP and NCE, but Ren *et al.* note “nitrogen deposition alone could compensate for the combined negative effects of O₃ and LCLUC in China.” They also report an

increase in NPP occurred in the CO₂-N combination simulation, which they write, “was consistent with previous studies (e.g., Ollinger *et al.*, 2002; Felzer *et al.*, 2004; Hanson *et al.*, 2005).” They suggest CO₂ and nitrogen deposition working together “could offset the combined negative effects of O₃ pollution, climate change and LCLUC on annual NCE.” It would appear the combination of atmospheric CO₂ enrichment and nitrogen deposition provide powerful antidotes for the negative effects of ozone pollution, land-cover/land-use change, and various deleterious climatic phenomena on NPP and NCE in China and, by inference, other parts of the world as well.

Su and Sang (2004) used an ecosystem process model to explore the sensitivity of the net primary productivity (NPP) of an oak forest near Beijing to the global climate changes projected to result from a doubling of the atmosphere’s CO₂ concentration from 355 to 710 ppm. They found the aerial fertilization effect of the increase in the atmospheric CO₂ content would raise the forest’s NPP by 14.0%; a concomitant temperature increase of 2°C would boost the NPP increase to 15.7%; and adding a 20% increase in precipitation would push the NPP increase to 25.7%. They also calculate a 20% increase in precipitation and a 4°C increase in temperature would boost the forest’s NPP by 25.7%.

Su *et al.* (2007) used a process-based model (BIOME-BGC) “to investigate the 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.” They modeled a double-CO₂-induced temperature increase of 2.6°C and a precipitation increase of 25%.

When they considered the predicted precipitation increase by itself, Su *et al.* found 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 only 2.7%. When the predicted increases in precipitation and temperature occurred together, forest NPP increased by 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 report forest NPP “increased dramatically, with an average increase of about 30.4%.”

Su *et al.* conclude the results derived from the various scenarios of their study indicate “the effects of precipitation and temperature change were simply

Earth's Vegetative Future

additive, but that the synergy between the effects of climate change and doubled CO₂ was important,” as it 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.”

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4.2.2.2.1.4 Grasslands

Noting the climate of China's temperate grasslands “experienced dramatic change in the past several decades,” Piao *et al.* (2006) investigated the impact of that climate change on the productivity of the country's grasslands. They analyzed normalized difference vegetation index (NDVI) data from the U.S. National Oceanic and Atmospheric Administration's very high-resolution radiometer at a spatial resolution of 8 x 8 km and at 15-day intervals from January 1982 to December 1999, comparing those results with temperature, precipitation, and Thornthwaite (1948) moisture index data generated from 680 well-distributed climate stations across China.

Piao *et al.* found little or no increase in precipitation and moisture index over the period of their study. For temperature, they found a least-squares linear warming of 0.89°C between 1982 and 1999 with $R = 0.59$ and $P = 0.009$, which they describe as “dramatic.” Even more dramatic, “mean growing season NDVI increased significantly ($R = 0.73$, $P = 0.001$) from 0.25 in 1982 to 0.28 in 1999,” or by approximately 12%.

At first glance it would appear the dramatic increase in temperature is what drove the dramatic increase in grassland productivity. But more detailed analyses revealed “the positive effect of temperature on the growth of grassland decreased as temperature rose.” Piao *et al.* suggest the “atmospheric CO₂ fertilization effect, increased nutrient deposition, and human activity such as grazing management [and] land abandonment due to migration into urban areas” may have compensated for the decreasing strength of the growth enhancement provided by the region's warming.

One year later, using national grassland resource inventory data, a normalized difference vegetation index (NDVI) time series dataset, and a satellite-based statistical model, Piao *et al.* (2007) identified changes in the size and distribution of the aboveground biomass carbon (C) stocks of China's

grasslands between 1982 and 1999. The authors report “aboveground biomass C stocks ... significantly increased from 136.3 Tg C in the early 1980s to 154.0 Tg C in the late 1990s,” for a total increase of 13% (Figure 4.2.2.2.1.4.1). They note “growing season average temperature for the study area increased by 0.052°C per year and growing season precipitation also tended to increase,” which led them to conclude “increased temperature may be associated with increasing C stocks and interannual changes in precipitation may be a factor in the fluctuations of C stocks.” In addition, the “atmospheric CO₂ fertilization effect and human activity such as land management may also partly account for the observed increase in biomass C stocks of China’s grassland.”

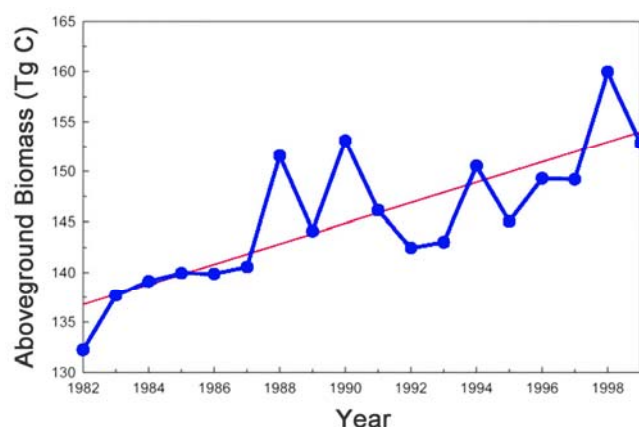


Figure 4.2.2.2.1.4.1. Interannual variations in aboveground biomass for China’s grassland during the years 1982–1999. Adapted from Piao *et al.* (2007).

Peng *et al.* (2010) used snow-depth measurements collected at 279 meteorological stations across China, plus collocated satellite-derived normalized difference vegetation index (NDVI) data, to investigate spatio-temporal changes in snow depth during the years 1980–2006 and the effects of those changes on vegetative growth the following spring and summer. The five researchers report, “over the past three decades, winter snow depth overall increased in northern China, particularly in the most arid and semiarid regions of western China where desert and grassland are mainly distributed,” and in those areas there were positive correlations between mean winter snow depth and spring NDVI data. They note Piao *et al.* (2005) determined the net primary productivity of the same desert and grasslands during 1982–1999 “increased by 1.6% per year and 1.1% per year, respectively,” and “desertification has been

reversed in some areas of western China since the 1980s,” citing Runnstrom (2000), Wu (2001), Zhang *et al.* (2003), and Piao *et al.* (2005).

Peng *et al.* write, the “increase in vegetation coverage in arid and semiarid regions of China, possibly driven by winter snow, will likely restore soil and enhance its antiwind-erosion ability, reducing the possibility of released dust and mitigating sand-dust storms,” noting the frequency of sand-dust storms has indeed “declined in China since the early 1980s (Qian *et al.*, 2002; Zhao *et al.*, 2004).”

As the world warmed over the past three decades, a climatic change across China above 40°N latitude (an increase in winter snow depth) has prompted a biological change (increased vegetative growth in desert areas and grasslands) that has prompted yet another climatic change (a reduction in sand-dust storms). All of these changes are positive developments.

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4.2.2.2.1.5 Tibetan Plateau

Taking a long temporal view of how vegetative productivity has fared in this region of China, Herzschuh *et al.* (2011) “critically review possible driving forces for early- to mid-Holocene vegetation shifts on the upper Tibetan Plateau (including precipitation, growing season length, radiation, human impact) with particular emphasis on changing CO₂ concentrations to better predict future environmental change and impacts on the Tibetan Plateau in a rapidly changing world.”

The four researchers report, “numerous pollen records from across the upper Tibetan Plateau indicate that *Kobresia*-dominated high-alpine meadow invaded alpine steppes during the mid- to late-Holocene.” Their investigation, which employed a pollen-moisture transfer function, indicates “this marked vegetation change cannot be satisfactorily explained by climate change.” In addition, they note “a literature review did not reveal convincing evidence for any widespread human impact on mid-Holocene vegetation.” They propose the reconstructed vegetation changes likely were “a response to Holocene CO₂ concentration changes,” with values rising from approximately 260 ppm in the early Holocene to near-present-day values on the order of 375 ppm.

Their conclusion is based on four lines of evidence: (1) “high-elevation vegetation is particularly sensitive to CO₂ changes due to lowered CO₂ partial pressure”; (2) “water conservation of steppe vegetation in response to experimental CO₂ enrichment was of the same order of magnitude as inferred from mid- to late-Holocene Tibetan pollen records”; (3) “modern remote sensing-aided vegetation monitoring of the Central Tibetan Plateau yielded an increase in biomass, most probably as a response to modern CO₂ increase,” even in spite of “increasing land-use by herding”; and (4) “experimental CO₂ fertilization of

dry grassland and desert vegetation performed in several regions world-wide has stimulated plant growth directly through enhanced photosynthesis and indirectly through enhanced water-use efficiency (Morgan *et al.*, 2004).”

Zhuang *et al.* (2010) used a process-based biogeochemistry model—the Terrestrial Ecosystem Model or TEM, which also employed a soil thermal model—to examine permafrost dynamics and their effects on the carbon dynamics of the Tibetan Plateau. They accomplished this by “parameterizing and verifying” the TEM using real-world data for soil temperature, permafrost distribution, and carbon and nitrogen distributions throughout the region, and then extrapolating the model and its parameters to the whole of the plateau.

The six scientists report, “during the 20th century, the Tibetan Plateau changed from a small carbon source or neutral in the early part of the century to a sink later” (Figure 4.2.2.2.1.5.1), noting “net primary production and soil respiration increased by 0.52 and 0.22 Tg C/year, respectively, resulting in a regional carbon sink increase of 0.3 Tg C/year,” so “by the end of the century, the regional carbon sink reached 36 Tg C/year and carbon storage in vegetation and soils is 32 and 16 Pg C, respectively.”

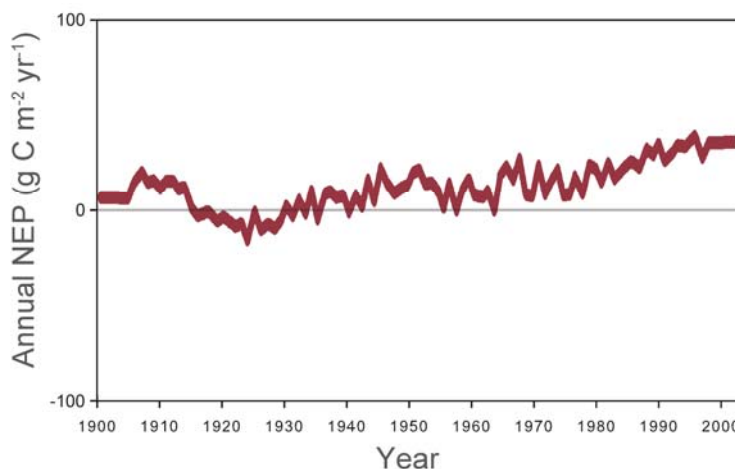


Figure 4.2.2.2.1.5.1. Five year running average of Net Ecosystem Production (NEP) on the Tibetan Plateau during the years 1901–2002. Negative values reveal the region to be a carbon source, positive values indicate it is a carbon sink. Adapted from Zhuang *et al.* (2010).

Zhuang *et al.* say the “increasing soil temperature and deepening active layer depth enhanced soil respiration, increasing the net nitrogen mineralization rate,” and “together with the [positive] effects of warming air temperature and rising CO₂ concentrations on photosynthesis, the stronger plant nitrogen

uptake due to the enhanced available nitrogen stimulate[d] plant carbon uptake, thereby strengthening the regional carbon sink as the rate of increase in net primary production was faster than that of soil respiration.” They say their study implies “future warming will increase thawing of the permafrost, increase soil temperature and dry up soil moisture,” and “these physical dynamics may enhance [the] future strength of the regional carbon sink, since the rate of increase of net primary production is higher than that of soil respiration on the Tibetan Plateau.”

Satellite-based measurements taken over the past three decades provide further evidence the productivity of the Tibetan Plateau’s vegetation has recently increased. Piao *et al.* (2006), for example, investigated net primary production (NPP) derived from a carbon model (Carnegie-Ames-Stanford approach, CASA) and its interannual change in the Qinghai-Xizang (Tibetan) Plateau using 1982–1999 NDVI data and paired ground-based information on vegetation, climate, soil, and solar radiation. Over the study period, NPP rose at a mean annual rate of 0.7%. Piao *et al.* report, “the NPP trends in the plateau over the two decades were divided into two distinguished periods: without any clear trend from 1982 to 1990 and significant increase from 1991 to 1999.”

The three researchers say their findings indicate “vegetation growth on the plateau in the 1990s has been much enhanced compared to that in [the] 1980s, consistent with the trend in the northern latitudes indicated by Schimel *et al.* (2001).” They write, “previous observational and NPP modeling studies have documented substantial evidence that terrestrial photosynthetic activity has increased over the past two to three decades in the middle and high latitudes in the Northern Hemisphere,” and “satellite-based NDVI data sets for the period of 1982–1999 also indicate consistent trends of NDVI increase,” citing multiple references. Piao *et al.*’s findings add to the growing body of evidence that reveals a significant greening of the Earth in response to the ongoing recovery of the planet from the growth-inhibiting chill of the Little Ice Age, which was likely the coldest period of the current interglacial; the aerial fertilization effect of the historical and still-ongoing rise in the atmosphere’s CO₂ concentration; and the growth-promoting effect of anthropogenic nitrogen deposition.

Zhou *et al.* (2007) investigated interannual variations of Tibetan Plateau vegetative productivity using a 21-year (1982–2002) normalized difference vegetation index (NDVI) dataset to quantify the

consequences of changes in temperature and precipitation for the regional ecosystem. They report, “the maximum, minimum and mean temperature fluctuations all present an increasing trend over the 21 years.” They note “the NDVI is comparatively large during the warm years, such as 1988, 1994, 1998, and 1999,” and “relatively small NDVI values are well coupled with the cold extreme and mean temperature in 1982, 1983 and 1997.” This relationship, they continue, “suggests a positive correlation between vegetation activity and surface air temperature on the plateau.” They report, “the correlation coefficient between the NDVI and the maximum, minimum and mean temperature reaches 0.674 (significant at the 99% level), 0.53 (significant at the 95% level) and 0.55 (significant at the 99% level), respectively.” In contrast, “the precipitation fluctuation does not show a detectable trend, and therefore its correlation with DNVI is not obvious.”

Zhou *et al.* conclude, “vegetation variability on the Tibetan Plateau might be mostly driven by thermal impacts (i.e., surface air temperature), whereas precipitation impact is less clear.” Overall, “vegetation activity demonstrates a gradual enhancement in an oscillatory manner during 1982–2002,” suggesting a significant positive impact of what IPCC calls “unprecedented” global warming on the Tibetan Plateau, which Zhou *et al.* describe as “one of the most prominent features on Earth.”

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4.2.2.2.2 All Other Asian Countries

This section examines how vegetative productivity has fared in Asian countries other than China over the past few decades.

Grunzweig *et al.* (2003) studied the Yatir forest, a 2,800-hectare stand of Aleppo and other pine trees, planted some 35 years earlier at the edge of the Negev Desert in Israel. They characterize the forest as growing in poor soil of only 0.2 to 1.0 meter's depth above chalk and limestone. Although it is located in an arid part of Asia that receives less annual precipitation than all of the other stations in the FluxNet global network of micrometeorological tower sites (Baldocchi *et al.*, 2001), the forest's annual net ecosystem CO₂ exchange was just as high as that of many high-latitude boreal forests and actually higher than those of most temperate forests.

Grunzweig *et al.* note the increase in atmospheric CO₂ concentration that has occurred since pre-industrial times should have improved water use efficiency (WUE) in most plants by increasing the ratio of CO₂ fixed to water lost via evapotranspiration. That this hypothesis is correct has been demonstrated by Leavitt *et al.* (2003) in the context of the long-term atmospheric CO₂ enrichment experiment of Idso and Kimball (2001) on sour orange trees. It also has been confirmed in nature by Feng (1999), who obtained results identical to the study of Leavitt *et al.* for 23 groups of naturally occurring trees across western North America for the years 1800–1985; a response,

Feng concludes, that “would have caused natural trees in arid environments to grow more rapidly, acting as a carbon sink for anthropogenic CO₂,” which is what Grunzweig *et al.* found in the Yatir forest on the edge of the Negev Desert. Grunzweig *et al.* also report, “reducing water loss in arid regions improves soil moisture conditions, decreases water stress and extends water availability,” which “can indirectly increase carbon sequestration by influencing plant distribution, survival and expansion into water-limited environments.”

Singh *et al.* (2011) used U.S. National Oceanic and Atmospheric Administration (NOAA) satellite-derived advanced very high resolution radiometer (AVHRR) data, together with the Global Production Efficiency Model (GloPEM) developed by Prince and Goward (1995), to calculate annual NPP over India for the years 1981–2000 (Figure 4.2.2.2.1). According to the five researchers, regression analysis of the 20-year NPP database showed a significant increase in the temporal trend of NPP over India ($r=0.7$, $p<0.001$), with the mean rate of increase being 10.43 gC/m²/year, which yields a mean rate-of-increase in carbon fixation of 34.3 TgC/year for the country, including its arid and semi-arid regions, its forests, and its dry-land and irrigated agricultural regions.

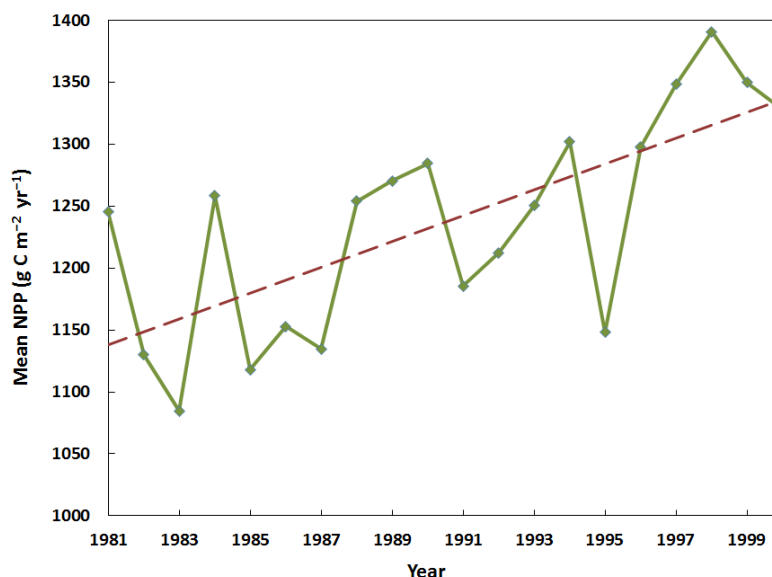


Figure 4.2.2.2.1. Average annual NPP estimated for India during the years 1981–2000 using NOAA-AVHRR data, as per Singh *et al.* (2011).

In Russia, in an area extending from 72°02'N to 72°40'N and from 101°15'E to 102°06'E—a total of approximately 36,000 ha that includes the Ary-Mas forest (the northernmost forest on the planet) plus

larch forests on southeastern slopes descending to the Khatanga River—Kharuk *et al.* (2006) analyzed remote-sensing images made by Landsat satellites in 1973 and 2000. They found “the most significant changes were observed in the class of normal larch stands (canopy density > 0.3): their area increased by 66%,” and “the areas of open and sparse forests (0.1 < canopy density < 0.3, and canopy density < 0.1) increased by 16 and 8%, respectively, whereas the background area became 19% smaller.” They report the rates of expansion of larch onto tundra “for sparse, open, and normal stands were estimated at 3, 9, and 11 m per year, respectively.” They remark, “since sparse stands are at the forefront of advancement to the tundra, the rate for this class (approximately 3 m per year) should be regarded as the rate of larch expansion in general,” and “the above rates reflect not only the expansion of trees into the tundra, but also an increase in the density of sparse and open stands.”

Kharuk *et al.* suggest the changes they reported were “induced by climatic trends” and the continuation of this process “will result in the expansion of larch to the Arctic coast,” which they describe as a “phenomenon that took place in the Holocene.” Thus the Ary Mas forest evidently is reclaiming what previously had been lost due to the progressive cooling of the planet after the Holocene Climatic Optimum, as this cooling culminated in the record interglacial cold of the Little Ice Age from which Earth and its biosphere are now recovering.

Lapenis *et al.* (2005) analyzed trends in forest biomass in all 28 ecoregions of the Russian territory, based on data collected from 1953 to 2002 in 3,196 sample plots comprising about 50,000 entries. This database, they write, “contains all available archived and published data.” Over the period 1961–1998, they write, “aboveground wood, roots, and green parts increased by 4%, 21%, and 33%, respectively,” such that “the total carbon density of the living biomass stock of the Russian forests increased by ~9%.” They also report a concomitant increase of ~11% in the land area of Russian forests. In addition, the U.S., Austrian, and Russian scientists note, “within the range of 50–65° of latitude [the range of 90% of Russian forests], the relationship between biomass density and the area-averaged NDVI is very close to a linear function, with a slope of ~1,” citing Myneni *et al.* (2001). They continue, “changes in the carbon density of live biomass in Russian forests occur at about the same rate as the increase in the satellite-based estimate in the seasonally accumulated NDVI.”

Acknowledging remote sensing data suggest

tundra vegetation in North America may be responding to recent warming via enhanced photosynthetic activity (Goetz *et al.*, 2005; Verbyla, 2008), Forbes *et al.* (2010) write, “at a circumpolar scale, the highest photosynthetic activity and strongest growth trends are reported in locations characterized by erect shrub tundra (Reynolds *et al.*, 2006),” noting “live leaf phytomass from deciduous shrubs, shown to have increased in northern Alaska during the second half of the last century (Sturm *et al.*, 2001; Tape *et al.*, 2006), is believed to be a key driver of the observed trends (Jia *et al.*, 2003; Goetz *et al.*, 2005; Verbyla, 2008).” Forbes *et al.* analyzed annual ring growth for 168 stem slices of 2- to 3-cm thickness they collected from 40 *Salix lanata* L. (*sensu lato*)—an abundant deciduous dioecious willow with nearly circumpolar geographic distribution from the northern boreal forest of Russia to the northern limits of the Low Arctic. Their samples were taken from 15 sites in an area of approximately 3 x 2.3 km located at about 68°40'N, 58°30'E.

The three researchers found “a clear relationship with photosynthetic activity for upland vegetation at a regional scale for the years 1981–2005, confirming a parallel ‘greening’ trend reported for similarly warming North American portions of the tundra biome,” and they write, “the standardized growth curve suggests a significant increase in shrub willow growth over the last six decades.” Noting “the quality of the chronology as a climate proxy is exceptional,” Forbes *et al.* state their findings “are in line with field and remote sensing studies that have assigned a strong shrub component to the reported greening signal since the early 1980s,” adding the growth trend agrees with the qualitative observations of nomadic reindeer herders, which suggest there have been “recent increases in willow size in the region.” Forbes *et al.* say their analysis “provides the best proxy assessment to date that deciduous shrub phytomass has increased significantly in response to an ongoing summer warming trend.”

Lioubimtseva *et al.* (2005) describe a number of findings generally not available to the international scientific community because of their publication in Russian. According to the four-member team of Russian and American scientists, “there has been a general warming trend in Central Asian republics on the order of 1–2°C since the beginning of the 20th century.” They note the trend is expressed most strongly in winter and “the amplitude of this trend seems to be comparable with Holocene climate variability,” suggesting it is nothing unusual nor does it require an anthropogenic explanation. Citing IPCC

(2001), they report precipitation has remained basically unchanged throughout the twentieth century, stating “there were no discernible trends in annual precipitation during 1900–95 for the region as a whole, nor in most parts of this region.”

In the face of unchanging precipitation and significant warming, it might be expected the aridity of Central Asia would have increased significantly in recent years, especially throughout the 1990s, when IPCC purports the world had its most oppressive heat of both the twentieth century and the past two millennia. However, Lioubimtseva *et al.* report, “analyses of the NOAA AVHRR temporal series since the 1980s showed a decrease in aridity from 1991–2000 compared to 1982–1990 in the northern part of the region and a southward shift of the northern boundary of the desert zone in Central Asia,” citing Zolotokrylin (2002). Lioubimtseva *et al.* suggest the cause of this unexpected development may have been the historical rise in the atmospheric CO₂ content.

The scientists note “an increased atmospheric CO₂ concentration has direct and relatively immediate effects on two important physiological processes in plants: it increases the photosynthetic rate, but decreases stomatal opening and therefore the rate at which plants lose water,” so “the combination of these two factors, increased photosynthesis and decreased water loss, implies a significant increase of water [use] efficiency (the ratio of carbon gain per unit water loss) and ... a reduction in the sensitivity to drought stress in desert vegetation as a result of elevated atmospheric CO₂,” citing Smith *et al.* (2000). They note these effects could “increase productivity and biomass of natural desert vegetation,” which would make the land less arid.

Buttressing this reasoning with experimental evidence from the region, Lioubimtseva *et al.* report, “CO₂-enrichment experiments (both chamber and free-air) conducted in the Kara Kum (Voznesensky, 1997) and Kyzyl Kum (Voznesensky, 1997; Zelensky, 1977) deserts showed a 2–4 times increase in the photosynthetic rate under the saturating CO₂ concentrations,” and “three Kara Kum species (*Eminium lehmanii*, *Rhemum turkestanuikum* and *Ephedra stobilacea*) responded with a six-fold increase in photosynthetic rate (Nechaeva, 1984).” They report, “the CO₂ fertilization effects included not only higher vegetation but also microphytic communities including mosses, lichens, fungi, algae, and cyanobacteria”; these communities, they write, “form biogenic crusts on the soil surface varying from a few millimeters to several centimeters in thickness

and play a significant role in the desert ecosystems controlling such processes as water retention and carbon and nitrogen fixation in soils.”

Zhou *et al.* (2001) analyzed satellite-derived normalized difference vegetation index (NDVI) data from July 1981 to December 1999, between 40 and 70° N latitude. They found a persistent increase in growing season vegetative productivity in excess of 12% over this broad contiguous swath of Asia stretching from Europe through Siberia to the Aldan plateau, where almost 58% of the land is forested. In a companion study, Bogaert *et al.* (2002) determined this productivity increase occurred at a time when this vast Asian region showed an overall warming trend “with negligible occurrence of cooling.”

Ichii *et al.* (2005) simulated and analyzed carbon fluxes during the years 1982–1999 “using the Biome-BGC prognostic carbon cycle model driven by National Centers for Environmental Prediction re-analysis daily climate data,” after which they “calculated trends in gross primary productivity (GPP) and net primary productivity (NPP).” They found solar radiation variability to be the primary factor responsible for inter-annual variations in GPP, followed by temperature and precipitation variability. In terms of GPP trends, the authors report, “recent changes in atmospheric CO₂ and climate promoted terrestrial GPP increases with a significant linear trend in all three tropical regions.” The rate of GPP increase for Asia was about 0.3 PgC year⁻¹ per decade. Ichii *et al.* favor carbon dioxide as the likely cause, reporting “CO₂ fertilization effects strongly increased recent NPP trends in regional totals.”

In a study examining a large portion of the Northern Hemisphere (East Asia, including China, Japan, Korea, and Mongolia), Piao *et al.* (2011) used three process-based ecosystem models—the Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ-DGVM) described by Sitch *et al.* (2003), the ORganizing Carbon and Hydrology In Dynamic Ecosystems (ORCHIDEE) model described by Krinner *et al.* (2005), and the Sheffield model (SDGVM) described by Woodward and Lomas (2004)—to investigate East Asia’s net primary productivity (NPP) response to the climatic change and rising atmospheric CO₂ concentration of the past century. They ran each of the three models for the years 1901 to 2002, using observed values of monthly climatology and annual global atmospheric CO₂ concentrations (Figure 4.2.2.2.2.2).

Between 1901 and 2002, modeled NPP “significantly increased by 5.5–8.5 Tg C per year (15–20% growth),” the authors write, and this

Climate Change Reconsidered II: Biological Impacts

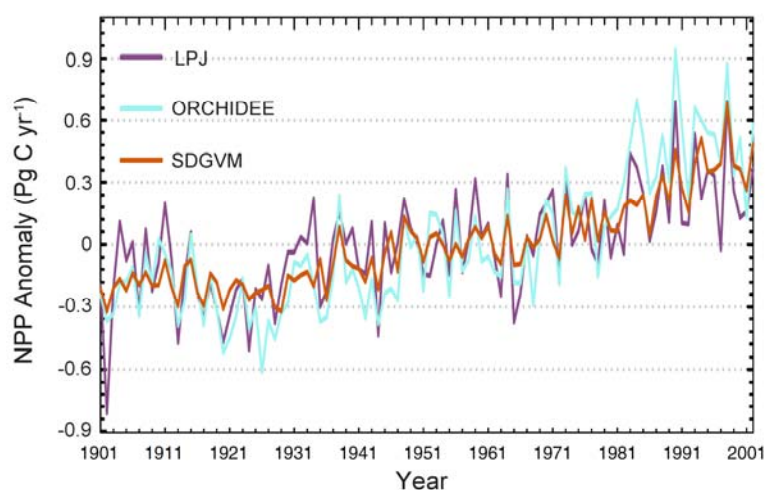


Figure 4.2.2.2.2. Terrestrial Net Primary Productivity anomalies for East Asia for the years 1901–2002 as determined from the three process-based ecosystem models described in the text (LPJ, ORCHIDEE, and SDGVM). Adapted from Piao *et al.* (2011).

increase in NPP “caused an increased cumulated terrestrial carbon storage of about 5–11 Pg C,” about 50–70% of which “is located in vegetation biomass.” In addition, “40–60% of the accumulated carbon uptake of the 20th century is credited to the period of 1980–2002,” the warmest two-decade interval of that century-long period, according to IPCC.

Thus Piao *et al.* demonstrate the rise of the air’s CO₂ concentration and temperature to their highest values of the past century enhanced the terrestrial vegetative productivity of East Asia. This and the many other observations described above indicate plant productivity in Asia is increasing as atmospheric CO₂ concentrations and temperatures rise.

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4.2.2.3 Australia

- Evergreen vegetation, woody plants, and other plant life have increased across Australia over the past 200 years as a result of CO₂ enrichment.

Banfai and Bowman (2006) note “a number of processes are thought to be threatening the ecological integrity of monsoon rainforests in Northern Australia,” testing this retracting-rainforest claim with a comprehensive repeat aerial photography study of the Northern Territory’s Kakadu National Park, where monsoon rainforest exists as an archipelago of hundreds of small patches within a larger eucalypt savanna matrix. The two Australian researchers from Charles Darwin University’s School for Environmental Research assessed changes to the boundaries of 50 monsoon rainforest patches using temporal sequences of digitized aerial photography taken in 1964, 1984, 1991, and 2004, to ascertain the relative importance of factors driving any change.

They found “rainforest patches increased in size between 1964 and 2004 by an average of 28.8%” (see Figure 4.2.2.3.1). After lengthy analyses of several phenomena that might have been responsible for the range increases, the two researchers conclude “the expansion is likely to have been primarily driven by increases in variables such as rainfall and atmospheric CO₂.” They note, “the average [area] change for dry rainforests from 1964 to 2004 was an increase of 42.1%, whereas for wet rainforests [the increase] was one-third of this at 13.1%.” With respect to dry rainforests, they found “an almost linear increase in rainforest area over the study period.”

In further support of the validity of their findings, and “contrary to the view that monsoon rainforests are contracting,” the two researchers note other repeat aerial photography studies conducted in Northern Australia also have revealed rainforest “expansion at the expense of more open vegetation.” These studies include those of monsoon rainforests in Litchfield

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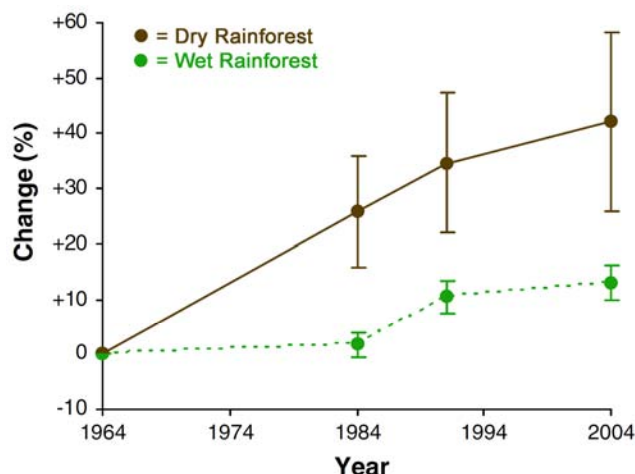


Figure 4.2.2.3.1. Average percentage change in rainforest area in Kakadu National Park, Northern Territory of Australia, relative to 1964 for dry rainforest (brown line) and wet rainforest (green dashed line). Standard errors are indicated. Adapted from Banfai and Bowman (2006).

National Park near Darwin (Bowman *et al.*, 2001)—where forest patches nearly doubled in size between 1941 and 1994—and in the Gulf of Carpentaria (Bowman *et al.*, 2006). Banfai and Bowman write, “these changes parallel the observed expansion of tropical rainforest on the east coast of Australia (Harrington and Sanderson, 1994; Russell-Smith *et al.*, 2004).”

Macinnis-Ng *et al.* (2011) note, “woody thickening” is typically defined as “the increase in woody standing biomass in a landscape already containing woody biomass.” Both it and woody plant invasion, they continue, “are global phenomena commonly observed in arid and semi-arid regions, including Australia (Bowman *et al.*, 2001; Burrows *et al.*, 2002; Asner *et al.*, 2003; Fensham *et al.*, 2005; Scott *et al.*, 2006; Witt *et al.*, 2009),” the “tropical rainforests of Central and South America (Phillips *et al.*, 1998), and temperate forests globally (Birdsey *et al.*, 1993).” Although “the cause of woody thickening remains debated,” they write, “there is an increasing awareness of potential roles for climate and changes in atmospheric CO₂ concentration in causing woody thickening (and woody invasion),” citing Fensham *et al.* (2005), Berry and Roderick (2006), Davis *et al.* (2007), and Sankaran *et al.* (2008).

The four researchers examined the responses of gross primary production (GPP) and water use of a typical Australian woodland using the soil-plant atmosphere (SPA) model of Williams *et al.* (1996), which they applied to the functioning of a temperate

open woodland in Australia (Zeppel *et al.*, 2008) that provided a methodology for testing the conceptual model of Eamus and Palmer (2007), which posits increasing atmospheric CO₂ concentration and declining evaporative demand “may explain the global phenomenon of woody thickening.”

Macinnis-Ng *et al.* demonstrate that as the atmosphere’s CO₂ content rises, plant stomatal conductance decreases, such that water use per tree decreases and, therefore, soil water content increases, leading to increases in leaf area index that allow more light to be intercepted, enabling existing trees to grow bigger, even in the case of photosynthetic acclimation. This set of phenomena constitutes the complex process of woody thickening. Noting their results “provide a valid mechanism for the conclusion of Berry and Roderick (2002) that evergreen vegetation has increased across Australia over the past 200 years as a result of CO₂ enrichment,” they conclude “woody thickening in Australia and probably globally can be explained by the changes in landscape GPP and soil moisture balance arising principally from the increased atmospheric CO₂ concentration.”

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4.2.2.4 Europe

- Over the last two decades of the twentieth century, Europe became greener and much of it is seeing an increase in its 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.

Using an empirically based mechanistic model of Mediterranean shrub vegetation, Osborne *et al.* (2000) set out to address two important questions: Has recent climate change, especially increased drought, negatively impacted Mediterranean shrublands? And has the historical increase in the air's CO₂ concentration modified this impact?

The data-based model they employed suggests the warming and reduced precipitation experienced in the Mediterranean area over the past century should have had negative impacts on net primary production and leaf area index. When the measured increase in atmospheric CO₂ concentration experienced over the period was factored into the calculation, however, these negative influences were overpowered: net primary productivity increased by 25% and leaf area index by 7%. These results, they write, "indicate that the recent rise in atmospheric CO₂ may already have had significant impacts on productivity, structure and water relations of sclerophyllous shrub vegetation, which tended to offset the detrimental effects of climate change in the region."

Model-predicted changes in Earth's precipitation regime indicate a doubling of the atmosphere's CO₂ content will lead to a modest intensification of the planet's hydrologic cycle. In the Mediterranean region over the past century, however, there has been a recent tendency toward drier conditions. Hence the specific case Osborne *et al.* investigated represents a much-worse scenario than what is predicted by

current climate models for Earth as a whole, yet the area's vegetation has grown even better than it did before the climatic change, thanks to the overpowering beneficial biological effects of the concurrent rise in atmospheric CO₂.

Cheddadi *et al.* (2001) employed a standard biogeochemical model (BIOME3)—which uses monthly temperature and precipitation data, certain soil characteristics, cloudiness, and atmospheric CO₂ concentration as inputs—to simulate the responses of various biomes in the region surrounding the Mediterranean Sea to changes in both climate (temperature and precipitation) and atmospheric CO₂ content. They first validated the model for two test periods, the present and 6,000 years before present (BP). They used recent instrumental records for atmospheric CO₂, temperature, and precipitation data for the present period; for 6,000 years BP, they used pollen data to reconstruct monthly temperature and precipitation values and ice core records to determine the atmospheric CO₂ concentration. They determined winter temperatures 6,000 years ago were about 2°C cooler than temperatures today, annual rainfall was approximately 200 mm less than today, and the air's CO₂ concentration averaged 280 ppm, considerably less than the 345 ppm the researchers used to represent the present—the midpoint of the period used for calculating 30-year climate normals at the time they wrote their paper. Applying the model to these two sets of conditions, they demonstrated “BIOME3 can be used to simulate ... the vegetation distribution under ... different climate and CO₂ conditions than today.”

Cheddadi *et al.* used their validated model to explore the vegetative consequences of an increase in anthropogenic CO₂ emissions that pushes the air's CO₂ concentration to a value of 500 ppm and its mean annual temperature to a value 2°C higher than today's mean value. The basic response of the vegetation to this change in environmental conditions was “a substantial southward shift of Mediterranean vegetation and a spread of evergreen and conifer forests in the northern Mediterranean.”

They write, “when precipitation is maintained at its present-day level, an evergreen forest spreads in the eastern Mediterranean and a conifer forest in Turkey.” Current xerophytic woodlands in this scenario become “restricted to southern Spain and southern Italy and they no longer occur in southern France.” In northwest Africa, “Mediterranean xerophytic vegetation occupies a more extensive territory than today and the arid steppe/desert boundary shifts southward,” as each vegetation zone becomes signifi-

cantly more verdant than it is today.

In identifying the cause of these positive developments, Cheddadi *et al.* write, “the replacement of xerophytic woodlands by evergreen and conifer forests could be explained by the enhancement of photosynthesis due to the increase of CO₂.” They also note, “under a high CO₂ stomata will be much less open which will lead to a reduced evapotranspiration and lower water loss, both for C₃ and C₄ plants,” adding “such mechanisms may help plants to resist long-lasting drought periods that characterize the Mediterranean climate.”

Contrary to what IPCC predicts for much of the world's moisture-challenged lands, the authors report, “an increase of CO₂, jointly with an increase of ca. 2°C in annual temperature would not lead to desertification on any part of the Mediterranean unless annual precipitation decreased drastically,” defining a drastic decrease as a decline of 30% or more. Equally important in this context, Hennessy *et al.* (1997) found a doubling of atmospheric CO₂ content would lead to a 5 to 10% increase in annual precipitation at Mediterranean latitudes, which is also what is predicted for most of the rest of the world. Thus the results of Cheddadi *et al.*'s study, where precipitation was held constant, may be considered a worst-case scenario, with the true vegetative response being even better than they projected.

Bellassen *et al.* (2011) write, “several parties to the United Nations Framework Convention on Climate Change (UNFCCC) are calling for ‘forward-looking baselines’” to develop country-specific scenarios based on forest age structure that can be used “to credit only the part of the forest sink going beyond business-as-usual practices.” They derived such a baseline for Europe.

Using ORCHIDEE-FM—a process-based vegetation model that differs from earlier versions of ORCHIDEE by “its explicit representation of stand growth and idealized forest management”—Bellassen *et al.* applied the model on a grid across Europe to “simulate changes in the net ecosystem productivity (NEP) of forests with and without changes in climate, CO₂ and age structure.” The six scientists report the model they used “simulates carbon stocks and volume increments comparable ... with inventory-derived estimates at country level for 20 European countries,” providing “an upwards trend of forest NEP of 1 ± 0.5 g C/m²/year between 1950 and 2000 across the EU 25,” ending with “a mean European forest NEP of 175 ± 52 g C/m²/year in the 1990s” (see Figure 4.2.2.4.1). They write, “61% of the change in NEP [over the last half of the 20th century] was attributed

Earth's Vegetative Future

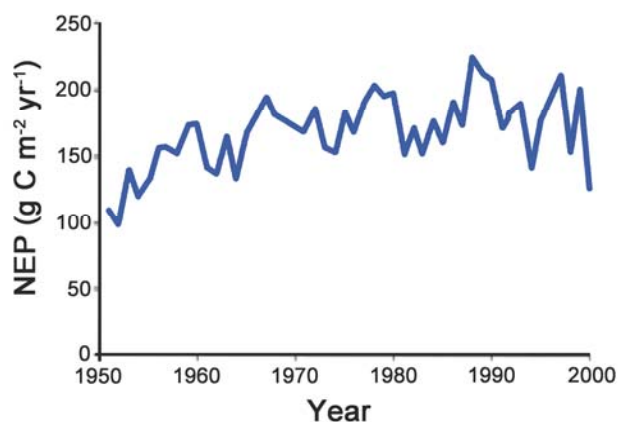


Figure 4.2.2.4.1. Simulated reconstruction of Net Ecosystem Productivity (NEP) in European forests for the years 1951–2000. Adapted from Bellassen *et al.* (2011).

to changes in CO₂, 26% to changes in climate, and 13% to changes in forest age structure.”

As intriguing as these model-based studies are, it is important to examine the issue through the lens of real-world data to see how plant productivity has actually responded to modern warming, which IPCC claims is unprecedented over the past one to two thousand years. A number of scientists have done just that.

Allen *et al.* (1999) analyzed sediment cores from a lake in southern Italy and from the Mediterranean Sea, developing high-resolution climate and vegetation datasets for this region over the past 102,000 years. They found rapid changes in vegetation were well-correlated with rapid changes in climate, such that complete shifts in natural ecosystems would sometimes occur over periods of less than 200 years. Over the warmest portion of the record (the 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 reveal the increased vegetative cover also led to less soil erosion during the more-productive woody-plant period of the Holocene. This study thus demonstrates the biosphere can respond successfully to rapid changes in climate. As the 15 researchers write, “the biosphere was a full participant in these rapid fluctuations, contrary to widely held views that vegetation is unable to change with such rapidity.” Their work also reveals warmer was always better in terms of plant growth, suggesting future warming in this region may return it to a level of biological productivity higher than it currently achieves.

Bert *et al.* (1997) calculated a 120-year (1860–

1980) history of intrinsic water-use efficiency (defined as the ratio of CO₂ assimilation rate to stomatal conductance for water vapor) for silver fir (*Abies alba* Mill.) trees, based on $\delta^{13}\text{C}$ data obtained from cores extracted from individual trees that grew within 208 pure stands in the Jura Mountains near the border that separates France and Switzerland. They found little net change in silver fir water-use efficiency from 1860 to 1930, but over the next half-century (1930 to 1980), when the atmosphere’s CO₂ concentration rose at a rate more than three times faster than its rate of rise over the earlier period, this important tree physiological property rose by approximately 30% (see Figure 4.2.2.4.2). The three researchers state their results—which were “obtained at the level of mature trees”—are “consistent with the physiological effects of increasing CO₂ concentrations as observed in controlled experiments on young seedlings” and are also “consistent with the strong increases in radial growth observed for *Abies alba* in western Europe over the past decades.”

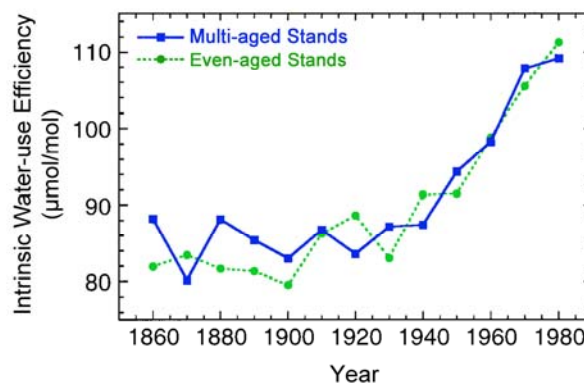


Figure 4.2.2.4.2. Intrinsic water-use efficiency (the ratio of CO₂ assimilation rate to stomatal conductance for water vapor) calculated from tree rings sampled in multi-aged and even-aged forest stands from the Jura Mountains in Eastern France for the years 1860–1980. Adapted from Bert *et al.* (1997).

Jandl *et al.* (2007) evaluated the growth rates of two Norway spruce (*Picea abies*) stands in the Bohemian Massif of Northern Austria over the prior four decades by analyzing the stem characteristics (height and diameter) of several trees they felled at two sites, and by comparing their results with data obtained from control plots of other experiments conducted there over an even longer period of time. The three researchers found “forest productivity is currently about two yield classes higher than it is in

Climate Change Reconsidered II: Biological Impacts

the regionally valid yield tables,” which were derived from data collected at the end of the nineteenth century, and “the height and diameter of dominant stems exceed expectations.” Jandl *et al.* conclude, “the sites are in a steady process of aggradation and that site productivity is rising.”

The Austrian researchers contend climate was unlikely to be the main driver of the elevated growth rates of the forest stands they studied, because neither air temperature nor precipitation were strong predictors of the increment rates at their experimental sites. In addition, they state the “ongoing improvement” was “not the mere consequence of a nitrogen-enriching effect.” Hence, they considered “the enriching effect of increasing CO₂ concentrations” and possibly changes in management practices (such as the abandonment of forest litter raking) to be the only viable alternative explanations for the steady historical increase in Norway spruce productivity at the sites they studied.

Leal *et al.* (2008) discovered “a very clear change in the sensitivity of the growth rate of [black pine (*Pinus nigra*)] tree stems to water availability in the late 20th century” in the Vienna basin of Austria in the European Eastern Alps, noting “trees previously sensitive to spring-summer drought show a lack of response to this climatic parameter in recent decades.” They explain “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.” They also 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 conclude by suggesting 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 different tree species, another indication of the propensity of the ongoing rise in the atmospheric CO₂ content to promote a greening of the Earth.

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 the southern limit of the distribution of the species.” This inventory “included a total of 10,664 plots randomly distributed throughout the forested area of Catalonia.” Scots pine was present in 30.2% of the plots and was the dominant tree species in 18.4%.

The researchers found “an overall increase of 84% in Scots pine BAI [basal area increment] during the 20th century (see Figure 4.2.2.4.3), consistent with most previous studies for temperate forests.” They state “this trend was associated with increased atmospheric CO₂ concentration,” which they characterize as “a fertilization effect.” The five scientists note over the same time period there was “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.” However, they found “its magnitude was not enough to counteract the fertilization effect.”

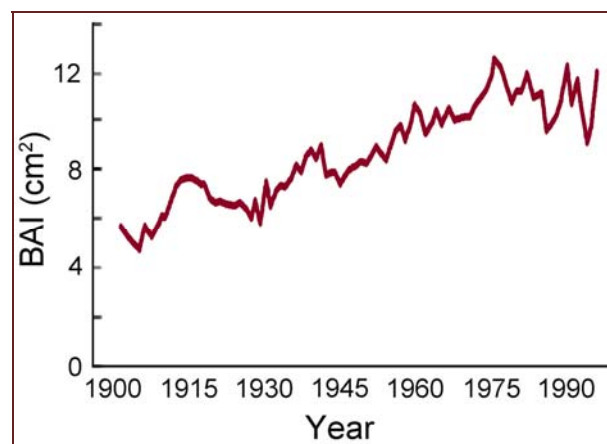


Figure 4.2.2.4.3. Basal area increment (BAI) for Scots pine trees growing in NE Spain during the years 1901–1997. Adapted from Martinez-Vilalta *et al.* (2008).

Noting “protected areas provide excellent opportunities for [determining] baseline descriptions and trends that ... can be used to evaluate the impact of global environmental change on terrestrial ecosystem functioning,” Alcaraz-Segura *et al.* (2008) employed satellite-derived normalized difference vegetation index (NDVI) data—which provide a measure of net primary production, “the most integrative indicator of ecosystem functioning”—to “evaluate the impact of global environmental change on terrestrial ecosystem functioning of [Spain’s] national parks.” This information provides a sound basis for determining what could have been expected

to have occurred throughout the rest of the country and much of Europe (Julien *et al.*, 2006) independent of confounding effects not related to global environmental change.

The four researchers from Argentina, Spain, and the United States report, “most parks showed areas with positive NDVI trends that tended to have higher proportions of Mediterranean coniferous and mixed forests, oro-Mediterranean scrublands, heathlands, maquis and garrigues,” whereas “negative trends were scarce.” Alcaraz-Segura *et al.* conclude “protected areas are changing in the short term and, at least in terms of vegetation greenness, they are changing in a directional way,” such that “a large part of the Spanish National Parks is intercepting more photosynthetically active radiation than in the past.”

Hallinger *et al.* (2010) studied male plants of the medium-sized *Juniperus nana* shrub at a site just three kilometers from the Abisko Scientific Research Station (68°21'N, 18°49'E) in the Northern Swedish Scandes. They collected the main stems of five to eight shrubs every hundred meters of elevation until the shrub zone ended. Ring-width measurements on these stems were then performed, they write, “to measure radial and vertical growth, to track growth changes over time, to age the shrub individuals and to correlate annual shrub growth with climate,” the characteristics of which were derived from records of the nearby Abisko Station.

The three researchers say their analysis “documented a distinct increase in radial and vertical growth rates of *J. nana* shrubs during recent decades in the subalpine zone of North Sweden” (see Figure 4.2.2.4.4), and “the age structure of shrubs along the elevational gradient provides evidence that an upslope advance of the altitudinal shrubline is underway.” They “observed significant, strong and stable correlations between annual ring width and summer temperatures (June, July, August),” and “the acceleration of radial and vertical growth since 1970 also coincides with the recent three decades of rising arctic air temperatures and the warming trend of 0.2°C per decade for the average temperature since 1956 at Abisko.” These findings, they write, add to the “mounting evidence that shrubs are expanding into alpine and arctic areas because of climate warming,” and “this expansion occurs in both evergreen and deciduous shrub types,” citing Forbes *et al.* (2009).

Kullman (2010a) presents “an integrative review of results from long-term monitoring of subalpine/alpine vegetation” in the Swedish Scandes, from which he derives “tentative projections of landscape transformations in a potentially warmer future,” based

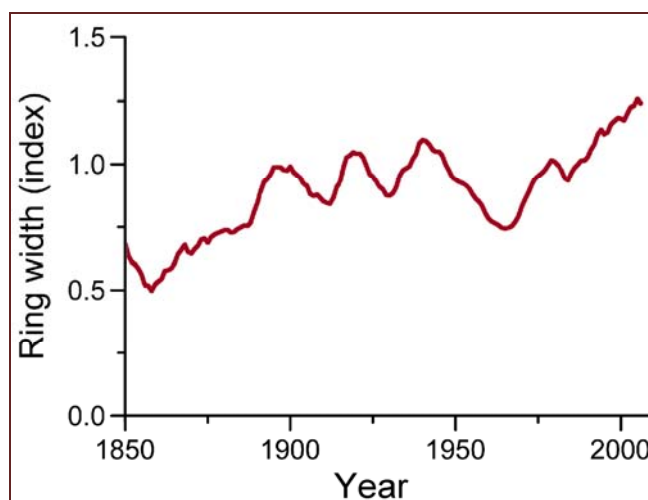


Figure 4.2.2.4.4. Indexed radial growth of juniper trees in the northern Swedish Scandes during the years 1850–2006, smoothed with a 10-year filter. Adapted from Hallinger *et al.* (2010).

on “actual observations and paleoecological data (Kullman and Kjallgren, 2006; Kullman 2006).” The professor of physical geography at Sweden’s Umea University writes post-Little Ice Age warming has broken “a multi-millennial trend of plant cover retrogression” and “floristic and faunal impoverishment, all imposed by progressive and deterministic neoglacial climate cooling.” He reports the “upper range margin rise of trees and low-altitude (boreal) plant species, expansion of alpine grasslands and dwarf-shrub heaths are the modal biotic adjustments during the past few decades, after a century of substantial climate warming.” Currently, “alpine plant life is proliferating, biodiversity is on the rise and the mountain world appears more productive and inviting than ever.” Kullman notes “in contrast to model predictions, no single alpine plant species has become extinct, neither in Scandinavia nor in any other part of the world in response to climate warming over the past century,” citing, in addition to his own studies, Pauli *et al.* (2001, 2007), Theurillat and Guisan (2001), and Birks (2008).

In a contemporaneous study published in the *Nordic Journal of Botany*, Kullman describes how extensive the recent proliferation of plant life has been (Kullman, 2010c). He reports the findings of species inventories he conducted on the uppermost 20 meters of four high-mountain summits in the Swedish Scandes (Kullman 2007a,b), the results of which he compared with the findings of “historical species inventories from the early 1950s, executed by a highly competent and experienced botanist (Kilander,

1955),” which “can be seen as an evaluation of a full-scale ‘natural experiment’ (cf. Grabherr *et al.*, 2001).”

Kullman (2010c) writes the species pools at the tops of the studied mountains have “increased by 60–170% since the 1950s,” “some of the invading species are new to the alpine tundra, with more silvine and thermophilic properties than the extant alpine flora,” and “not a single species of the original flora has disappeared from any of the summits.” Kullman concludes, “the alpine flora appears to be more adaptive and responsive to climate change than generally believed,” and “overall, a richer, greener and more productive alpine world has emerged in the wake of the recent climate warming episode (Kullman, 2010a, 2010b).”

Rundqvist *et al.* (2011) documented “rapid and substantial increases in the abundance of prominent tree and shrub species near [the] tree-line and forest-line in sub-Arctic Sweden,” on an east-facing slope of the Slattatjakka/Njulla mountains (68°21′N, 18°49′W) in the Abisko Valley about 200 km north of the Arctic Circle in Sweden. They “recorded an invasion by a thermophilic tree species not present in the plots 34 years ago.”

The seven Swedish scientists say their observations mesh well with those of many other researchers, noting “there is an indication that the shrub layer near the tree-line has expanded, since the 1930s, in the Abisko area (Enquist *et al.*, 1933; Sandberg, 1963),” and “data from Canada, Fennoscandia, Alaska and Russia reveal that there is a Pan-Arctic expansion of shrubs and trees in progress (e.g. Kullman, 2002; Tommervik *et al.*, 2004; ACIA, 2005; Tape *et al.*, 2006; Karlsson *et al.*, 2007; Olofsson *et al.*, 2009; Hallinger *et al.*, 2010; Hedenas *et al.*, 2011).” They state the change in shrubs and small trees they observed is “consistent with anticipated changes due to climate change and reduced herbivory,” and this change “could be interpreted as an ongoing natural re-establishment of plants at higher altitudes due to a natural increase in the temperature since the ‘Little Ice Age’ (Kammer *et al.*, 2007).”

Hedenas *et al.* (2011) state, “during the last 15 years, there has been an increasing focus on how climate change has and will affect

the distribution and extent of ecosystems around the globe including alpine and Arctic areas (e.g., Callaghan *et al.*, 2005).” They report, “field studies and remote sensing have revealed a recent increase in altitude of the tree line (e.g., Kullman, 2002),” as well as “an extension and increased cover of mountain birch forest (Tommervik *et al.*, 2009; Rundqvist *et al.*, 2011).” They say Tommervik *et al.* determined “tree biomass has doubled over a 43-year period, within an area of Finnmarksvidda, and Rundqvist *et al.* have observed an increased density and cover of mountain birch in the treeline over the last three decades, within an area near Abisko village.”

Hedenas *et al.* in 2010 re-surveyed shrub, tree, and vegetation data at 549 plots grouped into 61 clusters originally surveyed in 1997 in two areas close to the Abisko village approximately 200 km north of the Arctic Circle at 68°20′N, 18°50′E. They found “tree basal area and biomass increased by 19% between 1997 and 2010 with the main increase occurring in established birch forest” (see Figure 4.2.2.4.5), and this result “concurs with the results of other studies which suggest that there has been a general increase in cover and biomass of trees and shrubs in sub-Arctic and Arctic areas,” citing Sturm *et al.* (2001), Tape *et al.* (2006), Danby and Hik (2007), Forbes *et al.* (2010), Hallinger *et al.* (2010), and Van Bogaert *et al.* (2011). They found the 19% net

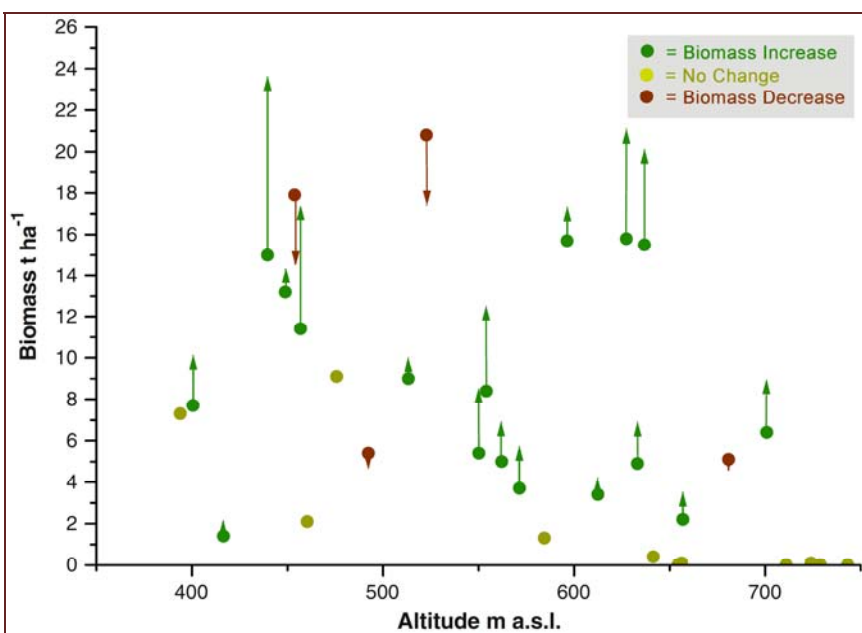


Figure 4.2.2.4.5. Change in mean tree biomass by altitude during the years 1997–2010 from various locations throughout the Swedish sub-Arctic. Colors reveal the direction of the change (green = biomass increase, yellow = no change, and red = biomass decrease), and arrows indicate the magnitude of the change over the 13-year period. Adapted from Hedenas *et al.* (2010).

increase in biomass occurred in spite of the increased browsing pressure provided by a growing reindeer population over the period of their study, as well as periodic outbursts of geometrid moths, which severely defoliated the birch trees in their study area in 2004 (Babst *et al.*, 2010). They write, “it has been suggested that increased nutrient availability associated with higher soil temperatures, and a longer growing season could underpin increased tree and shrub abundance and biomass in the Arctic (e.g., Chapin, 1983; Weih and Karlsson, 1997; Hartley *et al.*, 1999),” as a result of “a delayed re-expansion of shrubs and trees following the ‘Little Ice Age,’” as suggested by Grubb (2008).

Noting forests are exposed to a changing environment and “responses to recent climate change start to become visible if observation periods become long enough,” Pilegaard *et al.* (2011) present the results of continuous CO₂ flux measurements they made above a mature Danish beech stand in the Lille Bogeskov forest located near Soro on the island of Zealand (55°29'13"N, 11°38'45"E) during the years 1996–2009, describing the long-term changes they observed and relating them to possible causes.

They report observing “significant linear trends of increasing gross ecosystem exchange (GEE: 29 g C/m²/year) and increasing net ecosystem exchange (NEE: 23 g C/m²/year), while the positive trend for ecosystem respiration (RE: 5 g C/m²/year) was not significant.” They also state, “the length of the carbon uptake period increased by 1.9 day/year, whereas there was a non-significant increase of 0.3 day/year in the leafed period,” which means, they write, “the leaves stay active longer.” They say “the increase in the carbon uptake period explained only part of the increasing NEE (9 gC/m²/year).” And noting “the maximum rate of photosynthetic assimilation increased by 15% during the 14-year period,” they speculate the increase in canopy carbon uptake capacity “could be due to a combination of [the] increase in atmospheric CO₂, higher summer precipitation, and increased availability of nitrogen.”

Lopatin *et al.* (2006) collected discs and cores from 151 Siberian spruce trees and 110 Scots pines in the Komi Republic in the northeast European sector of Russia, from which they developed ring-width chronologies that revealed yearly changes in forest productivity. They developed satellite-based time series of NDVI for the months of June, July, and August of the years 1982–2001, correlated their site-specific ring-width-derived productivity histories with same-site NDVI time series, and used the resulting relationship to establish six regional forest pro-

ductivity histories for the years 1982–2001. They compared the six regional productivity trends over this period with corresponding-region temperature and precipitation trends. For all six vegetation zones of the Komi Republic, this work indicates the 1982–2001 trends of integrated NDVI values from June to August were positive, and the “increase in productivity reflected in [the] NDVI data [was] maximal on the sites with increased temperature and decreased precipitation.”

The three scientists write, “several studies (Riebsame *et al.*, 1994; Myneni *et al.*, 1998; Vicente-Serrano *et al.*, 2004) have shown a recent increase in vegetation cover in different world ecosystems.” What is special about their study, as they describe it, is “in Europe, most forests are managed, except for those in north-western Russia [the location of their work], where old-growth natural forests are dominant (Aksenov *et al.*, 2002).” They conclude “productivity during recent decades also increased in relatively untouched forests,” where non-management-related “climate change with lengthening growing season, increasing CO₂ and nitrogen deposition” are the primary determinants of changes in forest productivity.

Julien *et al.* (2006) “used land surface temperature (LST) algorithms and NDVI [normalized difference vegetation index] values to estimate changes in vegetation on the European continent between 1982 and 1999 from the Pathfinder AVHRR [advanced very high resolution radiometer] Land (PAL) dataset.” This analysis revealed arid and semi-arid areas (Northern Africa, Southern Spain, and the Middle East) have seen their mean LST increase and NDVI decrease, and temperate areas (Western and Central Europe) have suffered a slight decrease in LST but a more substantial increase in NDVI, especially in Germany, the Czech Republic, Poland, and Belarus. In addition, parts of continental and Northern Europe experienced either slight increases or decreases in NDVI while LST values have decreased. The Dutch and Spanish researchers conclude, over 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.”

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Climate Change Reconsidered II: Biological Impacts

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4.2.2.5 North America

As in Asia, a significant amount of terrestrial productivity research has been conducted for locations in North America. We group that research into these subsections: *Entire Continent*, *High Latitude Regions*, *Eastern USA*, *Central USA*, and *Western USA*.

4.2.2.5.1 Entire Continent

Zhou *et al.* (2001) determined the satellite-derived normalized difference vegetation index (NDVI) rose by 8.44% over the North American continent between 1981 and 1999. Noting the NDVI “can be used to proxy the vegetation’s responses to climate changes because it is well correlated with the fraction of photosynthetically active radiation absorbed by plant canopies and thus leaf area, leaf biomass, and potential photosynthesis,” Zhou *et al.* suggest the increases in plant growth and vitality implied by their NDVI data were driven primarily by increases in near-surface air temperature. Ahlbeck (2002) suggests the observed upward trend in NDVI was primarily driven by the rise in atmospheric CO₂ content over the period, since warming was rather muted in North America and in the United States in particular, where temperatures may have declined throughout the eastern part of the country over the period of the study. It is likely both parameters played a role in the observed productivity increase, although the CO₂ increase was more likely the predominant one given the lack of temperature increase over the period of time under study.

Hicke *et al.* (2002) computed net primary productivity (NPP) over North America for the years 1982–1998 using the Carnegie-Ames-Stanford Approach (CASA) carbon cycle model driven by a satellite NDVI record at 8 km spatial resolution. They found NPP increases of 30% or more occurred across the continent from 1982 to 1998. During this period,

the air’s CO₂ concentration rose by 25.74 ppm, as calculated from the Mauna Loa data of Keeling and Whorf (1998), which is 8.58% of the 300 ppm increase often used as a reference for expressing plant growth responses to atmospheric CO₂ enrichment. Consequently, for herbaceous plants that display NPP increases of 30–40% in response to a 300 ppm increase in atmospheric CO₂ concentration, the CO₂-induced NPP increase experienced between 1982 and 1998 would have been 2.6–3.4%. Similarly, for woody plants that display NPP increases of 60–80% in response to a 300 ppm increase in atmospheric CO₂ (Saxe *et al.*, 1998; Idso and Kimball, 2001), the expected increase in productivity between 1982 and 1998 would have been 5.1–6.9%. As both of these NPP increases are considerably less than the 30% or more observed by Hicke *et al.*, additional factors must have helped to stimulate NPP over this period. Those factors may have included concomitant increases in precipitation and air temperature, the tendency for warming to lengthen growing seasons and enhance the aerial fertilization effect of rising CO₂ concentrations, increasingly intensive crop and forest management, increasing use of genetically improved plants, the regrowth of forests on abandoned cropland, and improvements in agricultural practices such as irrigation and fertilization.

Lim *et al.* (2004) correlated the monthly rate of relative change in NDVI, derived from advanced very high resolution radiometer (AVHRR) data, with the rate of change in atmospheric CO₂ concentration during the natural vegetation growing season in three eco-region zones of North America (Arctic and sub-Arctic zone, humid temperate zone, and dry and desert zone, which they further subdivided into 17 regions) during the years 1982–1992. They explored the temporal progression of annual minimum NDVI during the years 1982–2001 throughout the eastern humid temperate zone of North America. In all of the regions but one, according to the researchers, “δCO₂ was positively correlated with the rate of change in vegetation greenness in the following month, and most correlations were high,” which they say is “consistent with a CO₂ fertilization effect” of the type observed in “experimental manipulations of atmospheric CO₂ that report a stimulation of photosynthesis and above-ground productivity at high CO₂.” 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.* say rising CO₂ could “increase minimum greenness by stimulating photosynthesis at

the beginning of the growing season,” citing Idso *et al.* (2000), who discovered that although new spring branch growth of sour orange trees began on exactly the same day of the year in both ambient (400 ppm) and CO₂-enriched (700 ppm) open-top chambers, the rate of new-branch growth was initially vastly greater in the CO₂-enriched trees. Three weeks after branch growth began in the spring, 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, and on a per-tree basis, more than six times more new-branch biomass was produced on the CO₂-enriched trees, before declining to an approximate 80% stimulation typical of the bulk of the growing season.

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, 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 yearly minimum greenness should have increased by an amount 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, the result is an increase of just over 40%, indicating Lim *et al.*'s data are not only qualitatively consistent with their hypothesis but on the mark quantitatively as well.

Xiao and Moody (2004) examined the responses of the normalized difference vegetation index integrated over the growing season (gNDVI) to annual and seasonal precipitation, maximum temperature ($T_{\max}$), and minimum temperature ($T_{\min}$) over an 11-year period (1990–2000) for six biomes in the conterminous United States (evergreen needleleaf forest, deciduous broadleaf forest, mixed forest, open shrubland, woody savanna, and grassland), focusing on within- and across-biome variance in long-term average gNDVI and emphasizing the degree to which this variance is explained by spatial gradients in long-term average seasonal climate. They found the greatest positive climate-change impacts on biome productivity were caused by increases in spring, winter, and fall precipitation and increases in fall and spring temperature, especially $T_{\min}$, which historically has increased at roughly twice the rate of $T_{\max}$ in the United States. They write, “if historical climatic

trends and the biotic responses suggested in this analysis continue to hold true, we can anticipate further increases in productivity for both forested and non-forested ecoregions in the conterminous US, with associated implications for carbon budgets and woody proliferation.”

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4.2.2.5.2 High Latitude Regions

- 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.

For many years, some researchers argued rising temperatures would change the Arctic from a carbon sink to a carbon source, further exacerbating the cause of ecosystem change—regional warming—by adding to the atmosphere's burden of greenhouse gases and hastening that portion of the biosphere's inevitable degradation (Oechel *et al.*, 1993, 1995).

In the early to mid-1970s, for example, when the first carbon balance studies of Alaskan Arctic ecosystems were conducted, wet-sedge communities and moist-tussock tundra were observed to be net sinks of carbon. By the mid-1980s and early 1990s, however, following significant increases in air temperature and surface water deficit, both ecosystems had become net sources of carbon. Then, between 1992 and 1996, in response to further warming and drying that resulted, Oechel *et al.* (2000a) write, in “the highest average summer temperature and surface water deficit observed for the entire 39-year period,” both ecosystems' net summer releases of CO₂ to the atmosphere declined, and they became CO₂ sinks.

How did it happen? Oechel *et al.* say their observations indicated “a previously undemonstrated capacity for ecosystems to metabolically adjust to long-term (decadal or longer) changes in climate.”

But how did *that* happen? Was there help along the way from the concomitant rise in atmospheric CO₂ content and its aerial fertilization and anti-transpirant effects? Although these well-documented consequences of atmospheric CO₂ enrichment are known to enable plants to better respond to the environmental challenges of warming and drying, Oechel *et al.* downplayed these effects, instead noting other plausible possibilities.

First, there is the likelihood that during the initial stages of warming and soil drying, younger and more labile carbon would be rapidly decomposed, shifting the net summer carbon balance of the ecosystems from carbon sequestration to carbon evolution. After this initial perturbation, Oechel *et al.* suggest “enhanced rates of net nitrogen-mineralization should eventually stimulate rates of gross primary production and atmospheric CO₂ sequestration.”

Another possibility is a gradual shift in plant species towards more productive types that would further reduce the large initial carbon losses over time. The researchers state, “there is evidence that the relative abundance of deciduous shrubs has increased in response to climate change over the past 1–2 decades in Alaskan moist-tussock tundra ecosystems,” which is also expected to occur as a consequence of the ongoing rise in atmospheric CO₂ content. Capers and Stone (2011), for example, report, in response to rising air temperatures, “trees have established where they did not previously occur, both in alpine areas (Wardle and Coleman, 1992; Peterson, 1994; Kullman, 2001, 2002), and in arctic tundra (Lescop-Sinclair and Payette, 1995; Danby and Hik, 2007),” while “increasing shrub abundance also has been reported in alpine (Klanderud and Birks, 2003) and arctic locations (Sturm *et al.*, 2001; Tape *et al.*, 2006; Wilson and Nilsson, 2009).”

Noting “canopy-forming shrubs are reported to be increasing at sites around the circumpolar Arctic,” Myers-Smith *et al.* (2011) examined historic photographs, repeated vegetation surveys, and conducted monitoring of long-term plots on Canada's Herschel Island (69.57°N, 138.91°W) to see what had occurred over the past century on this 100-km² parcel of land just off the western Arctic coast of Canada's Yukon Territory. They “found evidence of increases of each of the dominant canopy-forming willow species (*Salix richardsonii*, *Salix glauca* and *Salix pulchra*), during the twentieth century,” along with evidence “the majority of willow patches for each of these species became established between 1910 and 1960,” “with stem ages and maximum growth rates indicating that some patches could have established as late as the 1980s.”

The seven scientists note their observations are an example of the twentieth-century greening of the Circumpolar Arctic, noting “recent evidence indicates an expansion of canopy-forming shrubs at sites on the North Slope of Alaska (Sturm *et al.*, 2001; Tape *et al.*, 2006), on the coast of the Northwest Territories (Lantz *et al.*, 2009), in Northern Quebec (B. Tremblay *et al.*, personal communication), and in northern Russia (Forbes *et al.*, 2010a).” They write, “in Arctic Alaska, canopy cover of alder shrubs has increased by 14–20% on average within the last 40 years, with increases of up to 80% in some areas (Tape *et al.*, 2006).” Also, they note, “studies of population structures of shrub and tree species indicate advancing of shrubs up slopes in alpine tundra ecosystems in subarctic Sweden (Hallinger *et al.*, 2010),” as well as in sites in Norway (Hofgaard *et*

al., 2009), further noting “local indigenous Nenets people in the western Russian Arctic report increasing willow shrubs (Forbes *et al.*, 2010b)” and “similar observations of vegetation change by Inuit have been reported in Arctic Canada (Thorpe *et al.*, 2002).”

The team of Canadian researchers also states “pollen records indicate willows were widespread in Arctic ecosystems during warmer periods after the last glacial maximum (Brubaker *et al.*, 1983; Bigelow *et al.* (2003).” These observations seem to suggest the entire Circumpolar Arctic is in the process of returning to conditions of an earlier period when that part of the planet was a good deal greener—and a good deal livelier—than it has been for a long, long time.

Goetz *et al.* (2005) also documented increased plant growth in the high latitudes of North America. They transformed satellite-derived NDVI data obtained across boreal North America (Canada and Alaska) for the years 1982–2003 into photosynthetically active radiation absorbed by green vegetation and treated the result as a proxy for relative June–August gross photosynthesis (Pg), stratifying the results by vegetation type and comparing them with spatially matched concomitant trends in surface air temperature data. They found area-wide tundra experienced a significant increase in Pg in response to a similar increase in air temperature, and “this observation is supported by a wide and increasing range of local field measurements characterizing elevated net CO₂ uptake (Oechel *et al.*, 2000b), greater depths of seasonal thaw (Goulden *et al.*, 1998), changes in the composition and density of herbaceous vegetation (Chapin *et al.*, 2000; Epstein *et al.*, 2004), and increased woody encroachment in the tundra areas of North America (Sturm *et al.*, 2001).” For interior forest, they found no significant increase in air temperature and essentially no change in Pg, with the last data point of the series being essentially indistinguishable from the first. This seemingly aberrant observation is in harmony with the fact that at low temperatures the growth-promoting effects of increasing atmospheric CO₂ levels are often very small or even nonexistent (Idso and Idso, 1994), which is what appears to have been the case with North American boreal forests over that time period. As a result, the tundra ecosystems of Canada and Alaska exhibited increasing productivity over the past couple of decades, but their boreal forests did not.

Ropars and Boudreau (2012) state, “Myneni *et al.* (1997, 1998) were the first to report evidence of the pan-Arctic increase in vegetation cover,” noting, “by analyzing worldwide NDVI [normalized difference

vegetation index] trends between 1981 and 1991, they showed that the greatest increase in photosynthetic activity occurred in regions above 50°N,” and “since then, this phenomenon has been observed for different regions,” including Alaska (Silapaswan *et al.*, 2001; Jia *et al.*, 2003; Verbyla, 2008), Russia (Forbes *et al.*, 2010a), and Western Canada (Olthof and Pouliot, 2010), over a longer time span (Jia *et al.*, 2003; Goetz *et al.*, 2005; Verbyla, 2008; Forbes *et al.*, 2010a; Olthof and Pouliot, 2010), and at a better resolution (Jia *et al.*, 2003; Olthof and Pouliot, 2010). Focusing on an area near the Boniface River research station 35 km east of Hudson Bay and 10 km south of the treeline in subarctic Quebec (Canada), Ropars and Boudreau (2012) evaluated changes in shrub cover over a half-century, comparing two aerial photographs taken in July 1957 and a satellite image of the same area obtained in July 2008.

They found “both hilltops and terraces recorded an increase in shrub cover” (Figure 4.2.2.5.2.1), and “the increase was significantly greater on terraces than on hilltops (21.6% versus 11.6%),” further noting “this finding corroborates other studies using a similar method conducted in different regions of the Arctic,” including Alaska (Sturm *et al.*, 2001; Tape *et al.*, 2006), northern Quebec (Tremblay, 2010), and Russia (Forbes *et al.*, 2010), and studies that revealed a major increase of the NDVI over the past few decades (Jia *et al.*, 2003; Verbyla, 2008). Ropars and Boudreau conclude, “according to ground truthing, the shrub cover densification is associated mainly with an increase of *Betula glandulosa* Michx”—more commonly known as dwarf birch—and “the

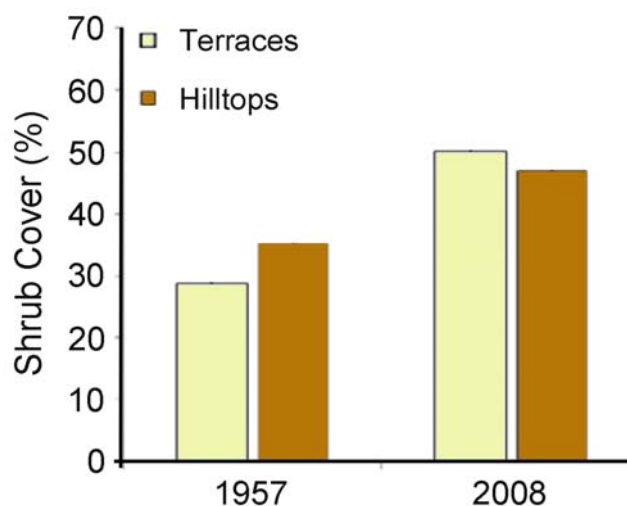


Figure 4.2.2.5.2.1. Percent shrub cover on terraces and hilltops in subarctic Quebec, Canada in 1957 and 2008. Adapted from Ropars and Boudreau (2012).

numerous seedlings observed during the ground truthing suggest that shrub densification should continue in the future.”

Hudson and Henry (2009) note the Arctic has warmed by about 1.6°C over the past four decades, citing McBean *et al.* (2005), and this temperature increase has “led the Arctic Climate Impact Assessment (ACIA) and Intergovernmental Panel on Climate Change (IPCC) to predict tundra ecosystems will be particularly threatened by climate change [i.e., warming] over the next century.” To provide real-world data with which to judge those predictions, Hudson and Henry measured biomass and composition changes in a heath community dominated by several vascular plants and bryophytes at an 8-km² coastal lowland adjacent to Alexandra Fiord on the east-central coast of Ellesmere Island, Nunavut, Canada. They did so over a period of 13 years (1995–2007), using a point-intercept method in permanent plots, and over a period of 27 years (1981–2008) using a biomass harvest comparison.

“Results from both methods,” the Canadian scientists write, “indicate the community became more productive over time,” that “bryophyte and evergreen shrub abundances increased,” and “deciduous shrub, forb, graminoid, and lichen cover did not change,” so “species diversity also remained unchanged.” Hudson and Henry further report, “satellite-based remote sensing models, such as green trends derived from the normalized difference vegetation index (NDVI; e.g., Myneni *et al.*, 1997; Zhou *et al.*, 2001; Stow *et al.*, 2004; Verbyla, 2008), and global vegetation and ecosystem process simulations of the terrestrial carbon cycle (e.g., Kimball *et al.*, 2006; Zhang *et al.*, 2008), indicate increasing trends in vegetation photosynthetic activity and net primary production in the Arctic over the past several decades.” They write, “it is likely that warming directly increased plant growth and reproduction and indirectly increased resource supply,” noting “increased temperatures also lengthened the growing season, increased soil temperature, deepened the active [soil] layer, and consequently may have influenced nutrient uptake in the plant community.”

Hudson and Henry (2010) used open-top chambers to passively warm an evergreen-shrub heath by 1.0–1.3°C over a period of 15 years, during which time there was also a significant background warming, at the same location at Alexandra Fiord, Nunavut, Canada (79°N), an effort they describe as “the longest-running passive warming experiment in the Canadian Arctic.” They report, “experimental

warming did not strongly affect vascular plant cover, canopy height or species diversity, but it did increase bryophyte cover by 6.3% and decrease lichen cover by 3.5%,” although “temporal changes in plant cover were more frequent and of greater magnitude than changes due to experimental warming,” as pointed out in their study published the year prior and highlighted above.

Madsen *et al.* (2011) compared the aboveground biomass of the graminoid marsh vegetation observed on Jameson Land, low Arctic, East Greenland in surveys conducted in 1982–1984 with similar surveys conducted in 2008, to see what had happened over the intervening period of significant global—and local—warming. The five researchers say the data they obtained in 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 1984. 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), adding “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.”

Villarreal *et al.* (2012) write, “climate warming is pronounced at high northern latitudes (ACIA, 2005; Serreze, 2010),” and “time series analysis of satellite remote sensing between 1982 and 2008 suggests that there has been a greening of arctic landscapes,” citing Bhatt *et al.* (2010). They note “remotely detected changes in the normalized difference vegetation index (NDVI) of the arctic coastal plain near Barrow, Alaska, appear to be among the most dramatic recorded for much of the Arctic,” again citing Bhatt *et al.* (2010).

Noting “there is a general scarcity of ground-based studies that examine vegetation change in the Arctic over decade time scales,” Villarreal *et al.* in 1999, 2008, and 2010 resampled for species cover and presence 330 marked plots at 33 sites established in 1972, as part of the International Biological Program, in an area near Barrow at the northernmost point of the Alaskan Coastal Plain (71°18′N, 156°40′W).

Over the 38-year study period, they found, ecosystem diversity “increased for most plant communities, and wetter communities changed more than dry and moist plant communities.” These findings, they say, support other observational

Earth's Vegetative Future

studies, such as Wilson and Nilsson (2009). Of the 19 species that made up more than 80% of the overall relative cover, they say five had higher relative cover in 2010 than in 1972. Their results for changes in shrub cover “are somewhat consistent with other long-term observations and experimental studies that report increased shrub abundance (Myers-Smith *et al.*, 2011; Tape *et al.*, 2006; Walker *et al.*, 2006; Sturm *et al.*, 2001),” as well as warming-induced “treeline advancement (Lloyd, 2005; Danby and Hik, 2007).”

Tape *et al.* (2006) analyzed repeat photography data from a photo study of the Colville River, Alaska conducted between 1945 and 1953, plus 202 new photos of the same sites obtained between 1999 and 2002, to determine the nature of shrub expansion in that region over the past half-century. They found “large shrubs have increased in size and abundance over the past 50 years, colonizing areas where previously there were no large shrubs.” They say their review of plot and remote sensing studies confirms “shrubs in Alaska have expanded their range and grown in size” and “a population of smaller, intertussock shrubs not generally sampled by the repeat photography, is also expanding and growing.” They conclude, “these three lines of evidence allow us to infer a general increase in tundra shrubs across northern Alaska.”

Tape *et al.* are inclined to attribute their findings to large-scale pan-Arctic warming, and from analyses of logistic growth curves, they estimate the expansion began about 1900, “well before the current warming in Alaska (which started about 1970).” Hence, they conclude “the expansion predates the most recent warming trend and is perhaps associated with the general warming since the Little Ice Age.” These inferences appear reasonable, although the 80 ppm increase in the atmosphere’s CO₂ concentration since 1900 likely played a role in the shrub expansion as well.

Elmendorf *et al.* (2012) note, “remote-sensing data indicate contemporary climate warming has already resulted in increased productivity over much of the Arctic,” and “normalized difference vegetation index (NDVI) values have increased over the tundra biome in recent years, indicating a greening of the tundra ecosystem coincident with climate warming trends,” citing Pouliot *et al.* (2009) and Bhatt *et al.* (2010). Because “plot-based evidence for vegetation transformation is not widespread,” they analyzed “change in tundra vegetation surveyed between 1980 and 2010 in 158 plant communities spread across 46 locations throughout the Arctic,” the majority of

which were in North America.

The 47 researchers from 12 countries found “biome-wide trends of increased height of the plant canopy and maximum observed plant height for most vascular growth forms; increased abundance of litter; increased abundance of evergreen, low-growing and tall shrubs, and decreased abundance of bare ground.” These data confirm the findings of prior satellite assessments of the vegetative transformation of Earth’s northernmost collection of landscapes over the past three decades, attributable not only to global warming but also to the aerial-fertilization and water-use-efficiency-enhancing effects of atmospheric CO₂ enrichment.

Wang *et al.* (2006) examined ring-width development in cohorts of young and old white spruce 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 younger trees slightly removed from the islands survived. “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,” while “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 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.

The researchers found the slope of the linear regression describing the rate of growth of the ring-width residuals for the later period (when the air’s CO₂ concentration was 15% greater and its rate-of-rise 285% greater) was more than twice that of the earlier period. The researchers say 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.” They note, “these results are consistent with expectations for CO₂-fertilization effects,” saying “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 the “postdrought growth response was much stronger for young trees (1970–1999) compared with old trees at the same development stage (1900–1929),” and the “higher atmospheric CO₂ concentration in the period from 1970–1999 may have helped white spruce recover from severe drought.” They report 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.”

The results presented here for the high latitude region of North America paint a picture of the planet’s terrestrial vegetation opposite of that promulgated by the models used by IPCC. Instead of a world heading toward environmental degradation and extinction, 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.

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4.2.2.5.3 Eastern USA

- 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.

Pan *et al.* (2009) examined “how changes in atmospheric composition (CO₂, O₃ and N deposition), climate and land-use affected carbon dynamics and sequestration in Mid-Atlantic temperate forests during the 20th century,” modifying and applying “a well-established process-based ecosystem model with a strong foundation of ecosystem knowledge from experimental studies.” They validated the model “using the U.S. Forest Inventory and Analysis (FIA) data.”

For previously harvested and currently regrowing forests, the calibrated model produced changes in net ecosystem productivity (NEP) due to observed changes in N deposition (+32%), CO₂ (+90%), O₃

Earth's Vegetative Future

(-40%), CO₂ + O₃ (+60%), CO₂ + N deposition (+184%), and CO₂ + N deposition + O₃ (+138%). Corresponding changes in NEP for undisturbed forests were +18%, +180%, -75%, +78%, +290%, and +208%. They report “the ‘fertilization’ effect of N deposition mainly stimulates carbon allocation to short-lived tissues such as foliage and fine roots,” but “the ‘fertilization’ effect by elevated CO₂ likely enhances more sustainable carbon storage such as woody biomass (including coarse roots).”

The four USDA Forest Service scientists say their findings indicate “the change in atmospheric composition, particularly elevated CO₂, will gradually account for more of the carbon sink of temperate forests in the Mid-Atlantic region,” and “such a significant ‘fertilization effect’ on the forest carbon sequestration could eventually result in a ‘greener world’ after a long period of chronic change in atmospheric composition and cumulative impact.”

Westfall and Amateis (2003) used mean height measurements made at three-year intervals over a period of 15 years from dominant stands of loblolly pine plantations growing at 94 locations across the southeastern United States to calculate a site index related to the mean growth rate for each of the five three-year periods. They expected the index would increase monotonically if growth rates were being enhanced above normal by some monotonically increasing factor that promotes growth. The researchers found, the “mean site index over the 94 plots consistently increased at each re-measurement period,” suggesting “loblolly pine plantations are realizing greater than expected growth rates.” They found the growth rate increases grew larger with each succeeding three-year period.

Westfall and Amateis considered attributing their findings to increases in temperature and precipitation in addition to rising atmospheric CO₂ concentrations, but they report a review of annual precipitation amounts and mean ground surface temperatures showed no trends in these factors over the period of their study. They also say if increased nitrogen deposition were the cause, “such a factor would have to be acting on a regional scale to produce growth increases over the range of study plots.” Hence, they favor the aerial fertilization effect of atmospheric CO₂ enrichment as being responsible for the accelerating pine tree growth rates.

McMahon *et al.* (2010) state, “there are

indications that forest biomass accumulation may be accelerating where nutrients and water are not limiting,” citing Myneni *et al.* (1997), Lewis *et al.* (2004), Lewis *et al.* (2009), Boisvenue and Running (2006), Delpierre *et al.* (2009), Salzer *et al.* (2009), and Chave *et al.* (2008). They further investigated the subject because of the great significance such growth portends for the planet’s carbon balance and the future course of potential CO₂-induced global warming.

Using unique datasets of tree biomass collected from 55 temperate forest plots with known land-use histories and stand ages ranging from five to 250 years (which were derived from knowledge of when the stands had begun to regrow following major disturbances such as significant logging, various natural disasters that had decimated large patches of trees, or the clearing of trees to make room for agriculture that was ultimately abandoned), McMahon *et al.* “estimated biomass change, while controlling for stand regeneration” (see Figure 4.2.2.5.3.1) in parts of a temperate deciduous forest in the vicinity of the Smithsonian Environmental Research Center, Edgewater, Maryland (USA). They compared recent (the prior 22 years or less) rates of biomass accumulation of the various stands with rates predicted for those age intervals by the overall growth function derived from the combined data of all of the stands. They compared their findings with “over 100 years of local weather measurements and 17 years of on-site atmospheric CO₂ measurements.”

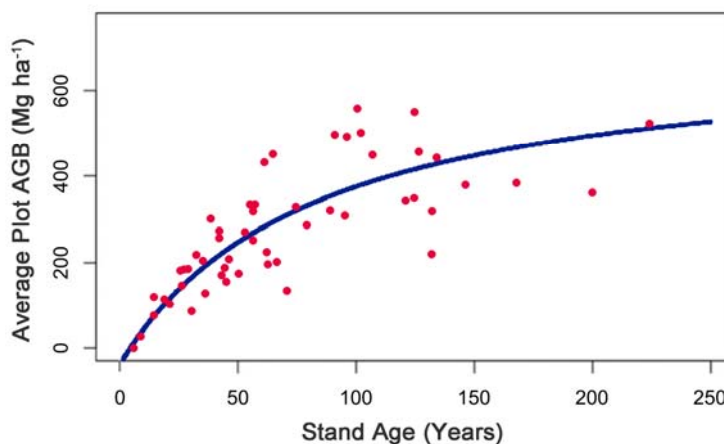


Figure 4.2.2.5.3.1. Graphic showing the relationship between above-ground biomass (AGB) and stand age of multiple-censused forest plots in a temperate deciduous forest in and near the Smithsonian Environmental Research Center in Edgewater, MD. The plot indicates younger trees are growing faster than older ones. Adapted from McMahon *et al.* (2010).

The authors report the results of their analysis reveal “recent biomass accumulation greatly exceeded the expected growth caused by natural recovery,” and they note in stands younger than 50 years the observed rate increase was generally at least one-third of total growth, and in older stands it typically was “the majority of growth,” even though past experience and the ensemble relationship of growth vs. age derived from their data suggest “old forests should grow very little as they approach equilibrium.”

The Smithsonian scientists write, “increases in temperature, growing season [which is largely driven by temperature], and atmospheric CO₂ have documented influences on tree physiology, metabolism, and growth,” and they state these factors may have been “critical to changing the rate of stand growth observed across stands.”

Capers and Stone (2011) “studied a community in western Maine, comparing the frequency and abundance of alpine plants in 2009 with frequency and abundance recorded in 1976,” noting “the 2009 survey was designed to provide a fair comparison with that of 1976,” which was conducted and described by Stone (1980). The two researchers found the 2009 survey “provided evidence of the increasing importance of woody plants—both trees and shrubs—in the alpine community” (Figure 4.2.2.5.3.2), commenting, “the most widespread tree species increased dramatically.” They “recorded an increase in total species richness of the community with the addition of four lower montane species that had not been recorded previously” and “found no evidence that species with high-arctic distributions had declined more than other species.”

Capers and Stone write the changes they recorded “are consistent with those reported in tundra communities around the world.” And although there is some concern the observed increase in species richness could turn out to be temporary if alpine species were to disappear because of competition from new species, they state, “species losses resulting from competition have not typically been found with rising richness in high alpine areas, possibly because newly arriving species occupy different micro-habitats,” citing Walther *et al.* (2005).

Ziska *et al.* (2004) characterized the gradual changes that occur in a number of environmental variables as one moves from a rural location (a farm approximately 50 km from the center of the city of

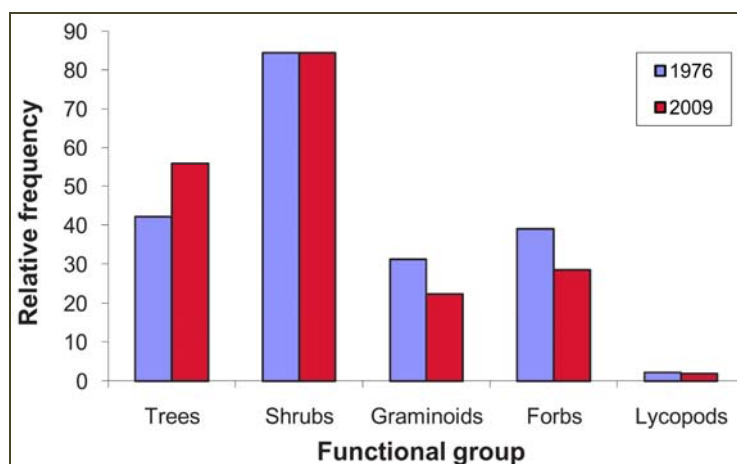


Figure 4.2.2.5.3.2. The relative frequency of five functional plant groups from surveys taken in 1976 and 2009 in a Northeast United States alpine plant community. The relative frequency of trees increased by a significant 14%, whereas the changes in forbs and graminoids were only marginally significant. Adapted from Capers and Stone (2011).

Baltimore, Maryland (USA)) to a suburban location (a park approximately 10 km from the city center) to an urban location (the Baltimore Science Center approximately 0.5 km from the city center). At each of these locations, four 2 x 2 m plots were excavated to a depth of about 1.1 m and filled with identical soils, the top layers of which contained seeds of naturally occurring plants of the general area. These seeds sprouted in the spring, and the plants they produced were allowed to grow until they senesced in the fall, after which all were cut at ground level, removed, dried, and weighed.

Along the rural to suburban to urban transect, the only consistent differences in the environmental variables Ziska *et al.* measured were a rural to urban increase of 21% in average daytime atmospheric CO₂ concentration and increases of 1.6 and 3.3°C in maximum (daytime) and minimum (nighttime) daily temperatures, respectively. These changes, they write, “were consistent with most short-term (~50 year) global change scenarios regarding CO₂ concentration and air temperature.” They write, “productivity, determined as final above-ground biomass, and maximum plant height were positively affected by daytime and soil temperatures as well as enhanced CO₂, increasing 60 and 115% for the suburban and urban sites, respectively, relative to the rural site.”

The three researchers say their results suggest “urban environments may act as a reasonable surrogate for investigating future climatic change in vegetative communities,” and those results

demonstrate rising air temperatures and CO₂ concentrations tend to produce dramatic increases in the productivity of the natural ecosystems typical of the greater Baltimore area and, by inference, probably those of many other areas as well.

The studies discussed above find 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.

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4.2.2.5.4 Central USA

- The late twentieth-century rise in temperature and CO₂ has improved the productivity of plant communities in the central region of the United States, notwithstanding model-based concerns to the contrary.

Voelker *et al.* (2006) studied two species of oak (*Quercus velutina* Lam. and *Quercus coccinea* Muench.) and one of pine (*Pinus echinata* Mill.) in the Ozark Mountains of Missouri (USA). They report since 1850 the stem growth of the three species has risen “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 (Figure 4.2.2.5.4.1). They note “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.” The four Department of Forestry researchers from the University of Missouri suggest a continual rise in the atmosphere’s CO₂ concentration, aided by continued nitrogen deposition, likely will “stimulate further increases in the rates of stand development and carbon storage.”

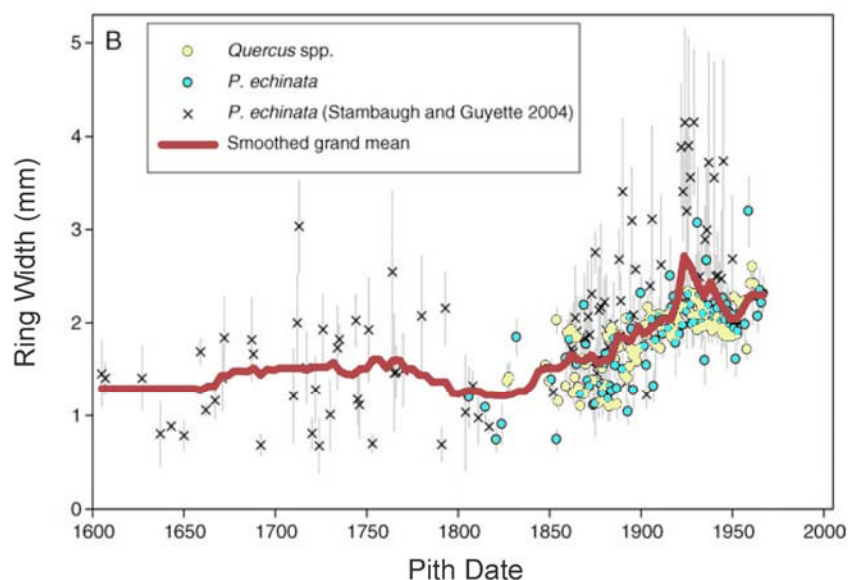


Figure 4.2.2.5.4.1. Mean ring width responses by pith date calculated across 11 equally spaced cambial ages from 1 to 50, for randomly sampled oak and pine trees in the Ozark Mountains of Missouri, USA. The means for *P. echinata* (Stambaugh and Guyette 2004) were calculated from three cambial ages but were shifted to the pith date for accurate intercomparisons among datasets (see Voelker *et al.*, 2006). The smoothed grand mean was calculated across each of the closest 14 ring widths. Adapted from Voelker *et al.* (2006).

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, “the most widely distributed tree species on the continent,” and 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).” They sought to determine how this keystone species may have responded to the increase in atmospheric CO₂ concentration that has occurred over the past several decades, especially in light of the climatic changes that occurred concurrently.

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, the scientists recorded trunk diameter at breast height for each sampled tree, a parameter, they write, “is very highly correlated with total biomass in aspen,” citing Bond-Lamberty *et al.* (2002).

The Minnesota and Wisconsin scientists report, “age-specific ring width increased over time” and “the greatest increase occurred for relatively young trees, so young trees grew faster in recent years than did young trees several decades ago.” During the past half-century, for example, they found the growth of trees 11–20 years old rose by 60% (Figure 4.2.2.5.4.2). They write, “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.” When they separated out the impacts of the two factors, they found “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.”

Cole *et al.* comment “the magnitude of the growth increase uncovered by this analysis raises the question of how much other major forest species have responded to the joint effects of long-term changes in CO₂ and precipitation.”

Woody plants in the U.S. Northern Great Plains

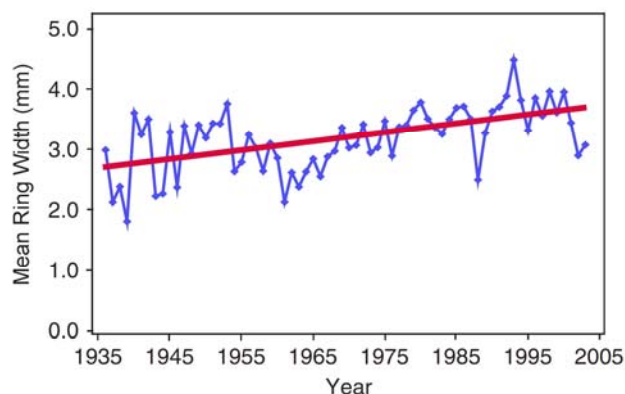


Figure 4.2.2.5.4.2. Mean ring width of quaking aspen trees sampled in Wisconsin, USA. Adapted from Cole *et al.* (2010).

also have responded positively to the twentieth-century increase in atmospheric CO₂ by expanding their ranges, and that expansion has led to greater benefits beneath the soil as well. Springsteen *et al.* (2012) note, “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 own investigation, Springsteen *et al.* examined near-surface (upper 15 cm) soil biogeochemistry along a 42-year (1963–2005) chronosequence, which encompassed grassland, woodland, and grassland-woodland transition zones in a northern Great Plains grassland at the USDA-ARS Northern Great Plains Research Laboratory near Mandan, North Dakota (USA), 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 chronosequence from grassland to woodland within the 0–15 cm soil depth, and total soil nitrogen content rose by 31%. 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, just a little more than doubled. Soil carbon sequestration driven by woody-plant invasions of grasslands, which are driven to a significant degree by the ongoing rise in the atmospheric CO₂ content, as well as the increases in soil nitrogen content required to sustain them, are growing with the passage of time.

In a vastly different type of study based on a 48-year record derived from an average of 17 measurements per year, Raymond and Cole (2003) demon-

strated the export of alkalinity, in the form of bicarbonate ions, from the USA’s Mississippi River to the Gulf of Mexico had increased by approximately 60% since 1953. “This increased export,” they write, was “in part the result of increased flow resulting from higher rainfall in the Mississippi basin,” which had led to a 40% increase in annual Mississippi River discharge to the Gulf of Mexico over the period. The remainder of the increased export of alkalinity had to have been due to increased rates of chemical weathering of soil minerals.

The two researchers note the mechanisms potentially responsible for this phenomenon include “an increase in atmospheric CO₂, an increase [in] rainwater throughput, or an increase in plant and microbial production of CO₂ and organic acids in soils due to biological responses to increased rainfall and temperature.” They don’t mention as a mechanism, but should have, the increase in terrestrial plant productivity produced by the increase in the aerial fertilization effect of the atmosphere’s rising CO₂ content, which also leads to an increase in plant and microbial production of CO₂ and organic acids in soils.

The findings presented above indicate the late twentieth-century rise in temperature and CO₂ has improved the productivity of plant communities in the central region of the United States, notwithstanding model-based concerns to the contrary.

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4.2.2.5.5 Western USA

- The late twentieth-century rise in temperature and CO₂ has 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.

Baron *et al.* (2000) used an empirically based hydro-ecological simulation model to evaluate the consequences of a doubling of atmospheric CO₂ content and 2 to 4°C increases in air temperature on ecosystem performance in a high-elevation Rocky Mountain watershed. They found “both photosynthesis and transpiration were highly responsive to doubled CO₂.” They also determined the positive effects of the 4°C temperature increase “were additive, so a warmer and carbon-rich environment increased plant growth by 30%.” The authors conclude, “forests will expand at the expense of tundra in a warmer, wetter, and enriched CO₂ world,” and observed increases in tree height and density in recent decades illustrate “the rapidity with which vegetation can respond to climate change.”

Because urban environments are affected by urban heat islands, carbon dioxide domes, and high-level nitrogen deposition, Shen *et al.* (2008) write, “to some extent they portend the future of the global ecosystem,” and they “provide a unique ‘natural laboratory’ to study potential ecosystem responses to anthropogenic environmental changes.” The team of four authors used a version of the Patch Arid Land Simulator-Functional Types (PALS-FT) process-based ecosystem model—originally developed for the Chihuahuan Desert but modified to represent the *Larrea tridentata*-dominated ecosystem characteristic of the Sonoran Desert in which Phoenix, Arizona (USA) is located—to investigate the impacts of previously documented city-to-desert gradients of atmospheric CO₂ concentration, air temperature (TA), and nitrogen deposition (N_{dep}) on aboveground net primary productivity (ANPP) and soil organic matter (SOM).

In response to the mean maximum rural-to-urban increases in CO₂ (160 ppm), N_{dep} (24 kg per ha/year) and TA (4.0°C) characteristic of Phoenix, mean ANPP changes of +52.5, +42.7 and -7.8 g dry matter (DM) per m²/year were obtained, respectively, from the 76.3 g DM per m²/year characteristic of desert conditions, when each of the three factors was increased individually. When all three parameters were increased together, the researchers found the net increase in ANPP was even greater than the sum of the three individual results: 108 vs. 87.4 g DM per m²/year, translating to respective percentage increases

of 142% vs. 115%. In the case of SOM, increases of 18.5, 12.3, and 1.2 g C per m²/year were obtained for mean maximum individual increases in CO₂, N_{dep}, and TA, respectively, and the combined increase was 30.9 g C per m²/year. These findings indicate that even in a desert region as hot as Phoenix, the types of CO₂, temperature, and nitrogen deposition increases predicted for the years ahead portend huge increases in indigenous ecosystem productivity and soil organic matter buildup.

Zavaleta and Kettley (2006) examined patterns of production, standing biomass, carbon (C) and nitrogen (N) storage, community composition, and soil moisture along a 25-year chronosequence of sites in an annual, exotic-dominated grassland at Stanford University's Jasper Ridge Biological Preserve in the interior foothills of the central coast range south of San Francisco, California (USA), various parts of which had been invaded at a number of different times over the past quarter-century by *Baccharis pilularis* shrubs.

The two researchers report increasing above- and below-ground biomass along the chronosequence "drove increases in ecosystem N sequestration of ~700% and in C storage of over 125%," including a 32% increase in total soil C over the 25-year period. They write, "increases in carbon storage also did not appear to be saturating at 25 years after shrub establishment in any pool, suggesting the potential for additional carbon gains beyond 25 years." *Baccharis* shrubs began to decline in prominence after about 20 years, as native oaks "with life spans of centuries" and the potential to drive even larger ecosystem changes began to grow in the shrub-dominated areas.

Zavaleta and Kettley note they "initially hypothesized *Baccharis*-invaded sites would experience increasing N limitation as N was immobilized in biomass and litter." However, they found "total soil N increased rapidly with shrub age" and "the magnitude of increase in total soil nitrogen was much larger than the increase in nitrogen immobilization in biomass and litter over time." They say their findings "illustrate the potential for important vegetation-mediated ecosystem responses and feedbacks to atmospheric CO₂ and climate change." In particular, they highlight the great potential for a CO₂-induced range expansion of trees, and they pretty much lay to rest the claim (Hungate *et al.*, 2003) that the availability of nitrogen, in forms usable by plants, will probably be too low for large future increases in carbon storage driven by CO₂-induced increases in plant growth and development.

Peterson and Neofotis (2004) grew velvet

mesquite (*Prosopis velutina* Woot.) seedlings for six weeks from their time of planting (as seeds) in small pots in environmentally controlled growth chambers maintained in a laboratory setting 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, by the end of their six-week study they observed a significant reduction of approximately 41% in the volume of water transpired by *P. velutina* in response to the experimental doubling of the atmospheric 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 pair of scientists from the Biosphere 2 Center near Oracle, Arizona (USA) say 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." They 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." They 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).

Among such studies could also be listed the work of Feng (1999), who derived variations in plant intrinsic water-use efficiency over the preceding two centuries from 23 carbon isotope tree-ring chronologies. Their results were nearly identical to the historical trend in the atmospheric CO₂ content, with plant intrinsic water-use efficiency rising by 10 to 25% from 1750 to 1970, during which time the air's CO₂ concentration rose by approximately 16%. Feng concludes, "in arid environments where moisture limits the tree growth, biomass may have increased with increasing transpiration efficiency," noting the enhanced growth of trees in arid environments may "have operated as a carbon sink for the anthropogenic CO₂" emitted during that period.

Soule and Knapp (2006) studied ponderosa pine trees 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 the sites they chose "fit several criteria designed to limit potential confounding influences associated with anthropogenic disturbance." They selected locations 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 also note all sites were located in areas "where ozone concentrations and nitrogen deposition are typically low."

At all eight of the 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, as they put it, "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 radial growth rates during matched wet and dry years pre- and post-1950.

Overall, the two researchers discovered a post-1950 radial growth enhancement "more pronounced during drought years compared with wet years, and the greatest response occurred at the most stressed site" (see Figure 4.2.2.5.5.1). As for the magnitude of the response, they write, "the relative change in growth [was] upward at seven of our [eight] sites, ranging from 11 to 133%."

Soule and Knapp say their results show "radial growth has increased in the post-1950s period ... while climatic conditions have generally been unchanged," which suggests "nonclimatic driving forces are operative." They say the "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 conclude their findings "suggest that elevated levels of atmospheric CO₂ are acting as a driving force for increased radial growth of ponderosa pine, but the overall influence of this effect may be enhanced, reduced or obviated by site-specific conditions."

Soule and Knapp note 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 they report their results "support these hypotheses." They conclude, "an atmospheric CO₂-driven growth-enhancement effect exists for ponderosa pine growing under specific natural conditions within the interior Pacific Northwest."

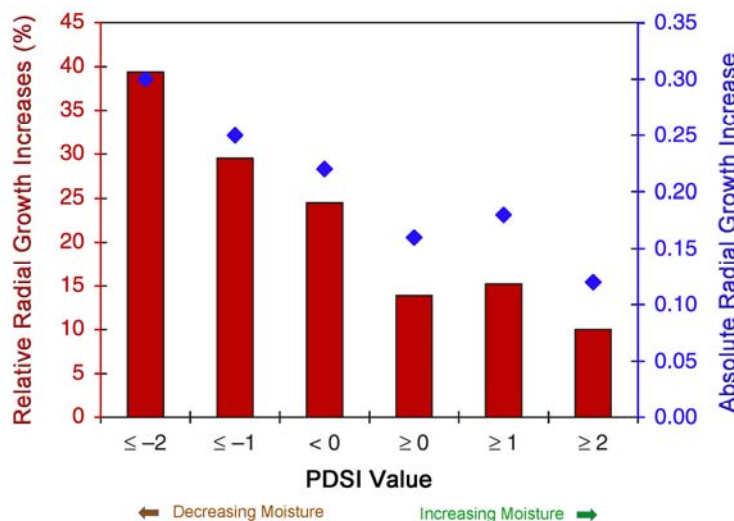


Figure 4.2.2.5.5.1. Relative and absolute radial growth increases of Ponderosa pine (*Pinus ponderosa*) in the Pacific Northwest, USA, post-1950 compared with pre-1950 during years falling into various Palmer Drought Severity Index (PDSI) categories of drought (moist) severity. Adapted from Soule and Knapp (2006).

The studies in this section document the late twentieth-century rise in temperature and CO₂ has 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.

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4.2.2.6 South America

- 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.

Beerling and Mayle (2006) investigated the Amazonian ecosystem's response to the large-scale environmental changes experienced during glacial-interglacial cycles via a series of 21,000-year simulations. They used a dynamic process-based ecosystem model for three scenarios: real-world glacial-to-interglacial changes in CO₂ concentration and climate, the real-world change in CO₂ with a constant preindustrial climate, and the real-world change in climate with a constant preindustrial CO₂ concentration.

During the last glacial maximum, the model suggests “total above-ground carbon storage in Amazonia was half preindustrial values, indicative of rain forests with markedly lower canopy densities and simpler structures due to lowered CO₂ levels, corroborating modeling studies by Cowling (2004) and Cowling *et al.* (2001).” Thereafter, they write, “biome

shifts in ecotonal areas since the last glacial maximum [“the competitive replacement of drought-adapted vegetation (e.g. savanna or deciduous/semideciduous dry forest) by rain forest”] were driven predominantly by climate change, while coincident, increased ecosystem carbon storage throughout the Amazon Basin was driven largely by CO₂.”

As to the contemporary relevance of these findings, Beerling and Mayle write, “the underlying cause for the observed trend of increasing biomass in long-term Amazonian forest plots over recent years, despite drought-induced El Niño events (Phillips *et al.*, 1998; Baker *et al.*, 2004a), has been a subject of considerable debate (Baker *et al.*, 2004a; Wright, 2005),” and they conclude “this biomass increase is part of a long-term historical trend driven by anthropogenically induced rising CO₂ levels since the 19th century.”

Ichii *et al.* (2005) “simulated and analyzed 1982–1999 Amazonian, African, and Asian carbon fluxes using the Biome-BGC prognostic carbon cycle model driven by National Centers for Environmental Prediction reanalysis daily climate data” and “calculated trends in gross primary productivity (GPP) and net primary productivity (NPP).” They found solar radiation variability to be the primary factor responsible for inter-annual variations in GPP, followed by temperature and precipitation variability. In terms of GPP trends, they report, “recent changes in atmospheric CO₂ and climate promoted terrestrial GPP increases with a significant linear trend in all three tropical regions.” In the Amazonian region, the rate of GPP increase was highest, at 0.67 PgC year⁻¹ per decade, and in Africa and Asia it was about 0.3 PgC year⁻¹ per decade. As Beerling and Mayle found, Ichii *et al.* say carbon dioxide was the major cause of increased growth, reporting, “CO₂ fertilization effects strongly increased recent NPP trends in regional totals.”

This finding is especially interesting because many scientists over the past century believed old-growth forests, such as those of Amazonia, were close to dynamic equilibrium. Just the opposite, however, has been observed repeatedly by several groups of researchers over the past two decades.

Phillips and Gentry (1994) analyzed the turnover rates—close correlates of net productivity (Weaver and Murphy, 1990)—of 40 tropical forests from around the world. They report the growth rates of

these already highly productive forests have been rising since at least 1960, and they have undergone an apparent acceleration in growth rate sometime after 1980. Pimm and Sugden (1994) report the consistency and simultaneity of the forest growth trends Phillips and Gentry documented on several continents led them to conclude “enhanced productivity induced by increased CO₂ is the most plausible candidate for the cause of the increased turnover.”

Phillips *et al.* (1998) analyzed forest growth rate data for the years 1958 to 1996 for several hundred plots of mature tropical trees around the world, finding tropical forest biomass, as a whole, increased substantially over the period of record (Figure 4.2.2.6.1). The increase in the neotropics (tropical Central and South America) was equivalent to approximately 40% of the missing terrestrial carbon sink of the entire globe. They identify the aerial fertilization effect of the ongoing rise in atmospheric CO₂ content as one of the primary factors likely to be responsible for this phenomenon.

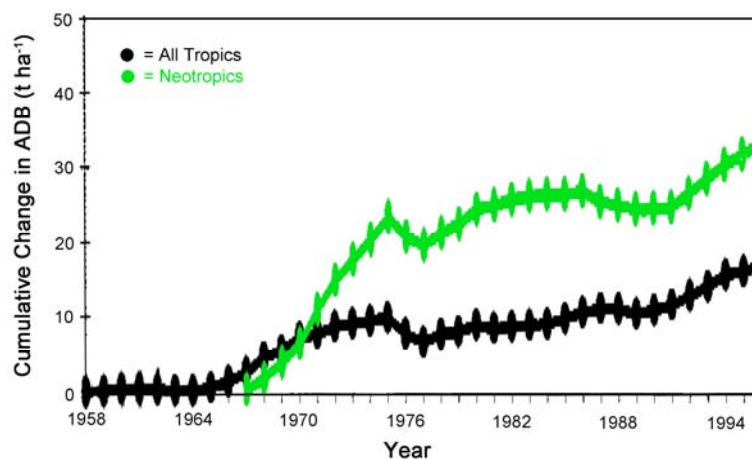


Figure 4.2.2.6.1. Cumulative aboveground dry biomass change (ADB) per year in humid forests in the entire Tropics since 1958 and in the Neotropics (tropical Central and South America) since 1967. Adapted from Phillips *et al.* (1998).

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. Laurance *et al.* (2005) 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).” They “interpreted these 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).” Noting Nelson (2005) challenged this conclusion, they considered his arguments in some detail, dismantling each one.

Lewis (2006) reports the increasing dynamism and productivity of intact tropical forests has had a long history, noting “across the paleotropics forest dynamism has been steadily increasing for five decades (Phillips and Gentry, 1994).” Among 50 old-growth plots across tropical South America, for example, he notes “stem recruitment, stem mortality, and biomass growth, and loss, all increased significantly (Lewis *et al.*, 2004a).” He reports “over approximately the last 20 years, long-term monitoring of 59 plots showed that above-ground biomass increased by 0.6 ± 0.2 tonnes C ha⁻¹ a⁻¹, or a relative increase of $0.50 \pm 0.17\%$ a⁻¹ (mean $\pm$ 95% confidence interval; Baker *et al.*, 2004a).” This rate of increase “is slightly higher than that documented by Phillips *et al.* (1998).” Lewis concludes there is no question “over the past two decades these forests have shown concerted changes in their ecology, becoming, on average, faster growing—more productive—and more dynamic, and showing a net increase in above-ground biomass.”

Lewis states “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).” The four resources he identifies are 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).” He writes, the explanation is in “the anthropogenic increase in atmospheric carbon dioxide concentrations, increasing forest net primary productivity leading to accelerated forest growth and dynamics.”

In spite of the forest growth optimism inherent in the studies cited above, some pessimists remained. 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.*, 2004a), and

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.*, 2004a).” They state this conclusion had been challenged by an overzealous application of the “Slow in, Rapid out” dictum, which relates to the fact that forest growth is a slow process, whereas mortality can be dramatic and singular in time, so sampling over relatively short observation periods may miss the more severe events, leading to positively biased estimates of aboveground biomass trends when either no trend or negative trends actually exist.

Gloor *et al.* statistically characterized 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, exploring the consequences of sampling artifacts using a data-based stochastic simulator. The authors report, “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.” 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.” 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.”

Bonal *et al.* (2011) write, “the impact of global change during the last century on the biology of tropical rainforest trees is largely unknown,” but “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). They note “the stimulating impact on photosynthesis of increased CO₂ concentrations in the air (Ca) could explain these growth patterns (Lloyd and Farquhar, 2008).”

Bonal *et al.* assessed the impacts of historical environmental changes “on leaf morphological (stomatal density, stomatal surface, leaf mass per unit area) and physiological traits (carbon isotope composition, $\delta^{13}\text{C}_{\text{leaf}}$, and discrimination, $\Delta^{13}\text{C}_{\text{leaf}}$, oxygen isotope composition, $\delta^{18}\text{O}_{\text{leaf}}$) of two tropical

rainforest species (*Dicorynia guianensis*; *Humiria balsamifera*) that are abundant in the Guiana shield (Northern Amazonia),” working with leaf samples from different international herbariums that covered a 200-year period (AD 1790–2004).

The 11 researchers found “a clear response of leaf physiological characteristics to increasing CO_2 for both species,” consistent with the findings of 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).” They say their results indicate “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. They write, “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.* further state the responses of the two tree species to increasing CO_2 appear to be “simply related to the availability of CO_2 in the air (fertilization effect),” and they note “this trend seems to be consistent with recent tree growth patterns in the Amazonian region.”

Silva *et al.* (2009) studied tree-ring data obtained from *A. angustifolia* trees growing in forest and grassland sites in southern Brazil, comparing changes in intrinsic water use efficiency—iWUE, defined as the ratio of the rate of CO_2 assimilation by the trees’ needles to their stomatal conductance—with concomitant historical changes in temperature, precipitation, and atmospheric CO_2 concentration over the past century. During the past several decades, the four researchers report, “iWUE increased over 30% in both habitats” (see Figure 4.2.2.6.2), and “this increase was highly correlated with increasing levels of CO_2 in the atmosphere.” Over the latter period, tree growth remained rather stable because of lower-than-normal precipitation and higher-than-normal temperatures, which would normally tend to depress the growth of this species; Katinas and Crisci (2008) describe *A. angustifolia* as being “intolerant of dry seasons and requiring cool temperatures.” Silva *et*

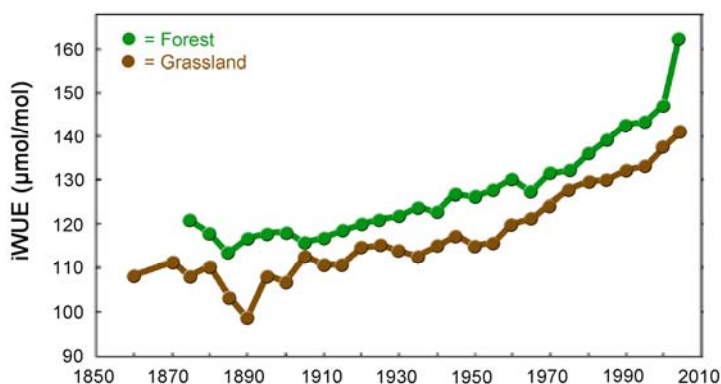


Figure 4.2.2.6.2. Intrinsic water-use efficiency (iWUE) in *Araucaria angustifolia* trees established into forest and grassland in southern Brazil (means of individuals per site in five-year total values). Adapted from Silva *et al.* (2009).

al. conclude the “climatic fluctuations during the past few decades,” which would normally 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 CO_2 and changes [i.e., increases] in iWUE.”

Phillips *et al.* (2009) investigated what effect a severe drought might have on South America’s surprisingly spry-for-its-age tropical mega-forest, especially a drought of the type the models predict will occur if anthropogenic CO_2 emissions are not significantly abated. The international team of scientists sought to determine 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 worst-case catastrophic scenarios of the models.

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. They derived the results plotted in Figure 4.2.2.6.3.

As Figure 4.2.2.6.3. shows, the Amazonian drought of 2005 only slightly impacted the strong upward trend of tree biomass accumulation that was exhibited over the prior two decades, which had occurred, as Phillips *et al.* note, through a multi-decadal period spanning both wet and dry episodes, the latter of which are not even detectable in their wood biomass data. Hence it would appear that

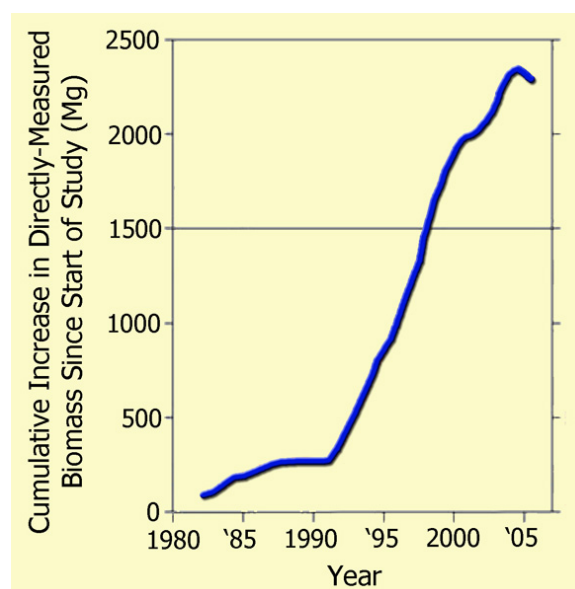


Figure 4.2.2.6.3. The post-1980 cumulative biomass increase of Amazon trees ≥ 10 cm in diameter as a function of the mid-date of each forest-plot census interval, portrayed as a 50-interval moving mean. Adapted from Phillips *et al.* (2009).

although extremely severe drought conditions can indeed stop 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 prowess 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) of nearly all woody plants as the atmospheric CO_2 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 CO_2 -induced stimulation of tree growth.” Phillips *et al.* (2008) add 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,” and “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 [its] concentration, the key role of CO_2 in photosynthesis, and the demonstrated effects of CO_2 fertilization on plant growth rates.”

The voluminous and undeniable real-world observations reported in the studies described above indicate forest productivity has been increasing along with the increasing CO_2 content of the air wherever tropical forests have not been decimated by the direct destructive actions of man, such as the felling and burning of trees. This productivity increase has persisted in spite of all concomitant changes in atmospheric, soil, and water chemistry and the twentieth-century global warming. Real-world evidence suggests the anthropogenic-induced increase in the atmospheric CO_2 content is primarily responsible for this beneficial state of affairs.

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4.2.3 Rising Temperatures and Biospheric Productivity

- 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 CO_2 . This response, coupled with expected increases in plant photosynthetic rates from the rise in the air's CO_2 concentration, is more than enough to compensate for any temperature-induced plant stress caused by global warming.

In spite of the overwhelming amount of evidence, presented in Section 4.2 of this report, demonstrating rising atmospheric CO_2 concentrations and warmer temperatures have enhanced the productivity of the biosphere, some scientists have expressed concern these trends will gradually decline—and eventually reverse—if temperatures rise toward the upper limits

projected in model-based scenarios of future global warming.

It is more likely, however, that the greening of the planet will continue in the future, even if the largest temperature increases predicted by the models do occur. This is 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.

Jurik *et al.* (1984) exposed bigtooth aspen leaves to atmospheric CO₂ concentrations of 325 and 1,935 ppm and measured their photosynthetic rates at a number of temperatures. Figure 4.2.3.1 below reproduces their results and slightly extends the two relationships defined by their data to warmer and cooler conditions.

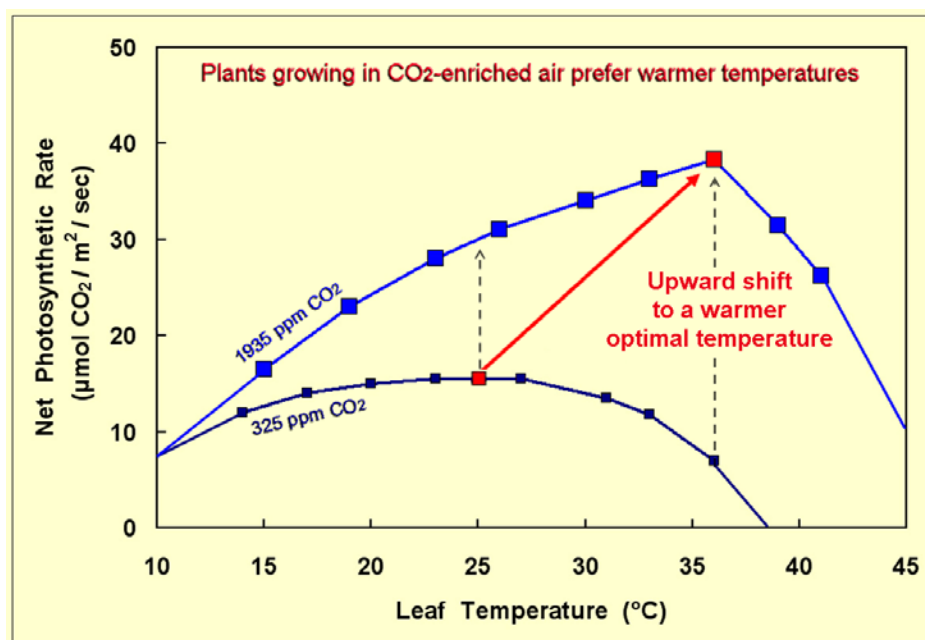


Figure 4.2.3.1. Net photosynthesis of big tooth aspen leaves growing under two concentrations of atmospheric carbon dioxide at various temperatures. Adapted from Jurik *et al.* (1984).

As the figure illustrates, at 10°C, elevated CO₂ has essentially no effect on net photosynthesis in this particular species, as Idso and Idso (1994) have demonstrated is characteristic of plants in general. At 25°C, however, where the net photosynthetic rate of the leaves exposed to 325 ppm CO₂ is maximal, the extra CO₂ of this study boosts the net photosynthetic rate of the foliage by nearly 100%, and at 36°C,

where the net photosynthetic rate of the leaves exposed to 1,935 ppm CO₂ is maximal, the extra CO₂ boosts the net photosynthetic rate of the foliage by 450%. The extra CO₂ increases the optimum temperature for net photosynthesis in this species by about 11°C: from 25°C in air of 325 ppm CO₂ to 36°C in air of 1935 ppm CO₂.

The warm-temperature extensions of the two relationships at the right-hand side of the figure show the transition from positive to negative net photosynthesis—which denotes a change from life-sustaining to life-depleting conditions—likely occurs somewhere in the vicinity of 39°C in air of 325 ppm CO₂ but somewhere in the vicinity of 50°C in air of 1935 ppm CO₂. Thus not only was the optimum temperature for the growth of bigtooth aspen greatly increased by the extra CO₂ of this experiment, so too was the temperature above which life cannot be sustained also increased, and by about the same amount: 11°C.

Other researchers have documented this important CO₂-induced plant benefit in other agricultural, grassland, and woody plant species. Nearly all of these studies indicate a 300 ppm increase in the atmospheric CO₂ content increases a plant's optimum temperature for growth and development by a mean of approximately 6°C (Bjorkman *et al.*, 1978; Berry and Bjorkman, 1980; Nilsen *et al.*, 1983; Jurik *et al.*, 1984; Seeman *et al.*, 1984; Harley *et al.*, 1986; Stuhlfauth and Fock, 1990; McMurtrie *et al.*, 1992; McMurtrie and Wang, 1993; Idso *et al.*, 1995; Cowling and Sykes, 1999; Gutierrez *et al.*, 2009). This response is more than enough to compensate fully for any temperature-induced plant stress caused by

the worst-case scenario of climate-model-predicted CO₂-induced global warming. Additional research indicates plants may be able to boost their optimum temperature for photosynthesis as the temperature warms, even in the absence of a concurrent increase in atmospheric CO₂.

Gunderson *et al.* (2010) investigated the “photosynthetic sensitivity to temperature and the

potential for acclimation in relation to the climatic provenance of five species of deciduous trees, *Liquidambar styraciflua* [sweetgum], *Quercus rubra* [northern red oak], *Quercus falcata* [southern red oak], *Betula alleghaniensis* [yellow birch] and *Populus grandidentata* [bigtooth aspen].” They conducted their experiment out-of-doors in open-top chambers at three temperature regimes—ambient, ambient plus 2°C, and ambient plus 4°C—for three years. The five scientists report, “warming treatments resulted in a shift in the temperature response curves for CO₂ assimilation, such that leaves in warmer treatments had higher temperature optima [T_{opt}].” An example of this phenomenon is depicted in Figure 4.2.3.2 for *Q. rubra* seedlings during one specific month.

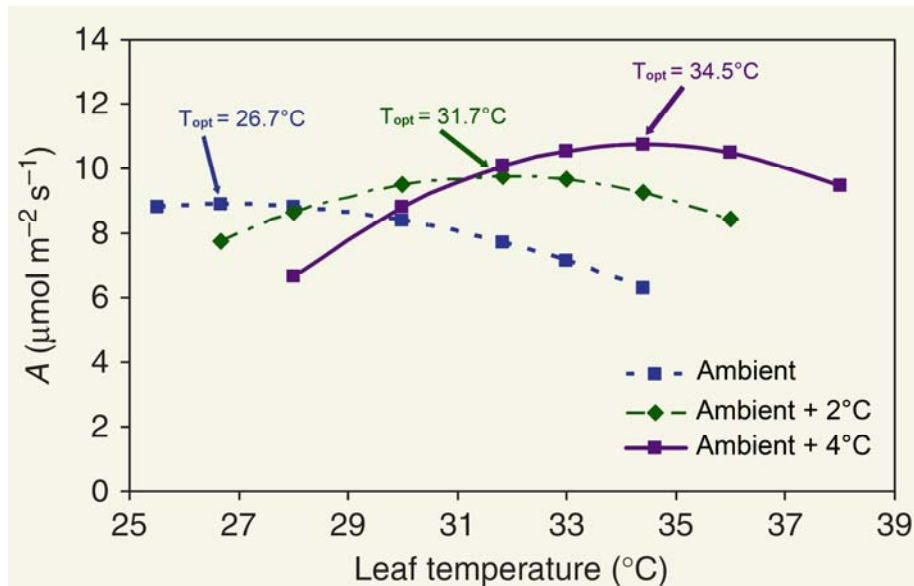


Figure 4.2.3.2. Net CO₂ assimilation rate vs. leaf temperature in *Quercus rubra* seedlings during June of 2003 in the ambient (A) and elevated (A+2°C and A+4°C) temperature treatments. Adapted from Gunderson *et al.* (2010).

As Figure 4.2.3.2 illustrates, the trees growing in progressively warmer environments had progressively higher T_{opt} values, and there was a tendency for the net CO₂ assimilation rates at those higher T_{opt} values to be a bit higher as well. Gunderson *et al.* found this adjustment in photosynthetic response was typically accomplished over a period of as little as two days, noting “others have found all or most acclimation within 2–6 days (Veres and Williams, 1984; Hill *et al.*, 1988; Battaglia *et al.*, 1996; Turnbull *et al.*, 2002; Froux *et al.*, 2004).” They state a similar “adjustment of thermal optima was confirmed in all species, whether temperatures varied with season or treatment,

and regardless of climate in the species’ range or provenance of the plant material,” and the “responses to the temperature manipulation were not different from the seasonal acclimation observed in mature indigenous trees.”

These observations indicate plants will be able to adjust their physiology to accommodate a warming of the magnitude and rate of rise IPCC predicts to accompany the projected future increase in atmospheric CO₂ content. If the planet’s flora can adjust their physiology to not only survive a modest instantaneous warming of 2–4°C, but to actually benefit from it, as has been demonstrated to be true of several trees examined by Gunderson *et al.*, there is every reason to believe they would respond to a similar warming projected to develop over a century

or more. When one factors in the aerial fertilization effect of rising atmospheric CO₂ concentrations, plus the transpiration-reducing effect that boosts plant water use efficiency, plus CO₂’s ability to also raise the T_{opt} values of most plants, it is clear the world’s vegetation is well-prepared for future warming. The recent greening of the planet should continue in the years and decades to come, notwithstanding model-based concerns to the contrary.

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4.3 Biodiversity

- Highly CO₂-responsive genotypes of a wide variety of plants—ranging from food crops to lumber crops—could be chosen to take advantage of their genetic ability to optimize growth in response to projected future increases in the atmospheric CO₂ content. Doing so is probably essential to the well-being of mankind and to the survival of much of the world's wildlands.

As human population grows, the demand for food rises as well, as does the need for land and water to grow that food. Unless something is done to enhance the per-acre productivity of the terrestrial biosphere, some species of plants and animals may be pushed out of existence by the midpoint of the current century.

A number of real-world experiments demonstrate many of Earth's food- and lumber-producing plants possess the genetic potential to grow better while using less water as atmospheric CO₂ content rises. In an important paper by 32 researchers from 12 countries, Ainsworth *et al.* (2008) made the case for breeding varieties of major food crops to best take advantage of the ongoing rise in the atmospheric CO₂ content. They note, "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," so "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, in their words, “a unique opportunity to increase the productivity of C₃ crops.”

The scientists point out “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.” They conclude, “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.”

Ziska *et al.* (1996) grew well-watered and well-fertilized plants of 17 cultivars of rice (*Oryza sativa* L.) from seed to maturity in glasshouses maintained at atmospheric CO₂ concentrations of either 373 ppm (ambient) or 664 ppm (elevated) in 24-L pots filled with local soil at two sets of day/night temperatures (29/21°C and 37/29°C), afterwards measuring total plant biomass and grain biomass. They found the degree of CO₂-induced enhancement of total plant biomass and the number of cultivars showing significant yield enhancement with elevated CO₂ decreased at the higher and more stressful set of growth temperatures, dropping from 12 of 17 cultivars with a mean biomass stimulation of 70% at the lower set of temperatures to eight of 17 cultivars with a mean biomass stimulation of 23% at the higher set of temperatures.

At the lower set of temperatures, a few cultivars exhibited no significant changes in response to the atmospheric CO₂ enrichment employed in the study, but the most responsive cultivar—a tropical japonica type from Brazil—exhibited a 265% increase in total plant biomass and a 350% increase in grain biomass.

The wide range of productivity enhancement exhibited in response to atmospheric CO₂ enrichment by the 17 cultivars of rice examined in this experiment indicates the tremendous potential in selecting rice varieties to take advantage of the aerial fertilization effect of atmospheric CO₂. That endeavor, Ziska *et al.* write, “could maximize productivity as CO₂ concentration increases.” Such a selection process likely will be an essential element of the race to feed humanity in the year 2050 without usurping vast tracts of tropical and temperate forests, savannas, and grasslands or commandeering all of the planet's remaining freshwater resources and destroy-

ing most of the world's remaining wildlands.

Bunce (2008) grew adequately fertilized plants of four varieties of the common garden bean (*Phaseolus vulgaris* L.)—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, making photosynthetic measurements of mature upper-canopy leaves in full sunlight at midday during the pod-filling stages of four growing seasons and assessing final seed yields and other plant characteristics at harvest. They found the 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 36% in the Red Hawk and Brown Beauty cultivars. The Matterhorn variety increased dry mass seed yield by about 39%, followed by Red Hawk at 21%, Brown Beauty at 18%, and Jaguar with a 10% decline in seed yield. As Bunce reported, “the highest yielding variety at ambient CO₂ [Jaguar] was out-yielded by a different variety at elevated CO₂ [Matterhorn].”

These findings demonstrate there is significant variability in seed yield response to atmospheric CO₂ enrichment among the four bean varieties Bunce tested. There was no *a priori* way of knowing which of the four cultivars would respond best, or that one of them would respond negatively. Bunce's work demonstrates the need to perform experiments on the world's most important crop plants to identify which of their many varieties should be selected for crop breeding work, to take full advantage of the increase in the atmosphere's CO₂ concentration likely to occur over the next several decades.

Yang *et al.* (2009) write, “rice (*Oryza sativa* L.) is unequivocally one of the most important food crops that feed the largest proportion of the world's population” and “the demand for rice production will continue to increase in the coming decades, especially in the major rice-consuming countries of Asia, Africa and Latin America, due to the population explosion and cropland reduction.” They note, “as sufficient intraspecific variation in yield response exists under field conditions, there is a pressing need to identify genotypes which would produce maximum grain yield under projected future CO₂ levels.”

Working at the National Institute for Agro-Environmental Sciences in Tsukuba, Japan, Lou *et al.* (2008) grew plants of four rice cultivars—Dular (a traditional indica variety), IR72 (an improved indica

variety), Koshihikari (a temperate japonica variety), and IR65598 (a new variety not yet released to farmers)—in growth chambers in submerged pots filled with a fertilized soil collected from the plough layer of a paddy field in Chiba Prefecture, Japan, at two atmospheric CO₂ concentrations: ambient (~370 ppm) and elevated (~570 ppm). They found the extra 200 ppm of CO₂ reduced the ultimate grain yield of Dular (by 0.7%) and increased the final grain yield of IR72 by 8.0%, of Koshihikari by 13.4%, and of IR65598 by 17.7%.

Yang *et al.* (2009) focused on a single two-line inter-subspecific hybrid rice variety (Liangyoupeijiu) produced as part of “a nationwide mega project” to develop what they called “super” hybrid cultivars that would “further break the yield ceiling.” In their three-year CO₂-enrichment study at the FACE facility at Yangzhou City, Jiangsu Province, China, which employed the same CO₂ levels as the study of Lou *et al.*, they found a much greater grain yield stimulation: a 28.4% CO₂-induced increase under a low nitrogen fertility treatment of 12.5 g N m⁻² and a 31.7% CO₂-induced increase under a high nitrogen fertility treatment of 25 g N m⁻².

Yang *et al.* state their hybrid cultivar “appears to profit much more from elevated CO₂ than inbred japonica cultivars.” Both the Japanese and Chinese FACE studies of inbred japonica cultivars found CO₂-induced grain yield enhancements on the order of only 13% for a 200 ppm increase in the air’s CO₂ concentration. Noting “there is a pressing need to identify genotypes which could optimize harvestable yield as atmospheric CO₂ increases,” Yang *et al.* conclude, “on the basis of available FACE data on rice,” the hybrid rice cultivar Liangyoupeijiu appeared “to be particularly promising.”

Mycroft *et al.* (2009) grew seedlings of 29 well-watered and fertilized white spruce (*Picea glauca* (Moench) Voss) tree genotypes in 2.83-liter pots filled with a mixture of peat and vermiculite between 10 May and 23 September 2006 in glasshouse compartments maintained at either ambient (370 ppm) or elevated (740 ppm) atmospheric CO₂ concentrations. They assessed plant performance by measuring final plant height, basal stem diameter, and total biomass production, including roots.

They found, “depending upon genotype, the increase in biomass at elevated CO₂ as a percentage of that at ambient CO₂ ranged from 23% to 108%, while increases in height ranged from 4% to 48%,” and “in the case of stem diameter, the effect of elevated CO₂ varied from a non-significant decrease of 6% to an increase of 32% depending upon

genotype.” The four researchers write, “similar to previous studies (e.g. Bazzaz *et al.*, 1995; Lindroth *et al.*, 2001; Moya *et al.*, 1998; Steinger *et al.*, 1997; Volk and Korner, 2001),” they discovered “significant genotype x CO₂ interactions for size-related traits.” They note their CO₂-induced biomass increases (+23% to +108%) were of a range similar to those Mohan *et al.* (2004) obtained for red maple (0% to +93%) and Wang *et al.* (2000) found for quaking aspen (-29% to +94%).

These observations demonstrate highly CO₂-responsive genotypes of a wide variety of plants, ranging from food crops to lumber crops, could be selected to take advantage of their genetic ability to optimize growth in response to projected future increases in atmospheric CO₂ content. Such measures probably will prove essential to the well-being of mankind and to the survival of much of the world’s wildlands.

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4.4 Extinction

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. One of the great horror stories associated with predictions of CO₂-induced global warming is of warming so fast and furious that many species of plants will not be able to migrate towards cooler regions—poleward in latitude, or upward in elevation—quickly enough to avoid extinction. Real-world observations of plants show they have many

ways of adjusting to changes in climate in addition to their ability to move from places of rising warmth to cooler habitats. These observations suggest the planet's current assemblage of plants is likely to be around longer than many theoretical models have predicted.

Under-yielding species appear to be buffered from extinction because growth enhancements of smaller plants tend to diminish the relative biomass advantages of larger plants in crowded conditions, and when species are rare in a local area, they have a higher survival rate than when they are common, resulting in the enrichment of rare species and increasing diversity with age and size class in complex ecosystems. In addition, diversity should increase as a group of individuals ages, because more common species are selectively removed by pathogens and predators, especially those commonly associated with them.

Also, individuals of a species compete more intensively with conspecifics than with individuals of other species, and diversity may increase if an individual benefits nearby non-conspecifics, as such facilitation makes interspecific interactions more positive than intraspecific interactions and thus provides an advantage to locally rare species. Similarly, common trees growing closer together are more prone to deadly infections, and they may also face stiffer competition for certain resources, whereas rarer trees, by depending on slightly different sets of resources, may not have this problem.

4.4.1 Migrating Plants

If Earth warms by a significant amount, for whatever reason, the best thing that could happen to the planet would be for the air's CO₂ concentration to rise concurrently, or shortly thereafter, because that would obviate the need for plants to migrate to cooler regions or at least reduce the required rate of migration and/or distance of travel well below what overly simplistic coupled climate-biology models have suggested. In a CO₂-enriched world, as air temperature increases, so too would the temperature at which most plants function at their optimum. Plants thus would be able to grow and reproduce in close proximity to where they grew when the air temperature first began to increase.

This is exactly how nature appears to operate during and after a glacial-to-interglacial transition. In response to the air temperature increase during such transitions, Earth's atmospheric CO₂ concentration

typically has risen by an amount sufficient to enable plants to cope with the warming of the globe. Cowling and Sage (1998) indicate a typical 180 ppm rise in atmospheric CO₂ concentration from a base level characteristic of glacial conditions can raise plant optimum growth temperature by about 4°–5°C, the temperature increase typically experienced during glacial terminations.

Cowling and Sykes (1999) conducted a review of the literature on the interactive effects of concurrent increases in atmospheric CO₂ and air temperature on plant growth and development. They report, “increases in CO₂ from 350 to 650 ppm are estimated to result in up to a 5°C rise in T_{opt} [plant optimal growth temperature], primarily because of a reduction in the rate of photorespiration at high temperatures.” They also state, “experiments with *Phaseolus vulgaris* [common garden bean] exposed to low CO₂ T_{opt} can decrease by approximately 4°–5°C with a reduction in CO₂ from 380 to 200 ppm,” citing Cowling and Sage (1998).

Cannariato *et al.* (1999) investigated the character, magnitude, and speed of biotic responses of benthic foraminifera to millennial-scale climate oscillations reconstructed from data obtained from a northeast Pacific Ocean sediment core that extended back in time some 60,000 years. This history revealed a number of rapid climatic switches throughout the record, representing periods of what they call “extreme environmental variability.” They report they observed no extinctions, and the benthic ecosystems “appear to be both resilient and robust in response to rapid and often extreme [changes in] environmental conditions.” They report faunal turnovers occurred within decades throughout the record “without extinction or speciation,” which led them to conclude “broad segments of the biosphere are well adapted to rapid climate change.”

Allen *et al.* (1999) examined an even longer period of time. After analyzing sediment cores from a lake in southern Italy and from the Mediterranean Sea, they developed high-resolution climate and vegetation datasets for this region covering the last 102,000 years. Their efforts revealed rapid changes in vegetation correlated well with rapid changes in climate, such that complete shifts in natural ecosystems would sometimes occur over periods of less than 200 years. They also report, over the warmest portion of the record (the Holocene), the total organic carbon content of the vegetation reached its highest level, more than doubling values experienced over the rest of the record, and during the more productive woody-plant period of the Holocene,

the increased vegetative cover also led to less soil erosion. As the 15 researchers state, “the biosphere was a full participant in these rapid fluctuations, contrary to widely held views that vegetation is unable to change with such rapidity.” They learned warmer was always better in terms of vegetative productivity.

Other studies based on more modern data have continued to demonstrate the unlikelihood of warming-induced plant extinctions. In July/August 2003, for example, Walther *et al.* (2005) resurveyed the floristic composition of the uppermost 10 meters of 10 mountain summits in the Swiss Alps, applying the same methodology used in earlier surveys of the same mountain tops by Rubel (1912), conducted in 1905, and Hofer (1992), conducted in 1985. Their analyses covered the bulk of the Little Ice Age-to-Current Warm Period transition (1905–2003), the warming IPCC claims to have been unprecedented over the past millennium or more in terms of both the rate of temperature rise and the level to which Earth’s temperature rose.

Whereas the mean increase in species numbers recorded by Hofer (1992) for the time interval 1905 to 1985 was 86%, “species numbers recorded in 2003 were generally more than double (138%) compared to the results by Rubel (1912) and 26% higher than those reported by Hofer (1992).” Walther *et al.* write, “the rate of change in species richness (3.7 species per decade) was significantly greater in the later period compared to the Hofer resurvey (1.3 species per decade).” They note “the observed increase in species numbers does not entail the replacement of high alpine specialists by species from lower altitudes, but rather has led to an enrichment of the overall summit plant diversity.”

In spite of the apparent reasonableness of the global warming extinction hypothesis, in which high-altitude species are expected to be “squeezed out of existence”—or “pushed off the planet,” as NASA’s James Hansen once described it, by other species migrating upwards from lower altitudes to escape the increasing stress of rising temperatures, Walther *et al.* could find no sign of this dire consequence over a century of supposedly unprecedented warming in the Swiss Alps.

Kullman (2007) analyzed the changing behavior of alpine and subalpine plants, together with shifts in their geographical patterns over the past century (when air temperatures rose by about 1°C in the Scandes of west-central Sweden), based on “repeat photography, individual age determinations and analyses of permanent plots.” Kullman reports, “at all

levels, from trees to tiny herbs, and from high to low altitudes,” as he describes it, “the results converge to indicate a causal association between temperature rise and biotic evolution,” indicating “this appears to be an ecosystem on the brink of profound and imminent transformation.”

Kullman reports treeline advance since the early twentieth century varied between 75 and 130 meters, depending on species and site, and subalpine and alpine plant species shifted upslope by an average of 200 meters. He writes, “present-day repetitions of floristic inventories on two alpine mountain summits reveal increases in plant species richness of 58 and 67%, respectively, since the early 1950s,” and “no species have yet become extinct from the highest elevations.” He states his results “converge with observations in other high-mountain regions worldwide,” citing Grabherr *et al.* (1994), Keller *et al.* (2000), Kullman (2002), Virtanen *et al.* (2003), Klanderud and Birks (2003), Walther *et al.* (2005), and Lacoul and Freedman (2006).

Kullman concludes the rapidity with which the observed ecosystem transformations occurred “contrasts with earlier assumptions and theoretical generalizations, stressing significant time-lags or inertial adaptations to changed climatic conditions.” His results demonstrate the capacity for vegetation to respond rapidly to climate change in dramatic ways that avert species extinctions and in fact can lead to increases in ecosystem species richness.

Three years later, Kullman reaffirmed his findings in additional works (Kullman, 2010a, 2010b, 2010c). In one of these (Kullman, 2010b), he describes how the post-Little Ice Age warming has broken “a multi-millennial trend of plant cover retrogression” and “floristic and faunal impoverishment, all imposed by progressive and deterministic neoglacial climate cooling.” He says “alpine plant life is proliferating, biodiversity is on the rise and the mountain world appears more productive and inviting than ever.”

Similar observations led Kullman to conclude (Kullman, 2010c), “the alpine flora appears to be more adaptive and responsive to climate change than generally believed,” and “overall, a richer, greener and more productive alpine world has emerged in the wake of the recent climate warming episode (Kullman, 2010a, 2010b).” He makes it very clear that “in contrast to model predictions, no single alpine plant species has become extinct, neither in Scandinavia nor in any other part of the world in response to climate warming over the past century” (Kullman, 2010b), citing, in addition to his own prior

studies, Pauli *et al.* (2001, 2007), Theurillat and Guisan (2001), and Birks (2008). As for the future, Kullman opines, “continued modest warming over the present century will likely be beneficial to alpine biodiversity, geological stability, resilience, sustainable reindeer husbandry and aesthetic landscape qualities” (Kullman, 2010b).

Holzinger *et al.* (2008) revisited areas of 12 mountains with summits between elevations of 2,844 and 3,006 meters in the canton of Grisons (Switzerland). In 2004 they made complete inventories of all vascular plant species they encountered, which they compared with similar inventories made by other researchers in 1885, 1898, 1912, 1913, and 1958, following the ascension paths of the earlier investigators “as accurately as possible.” The four researchers report mean summer temperatures in the studied region increased by at least 0.6°C between the time of the first study and the one they conducted in 2004.

Holzinger *et al.* detected plant upward migration rates of several meters per decade, and their data suggest vascular plant species richness increased by 11% per decade over the past 120 years on the mountain summits (defined as the upper 15 meters of the mountains) in the alpine-nival ecotone. This finding, they write, “agrees well with other investigations from the Alps, where similar changes have been detected (Grabherr *et al.*, 1994; Pauli *et al.*, 2001; Camenisch, 2002; Walther, 2003; Walther *et al.*, 2005).” Regarding the ominous prediction of “the extinction of a considerable number of high-alpine species” in “the context of climate warming,” they conclude this “outstanding threat for species to become out-competed ‘beyond the summits’ can neither be confirmed nor rejected with our data,” suggesting the threat may not be quite as outstanding as the climate models have typically made it out to be.

Erschbamer *et al.* (2009) documented and analyzed changes (from 2001 to 2006) in plant species number, frequency, and composition along an altitudinal gradient crossing four summits from the treeline ecotone to the subnival zone in the South Alps (Dolomites, Italy), where minimum temperatures increased by 1.1–2.0°C during the past century with a marked rise over the last decades. The four researchers report, “after five years, a re-visitation of the summit areas revealed a considerable increase of species richness at the upper alpine and subnival zone (10% and 9%, respectively) and relatively modest increases at the lower alpine zone and the treeline ecotone (3% and 1%, respectively).” They note, “during the last five years, the endemic species of the

research area were hardly affected,” and “at the highest summit, one endemic species was even among the newcomers.” The Austrian scientists conclude, “at least in short to medium time scales, the southern alpine endemics of the study area should not be seriously endangered.”

Kelly and Goulden (2008) compared two vegetation surveys (one made in 1977 and the other in 2006–2007) of the Deep Canyon Transect in Southern California’s (USA) Santa Rosa Mountains that spans several plant communities and climates, rising from an elevation of 244 meters to 2,560 meters over a distance of 16 km “through desert scrub, pinyon-juniper woodland, chaparral shrubland, and conifer forest.” They found “the average elevation of the dominant plant species rose by ~65 meters,” The 30-year mean temperature measured at seven stations around Deep Canyon rose by 0.41°C between 1947–1976 and 1977–2006, and the same metric rose by 0.63°C in the climate regions straddled by the transect, and by 0.77°C at the two weather stations nearest Deep Canyon. They conclude “surprisingly rapid shifts in the distribution of plants can be expected with climate change.”

Alsos *et al.* (2007) analyzed DNA fingerprinting (amplified fragment-length polymorphism) of 4,439 samples from most of the geographic ranges of nine plant species native to the Arctic, studying the Svalbard Archipelago—the islands of which were almost entirely glaciated during the last glacial maximum of 20,000 years ago. They used the genetic data thereby obtained to reconstruct past plant colonization patterns, determining “the frequency of effective long-distance dispersal events, [identifying] the source areas, and [assessing] whether dispersal ability is more limiting than establishment in a new area.”

The nine researchers found long-distance colonization of the Svalbard Archipelago “has occurred repeatedly and from several source regions,” with probable propagule dispersal vectors being “wind, drift wood and drifting sea ice, birds, and mammals.” They write, “the genetic effect of restricted colonization was strongly correlated with the temperature requirements of the species, indicating that establishment limits distribution more than dispersal.”

Given that dispersal mechanisms in existence during the early and mid-Holocene (from 9,500 to 4,000 years before present, when “the climate was 1 to 2°C warmer than today,” as Alsos *et al.* report) are probably “still operating,” they conclude “Arctic species seem to be able to track their potential niche

and ... unlimited dispersal models may be appropriate to estimate long-term range shifts for Arctic regions.”

Le Roux and McGeoch (2008) examined patterns of altitudinal range changes in the entire native vascular flora of sub-Antarctic Marion Island (46°54’S, 37°45’E) in the southern Indian Ocean, which warmed by 1.2°C between 1965 and 2003. Between 1966 and 2006, there was “a rapid expansion in altitudinal range,” with species expanding their upper elevational boundaries by an average of 70 meters. Because “the observed upslope expansion was not matched by a similar change in lower range boundaries,” they emphasize “the flora of Marion Island has undergone range expansion rather than a range shift.” They note “the expansion of species distributions along their cooler boundaries in response to rising temperatures appears to be a consistent biological consequence of recent climate warming,” citing several other studies that have observed the same type of response.

Another consequence of the stability of lower range boundaries together with expanding upper range boundaries is a greater overlapping of ranges, resulting in greater local biodiversity. Le Roux and McGeoch report, “the present species composition of communities at higher altitudes is not an analogue of past community composition at lower altitudes, but rather constitutes a historically unique combination of species,” indicating a world significantly richer, ecologically speaking, than the old one.

Stocklin *et al.* (2009) provide some insight into why plants in the real world tend to undergo a proliferation of species instead of extinction as temperature and atmospheric CO₂ concentration rise. They studied the consequences of the Swiss Alps’ highly structured alpine landscape for evolutionary processes in four plants (*Epilobium fleischeri*, *Geum reptans*, *Campanula thyrsoides*, and *Poa alpina*), testing for whether genetic diversity within their populations was related to altitude and land use while also seeking to determine whether genetic differentiation among populations was more related to different land use or to geographic distances.

The three Swiss scientists found within-population genetic diversity of the four species was high and mostly unrelated to altitude or population size. They also report genetic differentiation among populations was pronounced and strongly increased with distance, implying “considerable genetic drift among populations of alpine plants.” Stocklin *et al.* conclude “phenotypic plasticity is particularly pronounced in alpine plants,” and “because of the high heterogeneity of the alpine landscape, the pronounced

capacity of a single genotype to exhibit variable phenotypes is a clear advantage for the persistence and survival of alpine plants.” They write, “the evolutionary potential to respond to global change is mostly intact in alpine plants, even at high altitude.” These results make it much easier to understand why, despite significant twentieth-century global warming, no species of plants have been observed to have been pushed off the planet, especially in alpine regions.

In an invited paper in *Quaternary Science Reviews*, Vegas-Vilarrubia *et al.* (2011) write, “current extinction estimates for the near-future should be revised in light of palaeoecological information,” which in their view “shows that spatial reorganizations and persistence in suitable micro-refugia have been more common than extinction during the Quaternary.” The four researchers conclude “an interesting consequence is the possibility of new unknown species combinations with no modern analogues.”

Vegas-Vilarrubia *et al.* (2011) note the global warming that occurred at the end of the Younger Dryas (~13,000 to 11,500 years ago) is one of the more powerful analogues of projected future global warming “because both magnitude and rates of change parallel those predicted for the present century.” Although this prior real-world transformation “seems to have consisted of ecological reorganizations and changes in community composition because of differential species migration patterns and rates,” the four researchers point out “so far, it has not been possible to associate large-scale extinctions to the Younger Dryas climatic reversal.” Instead of a model-inspired increase in atmospheric CO₂ triggering catastrophic changes in climate, real-world data from the past suggest rising atmospheric CO₂ will help plants avoid climatic-induced extinctions.

Two phenomena come into play in these ecosystem transformations, according to the Spanish scientists: acclimation and adaptation, “with the first relying on phenotypic plasticity and the second involving genetic changes of potential evolutionary significance,” which have been proposed as “possible reactions to future global warming and as alternatives to extinction by habitat loss.” Vegas-Vilarrubia *et al.* note “some authors propose that spatial reorganizations without extinction will be the dominant biotic response to the near-future global changes.” They add, “it is also possible that ecosystems never attain equilibrium,” and “transient states perpetuate because of the recurrent action of environmental change.” They suggest “one of the main lessons to be learned from these considerations is that ecosystems may

express their resilience when confronted with environmental shifts by attaining several possible equilibrium states, as manifested in changes in biodiversity and/or composition, without losing their ecological functions.”

Willis and MacDonald (2011) note key research efforts have focused on extinction scenarios derived from “a suite of predictive species distribution models (e.g., Guisan and Thuiller, 2005)” —most often referred to as bioclimatic envelope models—that “predict current and future range shifts and estimate the distances and rates of movement required for species to track the changes in climate and move into suitable new climate space.” They report one of the most-cited studies of this type—that of Thomas *et al.* (2004)—“predicts that, on the basis of mid-range climatic warming scenarios for 2050, up to 37% of plant species globally will be committed to extinction owing to lack of suitable climate space.”

In contrast, Willis and MacDonald write, “biotic adaptation to climate change has been considered much less frequently.” This phenomenon—sometimes referred to as evolutionary resilience—they describe as “the ability of populations to persist in their current location and to undergo evolutionary adaptation in response to changing environmental conditions,” citing Sgro *et al.* (2010). They note this approach to the subject “recognizes that ongoing change is the norm in nature and one of the dynamic processes that generates and maintains biodiversity patterns and processes,” citing MacDonald *et al.* (2008) and Willis *et al.* (2009).

Willis and MacDonald examined the effects of significant and rapid warming on plants during several previous intervals of the planet’s climatic history that were as warm as, or even warmer than, what climate models typically predict for the next century. These intervals included the Paleocene-Eocene Thermal Maximum, the Eocene climatic optimum, the mid-Pliocene warm interval, the Eemian interglacial, and the Holocene.

In stark contrast to what IPCC typically does, this approach relies on empirical (as opposed to theoretical), data-based (as opposed to model-based) reconstructions (as opposed to projections) of the past (as opposed to the future). Willis and MacDonald found “persistence and range shifts (migrations) seem to have been the predominant terrestrial biotic response (mainly of plants) to warmer intervals in Earth’s history,” and “the same responses also appear to have occurred during intervals of rapid climate change.” They note “evidence for global extinctions or extinctions resulting from reduction of population

sizes on the scale predicted for the next century owing to loss of suitable climate space (Thomas *et al.*, 2004) is not apparent.” They report an increase in local biodiversity sometimes has been observed.

Feurdean *et al.* (2012) note species distribution models run at finer scales (Trivedi *et al.*, 2008; Randin *et al.*, 2009) or including representations of plant demography (Hickler *et al.*, 2009) and more accurate dispersal capability (Engler and Guisan, 2009) tend to predict much smaller habitat and species loss in response to climate model predictions than do more coarse-scale models (Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Araujo *et al.*, 2008).

The German and Romanian researchers analyzed “seven fossil pollen sequences from Romania situated at different elevations ... to examine the effects of climate change on community composition and biodiversity between 15,000 and 10,500 cal. yr BP in this biogeographically sensitive region of Europe.” This period “was characterized by large-amplitude global climate fluctuations occurring on decadal to millennial time scales (Johnsen *et al.*, 1992; Jouzel *et al.*, 2007),” which enabled them to explore “how repeated temperature changes have affected patterns of community composition and diversity” and to analyze “recovery processes following major disruptions of community structure.”

The four scientists report “community composition at a given time was not only the product of existing environmental conditions, but also the consequence of previous cumulative episodes of extirpation and recolonization.” They found “many circumpolar woody plants were able to survive when environmental conditions became unfavorable,” and “these populations acted as sources when the climate became more favorable again.” The latter behavior, they write, “is in agreement with modeling results at the local scale, predicting the persistence of suitable habitats and species survival within large-grid cells in which they were predicted to disappear by coarse-scale models.”

The findings of Feurdean *et al.* thus add to the growing number of studies demonstrating the shortcomings of “climate envelope” models of both vegetation and animal responses to rising temperatures, which are often used to predict massive species extinctions as a result of the “unprecedented” CO₂-induced global warming predicted by equally deficient climate models.

Dobrowski *et al.* (2013) write, “anthropogenic climate change is considered a threat to ecosystem services and to global biodiversity because of its magnitude, the potential for novel climatic conditions

(Williams *et al.*, 2007), and the rate at which it is occurring (Parmesan and Yohe, 2003; Montoya and Raffaelli, 2010).” They note, “species have always been subject to changing climatic regimes and have responded through adaptation (Davis and Shaw, 2001; Hoffman and Sgro, 2011), changes in phenology (Cleland *et al.*, 2007), range shifts (Davis and Shaw, 2001), and the use of climate refugia (Dobrowski, 2011; Hampe and Jump, 2011).” They write, “the fossil record suggests that widespread extinctions of plant species were rare during periods of rapid warming (~2–10°C/century) such as the Pleistocene-Holocene transition (Willis and MacDonald, 2011),” noting instead of species disappearing, “ecological turnover and range shifts were common responses to rapid climate changes of the past (Botkin *et al.*, 2010; Hof *et al.*, 2011; Willis and MacDonald, 2011).”

The seven U.S. scientists assessed “climate velocity (both climate displacement rate and direction) for minimum temperature, actual evapotranspiration, and climatic water deficit over the contiguous U.S. during the 20th century (1916–2005).” They discovered “a complex picture of the climate in the contiguous U.S.,” where “velocity vectors vary regionally, show variable and opposing directions among the variables considered, and shift direction through time.”

Dobrowski *et al.* found “ T_{min} vectors calculated over decadal and century scales demonstrate complex dynamics (e.g. northerly and southerly directions, direction reversal through time) that vary regionally,” and “climate displacement vectors for metrics of the water balance were predominantly oriented toward the west and south, showing regional variability.” They report “divergent climate vectors between temperature and water balance may help explain why roughly 10–30% of species assessed in previous climate change studies have not shifted their ranges whereas nearly 25% of species have shifted their ranges in a direction counter to expectations (Parmesan and Yohe, 2003; Chen *et al.*, 2011; Crimmins *et al.*, 2011).”

Dobrowski *et al.* say these results “suggest that the expectation of poleward and upward shifts associated with all taxa, previously referred to as a ‘globally coherent fingerprint’ (Parmesan and Yohe, 2003), may be derived from an oversimplification of the climate dynamics that have been observed over the 20th century.” They conclude their findings imply “a more full understanding of changes in multiple climatic factors, in addition to temperature, may help explain unexpected or conflicting observational evidence of climate-driven species range shifts.” They

Earth's Vegetative Future

say “moving away from viewing climate as simple monotonic changes in temperature is a necessary step in advancing our understanding of how species have and will respond to climate shifts.”

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Climate Change Reconsidered II: Biological Impacts

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4.4.2 Stationary Plants

- 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.

The “acid test” for any extinction hypothesis is to examine what appears to be happening—or to have

happened—in the real world. Here we discuss studies of plants fighting to survive under experimental settings or real-world locations where they periodically face threats to their survival and are unable to spread to other areas to escape competition, predation, high temperatures, or other threats.

An experiment that broached the subject of plants threatened by external biological and climatic factors was established in spring 1994 at the Cedar Creek Natural History Area in central Minnesota (USA), where a decade later Lambers *et al.* (2004) quantified the temporal evolution of the productivity and “staying power” of 14 species of plants across an experimental grassland diversity gradient. Over the course of that long-term study, the five researchers learned certain species were over-yielders—plants that grow better and produce more biomass when grown in competition with other species than when grown by themselves. They found six such species: a C_3 grass, three C_4 grasses, and two legumes. The five researchers note these “over-yielding species were either superior N competitors (C_4 grasses) or N fixers (legumes).” They also found five under-yielding species, four of which were forbs that typically grew less robustly when in the presence of other species. The scientists report the over-yielding species were not displacing the under-yielding species over time.

Lambers *et al.* conclude diversity-promoting interactions played a role in this experiment, and “under-yielding species appear to be buffered from extinction.” No one knows how common this phenomenon is, but its operation in this study suggests plants may be much better “buffered from extinction” than many have long supposed. More research should be directed toward elucidating the “diversity-promoting interactions” that maintain the existence of under-yielding species in the face of what might logically be presumed to be significant competitive pressure from average and over-yielding species.

Stinson and Bazzaz (2006) grew well-watered stands of ragweed (*Ambrosia artemisiifolia*) out-of-doors in open-top-chambers maintained at either 360 or 720 ppm CO_2 from their seedling stage to the onset of senescence, then harvested the plants and determined the dry masses of their shoots, roots, and reproductive structures. Prior to this time—at 14, 33, and 52 days after the start of the experiment—they also measured the heights and numbers of leaves of all the plants. The scientists found doubling the atmosphere's CO_2 concentration increased the mean stand-level biomass of the shoots of the ragweed plants by 44% and increased the biomass of their

roots and reproductive structures by 46% and 94%, respectively, for a total CO_2 -induced biomass increase of 70%. They also found the extra CO_2 “reduced the coefficients of variation for all aspects of plant growth, especially reproductive biomass,” so the CO_2 -induced growth enhancements were “more pronounced in small, rather than large plants.” They report, “growth enhancements to smaller plants diminished the relative biomass advantages of larger plants in increasingly crowded conditions,” and “ CO_2 -induced growth gains of subordinate *A. artemisiifolia* plants minimize differences in the reproductive output of small and large plants.”

The Harvard University scientists conclude, “more homogeneous reproduction between subordinates and dominants also implies that a larger number of individuals will contribute propagules to future generations.” This phenomenon, they write, “could in turn affect evolutionary and population dynamics.”

An international team of 33 researchers (Wills *et al.*, 2006) analyzed seven forest dynamics plots located throughout the New and Old World tropics, with a wide range of species richness and tree densities, all of which had been visited and “censused” more than once over the past few decades. For all of the plots they studied, they found “rare species survive preferentially, which increases diversity as the ages of the individuals increase” and “when species were rare in a local area, they had a higher survival rate than when they were common, resulting in enrichment for rare species and increasing diversity with age and size class in these complex ecosystems.”

The researchers offer several explanations for their findings. They note “diversity should increase as a group of individuals ages, because more common species are selectively removed by pathogens and predators,” especially those commonly associated with them. They also note “individuals compete more intensively with conspecifics than with individuals of other species” and “diversity may increase if an individual facilitates (benefits) nearby non-conspecifics.” This facilitation may have “the effect of making interspecific interactions more positive than intraspecific interactions and thus provides an advantage to locally rare species.”

Similarly, in a commentary on these important findings and the phenomena underpinning them, Pennisi (2006) write, “being closer together, common trees are more prone to deadly infections,” and “they may also face stiffer competition for certain resources,” whereas “rarer trees, by depending on

slightly different sets of resources, may not have this problem.” Pennisi quotes Scott Armbruster of the UK’s University of Portsmouth as saying the fact “these patterns are found to be so consistent across so many distant tropical forests suggests to me that the conclusion may eventually be found to hold for other diverse ecosystems as well.”

Londre and Schnitzer (2006) write, woody vines (lianas) around the globe are “competing intensely with trees and reducing tree growth, establishment, fecundity, and survivorship,” possibly because “increasing levels of CO₂ may enhance growth and proliferation of temperate lianas more than of competing growth forms (e.g., trees),” and possibly because “warmer winter temperatures may also increase the abundance and distribution of temperate lianas, which are limited in their distribution by their vulnerability to freezing-induced xylem embolism in cold climates.” The two researchers investigated whether these phenomena had impacted liana abundance and distribution over the prior 45 years in 14 temperate deciduous forests of southern Wisconsin (USA), during which time (1959–1960 to 2004–2005) the atmosphere’s CO₂ concentration rose by 65 ppm, mean annual air temperature in the study region rose by 0.94°C, mean winter air temperature rose by 2.40°C, and mean annual precipitation did not change.

Contrary to their initial hypothesis, the researchers found “liana abundance and diameter did not increase in the interiors of Wisconsin (USA) forests over the last 45 years.” They report *Toxicodendron radicans*—a liana popularly known as poison ivy, which “grew markedly better under experimentally elevated CO₂ conditions than did competing trees (Mohan *et al.*, 2006)” —decreased in abundance over this period, and did so significantly.

Londre and Schnitzer write, “the lack of change in overall liana abundance and diameter distribution in [the] study suggests that lianas are limited in the interiors of deciduous forests of Wisconsin by factors other than increased levels of CO₂,” suggesting it was likely the interior-forest lianas were limited by the enhanced tree growth provided by the CO₂ increase, which likely resulted in the trees becoming more competitive with the vines because of CO₂-induced increases in tree leaf numbers, area, and thickness. These factors would have reduced the amount of light being transmitted to the lianas growing beneath the forest canopy, negating the enhanced propensity for growth provided to the vines by the historical increase in the atmosphere’s CO₂ concentration.

In support of this net-zero competing effects

hypothesis, Londre and Schnitzer found, “compared to the forest interior, lianas were >4 times more abundant within 15 m of the forest edge and >6 times more abundant within 5 m of the forest edge,” and this “strong gradient in liana abundance from forest edge to interior was probably due to light availability.” They report their results “are similar to findings in tropical forests, where liana abundance is significantly higher along fragmented forest edges and within tree fall gaps,” and where the interior tropical trees have not suffered what some have claimed would be the negative consequences of CO₂-induced increases in liana growth, as described in the review of the study of Phillips *et al.* (2002).

Londre and Schnitzer write, because “forest fragmentation (and thus edge creation) has increased significantly over the last half-century, particularly in the northeastern and midwestern United States (e.g., Ritters and Wickham, 2003; Radeloff *et al.*, 2005), liana abundance has likely increased in temperate forests due to forest fragmentation.” Consequently, “as forest fragmentation continues, liana abundance will also likely continue to increase, and the effects of lianas on temperate forests, such as intense competition with trees (Schnitzer *et al.*, 2005), reduced tree growth rates and biomass sequestration (Laurance *et al.*, 2001), and the incidence of arrested gap-phase regeneration (Schnitzer *et al.*, 2000) may become even more pronounced.”

These latter observations remind us that a major cause of biodiversity reductions is not rising atmospheric CO₂ concentrations, but instead the direct encroachment of man upon the world of nature (Waggoner, 1995; Tilman *et al.*, 2001, 2002; Raven, 2002). Such encroachment could deplete the globe’s forests and drive innumerable species of both plants and animals to extinction, unless we can dramatically increase the water use efficiency of our crop plants so we are not forced to encroach further upon forests to obtain the additional land and water resources (Wallace, 2000) we will otherwise need to grow the greater quantities of food required to sustain the growing human population.

Regarding this challenge, Feeley and Silman (2009) write, “ongoing development of the Amazon, including natural gas and oil production, large-scale cattle ranching, soy farming, extended networks of improved roads, and the various synergistic activities that invariably accompany increased access, is causing the rapid loss and degradation of natural habitat,” which can lead to the extinctions of species that live there. The two researchers used various collections of pertinent data to map the potential

ecoregion-based distributions of the more than 40,000 vascular plant species for which collections were available from the Amazon. They estimated rates of habitat loss due to future land-use changes, based on projections made by Soares-Filho *et al.* (2006) of areas that will be deforested by 2050 under business-as-usual and more-optimistic governance scenarios, which they translated into estimated extinction risks for the year 2050.

By AD 2050, they found, human land-use practices will have reduced the habitat available to Amazonian plants by approximately 12–24%, resulting in 5–9% of species becoming “committed to extinction” at that time.

Some regions will suffer more than others. For the largest Amazonian ecoregion—the seasonal Cerrado savannahs of southwestern Brazil that cover about two million square kilometers—Feeley and Silman calculated a habitat loss of 1.5%/year as characteristic of the past three decades, but “habitat loss in the Cerrado has actually accelerated to 3.1–4.3%/year.” They state if they include “historic habitat loss and use a contemporary habitat loss rate of 3.7%, extinction risk for Cerrado species rises to more than 2 times greater than for non-Cerrado species.”

The Cerrado has been losing “natural habitat to agricultural and pastoral land over the past three decades,” Feeley and Silman note, and with the push for greater biofuel production, those habitat losses will accelerate. These incursions, not the ongoing rise in atmospheric CO₂ content, are the great threat to the Amazon’s biodiversity.

Short *et al.* (2011) write about a different species of plants facing extinction threats. They write, “seagrasses, a functional group of marine flowering plants rooted in the world’s coastal oceans, support marine food webs and provide essential habitat for many coastal species, playing a critical role in the equilibrium of coastal ecosystems and human livelihoods.” Seagrasses are also “a component of more complex ecosystems within marine coastal zones, contributing to the health of coral reefs and mangroves, salt marshes and oyster reefs,” they write, citing Dorenbosch *et al.* (2004), Duke *et al.* (2007), Heck *et al.* (2008) and Unsworth *et al.* (2008).

They report that for the first time, “the probability of extinction [has been] determined for the world’s seagrass species under the Categories and Criteria of the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species.” They describe this effort as “a four-year process involving seagrass experts internationally, compila-

tion of data on species’ status, populations, and distribution, and review of the biology and ecology of each of the world’s seagrass species.”

The 26 seagrass experts from 11 countries determined 10 seagrass species (comprising 14% of all seagrass species) are at elevated risk of extinction, with three other species qualifying as endangered. They identified several possible causes of the problem, including suspended sediments and siltation (Dennison *et al.*, 1993; de Boer, 2007), coastal construction, land reclamation, shoreline hardening, and dredging (Erftemeijer and Lewis, 2006), damaging fisheries practices such as trawling and aquaculture (Pergent-Martini *et al.*, 2006), mechanical damage from boats, boat moorings and docks (Burdick and Short, 1999; Kenworthy *et al.*, 2002), introduced species (Williams, 2007) that compete for space and resources (Heck *et al.*, 2000), and certain diseases (Rasmussen, 1997). They conclude “the most common threat to seagrasses is human activity,” not CO₂-induced global warming or ocean acidification.

Mosses offer another example of species under threat of extinction due to human activity, but not CO₂. Gerdol and Vicentini (2011) write, “*Sphagnum* mosses are a fundamental component of bog vegetation in northern regions, where these plants play a major role in controlling important ecosystem processes.” Noting “heat waves are expected to become increasingly intense and frequent, especially in cold territories,” they attempted to ascertain the ability of the mosses to survive such conditions.

The two researchers collected cores of two *Sphagnum* species—*S. fuscum* and *S. magellanicum*—from three mountain heights in the southeastern Alps of the Italian province of Bolzano above sea level: low (1,090 m), intermediate (1,780 m), and high (2,100 m). The locations spanned, they write, “almost the whole altitudinal range known for these species in mountainous regions of central-southern Europe.” In the laboratory, they grew portions of the six cores for four consecutive days at three 12-hour daytime temperature levels—ambient temperature (AT, 25°C), medium temperature (MT, 36°C), and high temperature (HT, 43°C)—and measured net CO₂ exchange and chlorophyll *a* fluorescence, as well as plant tissue chemistry.

The two Italian scientists report normalized net CO₂ exchange rates did not vary among species nor with altitude. Net CO₂ exchange rates in the plants under the MT treatment declined during treatment but recovered noticeably six days after treatment stopped. Despite receiving “severe damage,” the plants experiencing the HT treatment also exhibited a

capacity to recover six days after the conclusion of the temperature treatment. Noting their study suggests “the two *Sphagnum* species possess moderate altitudinal plasticity to increased temperature,” they conclude, “heat waves, even stronger than ever recorded, will unlikely bring about die-off of *Sphagnum* mosses in bog ecosystems unless high temperatures are coupled with drought.”

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Earth's Vegetative Future

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4.5 Evolution

- As good as things currently are for world agriculture, and as significantly better as they are expected to become as the atmosphere's CO₂ content continues to rise, there may be additional substantial room for natural selection and bio-engineering to remove the remaining constraints of low CO₂ adaptation in several important agricultural crops and thereby create novel genotypes able to exploit high CO₂ conditions.

4.5.1 A Major Opportunity

Sage and Coleman (2001) reviewed what is known about plant responses to increases and decreases in atmospheric CO₂ content. They note plants generally photosynthesize at reduced rates and produce less biomass at lower-than-current atmospheric CO₂ levels, and they photosynthesize at enhanced rates and produce more biomass at higher-than-current CO₂ concentrations. At optimal temperatures for C₃-plant photosynthesis, for example, the two researchers write, “reducing atmospheric CO₂ from the current level to 180 ppm [an approximate 50% reduction at that time] reduces photosynthetic capacity by approximately half” and “causes biomass to decline by 50%.” Doubling the atmosphere's CO₂ concentration typically increases photosynthesis and biomass production by 30 to 50%.

Sage and Coleman also report, “high CO₂ concentrations reduce the impact of moderate drought, salinity and temperature stress, and can indirectly reduce low nutrient stress by promoting root growth, nitrogen fixation and mycorrhizal infection.” These phenomena boost the basic CO₂-induced productivity increase still more, as Idso and Idso (1994) noted in an earlier review of the literature. These observations are common knowledge among plant biologists and serve merely as introductory material for Sage and Coleman's hypothesis that modern bioengineering techniques might help make plants even more responsive to increases in atmospheric CO₂ content.

Their reasoning is as follows. During the peak of the last ice age, and throughout the bulk of all prior ice ages of the past two million years, atmospheric

CO₂ concentrations tended to be approximately 180 ppm. This value, according to Sage and Coleman, might not be much above the “critical CO₂ threshold at which catastrophic interactions occur.” Thus they speculated plants of the late Pleistocene “might have been adapted to lower CO₂ concentrations than currently exist.” And in light of the short period of evolutionary time that has elapsed since the last of these low-CO₂ conditions prevailed, the two researchers suggest “many if not most plants might still be adapted to CO₂ levels much lower than those that exist today.”

Literally thousands of laboratory and field experiments have demonstrated Earth’s vegetation responds in dramatic positive fashion to atmospheric CO₂ enrichment far above what is characteristic of the CO₂ conditions of the present. Hence Sage and Coleman conclude as good as things currently are, and as significantly better as they are expected to become as the atmospheric CO₂ content continues to rise, there may be additional “substantial room for natural selection and bioengineering to remove the constraints [of low CO₂ adaptation], thereby creating novel genotypes able to exploit high CO₂ conditions to best advantage.”

That such is possible and even probable is borne out by Ziska *et al.* (1996), who grew well-watered and well-fertilized plants of 17 cultivars of rice from seed to maturity in glasshouses maintained at atmospheric CO₂ concentrations of either 373 or 664 ppm in soil-filled pots kept at two different sets of day/night temperatures (29/21°C and 37/29°C), after which they measured total plant biomass and grain biomass. They report the degree of CO₂-induced enhancement of total plant biomass and the number of cultivars showing significant enhancement with elevated CO₂ decreased at the higher and more stressful set of growth temperatures, dropping from 12 of 17 cultivars with an average biomass stimulation of 70% at the lower set of temperatures to eight of 17 cultivars with a mean biomass stimulation of 23% at the higher set of temperatures. A few cultivars exhibited no significant changes in response to the atmospheric CO₂ enrichment employed in the study, while the most responsive cultivar exhibited a 265% increase in total plant biomass and a 350% increase in grain biomass. The variability in productivity enhancement exhibited by the 17 rice cultivars clearly demonstrates the selection of rice varieties has tremendous potential to take advantage of the aerial fertilization effect of rising atmospheric CO₂ content, which “could maximize productivity as CO₂ concentration increases,” Ziska *et al.* write.

Also noting there is “considerable variability among current rice cultivars in their responses to CO₂ and temperature (Ziska and Teramura, 1992; Ziska *et al.*, 1996; Moya *et al.*, 1998) leading to the possibility of selecting rice cultivars against these two environmental variables for yield increases and/or stability in a possibly warmer, but almost certainly higher future CO₂ world,” Baker (2004) grew the Southern United States rice cultivars Cocodrie, Jefferson, and Cypress for an entire season in outdoor, naturally sunlit, controlled-environment chambers at a constant day/night temperature of 28°C at CO₂ concentrations of 350 and 700 ppm. In the following year he grew the cultivar Lamont under the same conditions, but at day/night temperatures of 27/23°C, as a main crop and ratoon (stubble) crop.

In the first of these experiments, grain yield per plant rose by 46%, 57%, and 71% in response to the doubling of the atmospheric CO₂ content in the Cocodrie, Jefferson, and Cypress cultivars, respectively. In the second experiment, with the Lamont cultivar, it rose by 12% when the rice was grown as a main crop but by 104% when it was grown as a ratoon crop. Baker concludes, “the wide range in grain yield responsiveness to CO₂ enrichment found among these four US rice cultivars points to the potential for selecting or developing high yielding US rice cultivars with the ability to take advantage of expected future global increases in CO₂,” noting “CO₂ enrichment could have potentially large positive effects on ratoon crop yields.”

Sage and Coleman note the low CO₂ levels of the past “could have had significant consequences for much of the Earth’s biota.” They suggest the origin of agriculture itself “might have been impeded by reduced ecosystem productivity during low CO₂ episodes of the late Pleistocene.” Since then, the increase in atmospheric CO₂ content has essentially doubled the biological prowess of the planet’s vegetation, and projected increases in atmospheric CO₂ content could readily lead to a tripling of the productivity of Earth’s ice-age past. In addition, the three studies reviewed above suggest there may be other opportunities to improve plant performance even more by using modern bioengineering techniques to overcome genetic constraints linked to adaptations to low levels of CO₂ that may persist in many plants. For agriculture, Sage and Coleman suggest, “this could be a major opportunity to improve crop productivity and the efficiency of fertilizer and water use.”

These studies demonstrate we are living in an age of unparalleled biological promise. The fullness of

that promise has yet to be achieved, and how effectively we exploit the opportunities to do so, as Sage and Coleman write, “will depend on our ability to conduct the basic research [needed] to identify the genes controlling acclimation and adaptation to CO₂ variation.”

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4.5.2 CO₂-Induced

- The ongoing rise in atmospheric CO₂ content likely is exerting significant selection pressure on Earth's naturally occurring terrestrial plants, which should improve their resistance to various environmental stressors via the process of micro-evolution as the air's CO₂ concentration continues to rise in the years and decades ahead.

The ongoing rise in atmospheric CO₂ content likely is exerting significant selection pressure on Earth's naturally occurring terrestrial plants, which should improve their resistance to various environmental stressors via the process of micro-evolution. Plants may be much better prepared than we have commonly believed to meet whatever climatic challenges,

including global warming, the future may pose for them. Moreover, 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.

Two decades ago, Root and Schneider (1993) 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.” 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, especially as it pertains to CO₂-induced changes in natural (i.e., non-agricultural) terrestrial vegetation, the topic examined in the scientific studies reviewed below.

Rae *et al.* (2007) note various studies “are beginning to identify genes that appear sensitive to elevated CO₂ (Gupta *et al.*, 2005; Taylor *et al.*, 2005; Ainsworth *et al.*, 2006),” while “leaf growth responses to elevated CO₂ have been found in *Populus*” and “quantitative trait loci (QTL) for this response [have been] determined (Rae *et al.*, 2006).” Continuing this endeavor, they studied a three-generation *Populus* pedigree generated by the hybridization of two contrasting *Populus* species—where two full-siblings from the resulting F1 family were crossed to form an F2 family—growing cuttings of the different generations for 152 days out-of-doors in open-top chambers maintained at either the ambient CO₂ concentration or concentrations on the order of 600 ppm. They measured various plant properties and physiological processes and determined QTL for above- and below-ground growth and genotype-by-environment interactions.

The four UK researchers report, “in the F2 generation, both above- and below-ground growth showed a significant increase in elevated CO₂,” and “three areas of the genome on linkage groups I, IX and XII were identified as important in determining above-ground growth response to elevated CO₂, while an additional three areas of the genome on linkage groups IV, XVI and XIX appeared important in determining root growth response to elevated CO₂.” Consequently, stating their results “quantify and identify genetic variation in response to elevated CO₂ and provide an insight into genomic response to the changing environment,” they conclude further work in this area “should lead to an understanding of

micro-evolutionary response to elevated CO₂,” as subsequent studies have further demonstrated.

Springer *et al.* (2008) grew well-watered and well-fertilized plants of two closely related out-crossed genotypes (SG and CG) of *Arabidopsis thaliana*, generated via artificial selection, in controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 380 or 700 ppm. They selected genotype SG for high seed number at elevated CO₂ over five generations, and they randomly chose genotype CG to serve as a control. They measured time to flowering, number of leaves at flowering, and total biomass at flowering, as well as foliar sugar concentrations. In a second experiment conducted under the same growing conditions, they characterized the expression patterns of several floral-initiation genes.

They found “SG delayed flowering by 7–9 days, and flowered at a larger size (122% higher biomass) and higher leaf number (81 more leaves) when grown at elevated versus current CO₂ concentration,” but “flowering time, size and leaf number at flowering were similar for CG plants grown at current and elevated CO₂.” They note “SG plants had 84% higher foliar sugar concentrations at the onset of flowering when grown at elevated versus current CO₂, whereas foliar sugar concentrations of CG plants grown at elevated CO₂ only increased by 38% over plants grown at current CO₂.” They report, “SG exhibited changes in the expression patterns of floral-initiation genes in response to elevated CO₂, whereas CG plants did not.”

Noting “delayed flowering increases production of vegetative resources that can be subsequently allocated to reproductive structures,” the researchers conclude “such evolutionary responses may alter total carbon gain of annual plants if the vegetative stage is extended, and may potentially counteract some of the accelerations in flowering that are occurring in response to increasing temperatures.” Their results demonstrate the ability of elevated CO₂ to alter the expression of plant genes in ways that may enable plants to take better advantage of the ongoing rise in atmospheric CO₂ content.

Lau *et al.* (2008) measured the amount of pathogen damage caused by *Pythium* or *Fusarium* spp. to the common prairie legume *Lespedeza capitata* growing in ambient and elevated (560 ppm) CO₂ treatments in the seventh and eighth full years (2004 and 2005) of the BioCON study (Reich *et al.*, 2001) conducted at the Cedar Creek Natural History Area in Minnesota (USA), where they applied the CO₂ treatments during the daylight hours of each

growing season. They found disease incidence was lower in the elevated CO₂ environment (down by 10% in 2004 and 53% in 2005). “Because disease caused major reductions in reproductive output,” the five researchers conclude, “the effects of CO₂ on disease incidence may be important for *L. capitata* evolution and population dynamics.” They note Strengbom and Reich (2006), “working in the same experimental site ... also found that elevated CO₂ ... reduced disease incidence on *Solidago rigida*.”

Kaligarić *et al.* (2008) investigated fluctuating asymmetry (FA), which describes the magnitude of random deviations from perfect symmetry in morphological traits of both plants and animals that “offers a unique tool for comparative studies of developmental stability (Møller and Swaddle, 1997)” and has been used as “an indicator of genetic and environmental stress (Martel *et al.*, 1999; Cornelissen and Stiling, 2004)” in plants. They 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* 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 meters, respectively, from the CO₂ source.

The four researchers 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).” They report, “*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 atmospheric CO₂ content increased. They conclude “adaptation and selection could explain the tendency towards decreased leaf FA in plants from the CO₂ spring relative to ambient conditions,” because “the more symmetrical leaves under long-term elevated CO₂ concentration were more developmentally stable in these conditions.”

Onoda *et al.* (2009) write the ongoing rise in atmospheric CO₂ content “is likely to act as a selective agent” among 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 add, “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 by studying plants growing around natural CO₂ springs, where they “have been exposed to a CO₂-enriched atmosphere over many generations,” providing what the researchers call “a unique opportunity to explore the micro-evolutionary response of wild plants to elevated CO₂.”

Onoda *et al.* 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.” They assessed the plants’ photosynthetic nitrogen use efficiency (PNUE), water use efficiency (WUE), and the degree of carbohydrate accumulation in the plants’ leaves, which if too large can lead to 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 identify “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.” They write, a molecular study “also found relatively large genetic differentiation across the CO₂ gradient in these plants.” 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 atmospheric CO₂ content continues to rise. This phenomenon should enable plants to fare even better in the CO₂-enriched air of the future than they do today.

Cseke *et al.* (2009) note certain perceived “genetic and environmental bottlenecks” may limit a plant’s capacity to allocate assimilated carbon to

greater biomass production. However, it is plausible that numerous species may possess the genetic diversity needed to overcome these potential roadblocks and thereby benefit more than is commonly anticipated from the enhanced growth known to be possible in a CO₂-enriched atmosphere.

Working at the Aspen FACE site near Rhinelander, Wisconsin (USA), Cseke *et al.* grew two quaking aspen (*Populus tremuloides* Michx.) clones (216 and 271) from the seedling stage in replicate plots maintained at either 372 or 560 ppm CO₂ throughout each year’s growing season (May–September), assessing their stem volume (a surrogate for biomass) annually for a period of eight years. They measured the trees’ maximum light-saturated rates of leaf net photosynthesis, the transcriptional activity of leaf elevated-CO₂-responsive genes, and numerous leaf primary and secondary carbon-based compounds. The CO₂-induced increase in the maximum light-saturated rate of leaf net photosynthesis in clone 216 was more than twice as great as that of clone 271 (37% vs. 17%, as best as can be determined from Cseke *et al.*’s bar graphs); they found just the opposite relationship in the CO₂-induced increases in the trees’ stem volumes, which increased only 0–10% for clone 216 but. 40–50% for clone 271.

The researchers’ transcript abundance and carbon/nitrogen biochemistry data suggest “the CO₂-responsive clone (271) partitions carbon into pathways associated with active defense/response to stress, carbohydrate/starch biosynthesis and subsequent growth,” whereas “the CO₂-unresponsive clone (216) partitions carbon into pathways associated with passive defense and cell wall thickening.” The seven scientists conclude there was “significant variation in expression patterns between different tree genotypes in response to long-term exposure to elevated CO₂,” and “future efforts to improve productivity or other advantageous traits for carbon sequestration should include an examination of genetic variability in CO₂ responsiveness.” As the atmosphere’s CO₂ concentration continues to rise, manifestations of these fitness-promoting traits will appear on their own, brought forth naturally by the changing environment, as plants appear to be genetically programmed to respond positively to atmospheric CO₂ enrichment. Plants are innately well-prepared to use the ongoing rise in the air’s CO₂ concentration to their advantage.

Nakamura *et al.* (2011) suggest “evolutionary responses to elevated CO₂ in wild plants are, in general, difficult to detect using growth experiments, because the duration of experiments is often too short

Climate Change Reconsidered II: Biological Impacts

compared to the time required for evolution.” They note areas around natural CO₂ springs—and locations nearby but beyond the influence of the additional CO₂—provide ideal sources of plants for such studies, as the plants near the springs have “been exposed to high CO₂ over an evolutionary time scale,” citing Miglietta *et al.* (1993) and Raschi *et al.* (1999).

Nakamura *et al.* conducted experiments designed to reveal numerous characteristics of *Plantago asiatica* plants (a C₃ rosette perennial herb) acquired from locations at different distances from a stream emerging from a CO₂-emitting spring situated at the foot of Mount Gassan (Japan), where the plants had been exposed to normal ambient (370 ppm) and several elevated (726, 771, 1,044, and 5,339 ppm) CO₂ concentrations, as measured in late August and early September in two years presumed to have been typical of CO₂ concentrations at those locations over what they called “an evolutionary time scale.”

The six scientists “found phenotypic differences between populations in areas with high and normal CO₂, some of which were heritable,” indicating “an evolutionary differentiation occurred in the *P. asiatica* population across a CO₂ gradient.” One of these differences was in plant relative growth rate, which, they write, “was higher in parent plants that originated in areas with higher CO₂, suggesting that plants from higher-CO₂ populations had an inherent potential for higher productivity.” They conclude “a higher potential of biomass production contributes to fitness and has selective advantages.”

Noting their results are “consistent with those of previous experiments, wherein artificial selection increased seed production under the respective CO₂ condition compared to non-selected plants (Ward *et al.*, 2000; Ward and Kelly, 2004),” Nakamura *et al.* conclude their study “clearly shows that phenotypic and genetic differences have occurred between high and normal CO₂ populations.”

The scientific findings described above indicate the ongoing rise in atmospheric CO₂ content is exerting significant selection pressure on naturally occurring terrestrial plants, which should improve their resistance to environmental stressors via the process of micro-evolution as atmospheric CO₂ concentrations continue to rise.

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4.5.3 Warming-Induced

- Plants may exhibit a rapid evolutionary response to temperature modifications, making them much better prepared than scientists have long believed to meet whatever possible challenge higher temperatures might pose.

IPCC contends CO₂-induced global warming will result in mass plant extinctions because many species will not be able to migrate poleward in latitude or upward in altitude fast enough to find temperature regimes suitable for their continued existence. That scenario assumes plants cannot evolve quickly enough to increase their ranges to keep up with the effects of warming, and that they cannot adjust their inner workings to be able to tolerate more heat than they seem capable of enduring at present. The papers reviewed below explore those possibilities.

Gunter *et al.* (2000) note many models of actual or attempted range shifts in response to global warming lack a thorough understanding of “the role that acclimation and genetic adaptation may have in a species’ response to predicted climate regimes,” stating if populations “have a greater capacity for adjustment to higher temperatures, and if they are not

constrained by complete genetic isolation from other populations, then the effects of global warming will probably be less severe than what may be predicted from a simple temperature-response curve applied without regard to spatial or temporal genetic variation.”

The four researchers employed random amplified polymorphic DNA markers to evaluate population-level genetic structure as an indirect indicator of the capacity for response to environmental change by sugar maple trees from three geographical locations representing a north-south gradient of that species’ current distribution. They found “genetic diversity, as indicated by estimates of percent polymorphic loci, expected heterozygosity, fixation coefficients, and genetic distance, is greatest in the southern region, which consists of populations with the maximum potential risk due to climate change effects.” They say “the high degree of variation within sugar maple implies that it may contain genetic mechanisms for adaptation.”

Gunter *et al.* note sugar maple range shift potentials derived by the Goddard Institute for Space Studies (Hansen *et al.*, 1983) and NASA’s Geophysical Fluid Dynamics Laboratory (Manabe and Wetherald, 1987)—as described by Davis and Zabinski (1992)—“assume that a species grows only in a climate with temperature and precipitation identical to its current range.” In a significant rebuff of those studies and their alarmist implications, Gunter *et al.* note existing “high levels of genetic variation among families indicate that vegetational models designed to predict species’ responses to global-scale environmental change may need to consider the degree and hierarchical structure of genetic variation when making large-scale inferences.” The ability of species to adapt to a changing environment may be far greater than what is presumed by the outdated climate envelope approach.

Hamrick (2004) also noted concerns that “expected changes may be of such an extent that tree species will not have adequate genetic variation to adapt to the modified conditions (Critchfield, 1984; Davis and Zabinski, 1992)”; “environmental changes may occur at such a rapid rate that trees, with their long generation times, could not adapt quickly enough to keep pace with predicted changes (Davis and Shaw, 2001)”; and trees “may not be capable of dispersing into newly available habitats quickly enough to match the rate of environmental change (Clark, 1998).”

In reviewing the findings of several studies that focused on the responses of trees to conditions

analogous to those of computer-generated simulations of rapid global warming, Hamrick found “trees combine life-history traits and levels of genetic diversity that will allow them to adapt relatively quickly to environmental changes,” noting they have high genetic mobility via pollen. The plant biology and genetics professor also notes “tree species have faced large-scale global environmental changes many times during their evolutionary histories,” and even though these changes “occurred quite quickly, most tree species have survived,” maintaining traits that “may allow many tree species to survive predicted global climatic changes while preserving much of their genetic diversity.”

Jump *et al.* (2006) write, “one of the basic assumptions in the study of plant adaptation to environment (genecology) is that natural selection in different environments generates genetic clines that correlate with environmental clines.” They point out “temperature is of major importance as a selective agent causing population differentiation over altitudinal and latitudinal clines (Saxe *et al.*, 2001),” and “temporal changes in gene frequency that result from global warming should therefore mirror spatial changes observed with decreasing altitude and latitude.” These changes, they write, are typically manifest in particular alleles that “may be confined to, or occur preferentially in, different sites with contrasting environmental conditions.”

The four researchers “combined population genomic and correlative approaches to identify adaptive genetic differentiation linked to temperature within a natural population of the tree species *Fagus sylvatica* L. [European beech] in the Montseny Mountains of Catalonia, northeastern Spain,” concentrating on three areas: the upper treeline (high *Fagus* limit, HFL), the lower limit of *F. sylvatica* forest (low *Fagus* limit, LFL), and an area of the forest interior.

Jump *et al.* note the 648-meter altitudinal difference that separates the HFL and LFL locations “equates to a mean temperature difference of 3°C ... based on the altitudinal lapse rate of 0.51°C per 100 meters reported by Peñuelas and Boada (2003) for Montseny.” Regarding the change in temperature due to the region’s manifestation of twentieth-century global warming, they write, “by 2003, temperatures had increased by approximately 1.65°C when compared with the 1952–1975 mean,” and this temperature change, they remark, was “likely to represent a strong selection pressure.”

Numerous tests conducted by Jump *et al.* on the data they collected reveal the frequency of a

particular *F. sylvatica* allele shows a predictable response to both altitudinal and temporal variations in temperature, with a declining frequency and probability of presence at the HFL site the Spanish research team determined to be “in parallel with rising temperatures in the region over the last half-century.” They say their work “demonstrates that adaptive climatic differentiation occurs between individuals within populations, not just between populations throughout a species geographic range,” which further suggests “some genotypes in a population may be ‘pre-adapted’ to warmer temperatures (Davis and Shaw, 2001).”

Jump *et al.* also contend “the increase in frequency of these genotypes,” which occurred in their study in parallel with rising temperatures, “shows that current climatic changes are now imposing directional selection pressure on the population,” and “the change in allele frequency that has occurred in response to this selection pressure also demonstrates that a significant evolutionary response can occur on the same timescale as current changes in climate,” citing Davis *et al.* (2005), Jump and Peñuelas (2005), and Thomas (2005).

Jump *et al.* conclude an evolutionary response to global warming of the type they describe is likely already “underway,” which further suggests many species of plants probably will not be forced to migrate either poleward in latitude or upward in altitude in response to global warming, as climate models suggest they will be forced to do. Instead, they will adjust their ranges (meaning, expand them) at the cold-limited boundaries of their ranges, and they may not be forced to make any major changes at the heat-limited boundaries of their ranges.

Keller *et al.* (2011) note “studies on the evolution of plant populations during historical fluctuations in climate can reveal the capacity for and constraints on adaptive evolution and may help inform predictions about evolutionary responses to future environments.” They tested for adaptive variation in 13 ecophysiology and phenology traits on clonally propagated genotypes of balsam poplar (*Populus balsamifera* L.) trees originating from a range-wide sample of 20 subpopulations that developed during the warming of climate conditions that marked the end of the last glacial maximum (~18 thousand years ago), when there was a rapid environmental change that increased population sizes and led to range expansions in many plant species. This “wave of migrations,” they write, “affected genomic diversity within populations, as colonists sub-sampled alleles from the ancestral gene pool during the process of expansion,” as described

by Lascoux *et al.* (2004), Petit *et al.* (2004), and Savolainen and Pyhajarvi (2007). The six scientists report, “evidence for divergence in excess of neutral expectations was present for eight of thirteen traits,” noting “strong correlations were present between traits, geography [extending across the whole of Canada from the Atlantic to Pacific Oceans], and climate.” These results, they conclude, reveal “a general pattern of northern subpopulations adapted to shorter, drier growing seasons compared with populations in the center or eastern regions of the range.”

Keller *et al.* say their study “demonstrates pronounced adaptive variation in ecophysiology and phenology among balsam poplar populations,” suggesting “as this widespread forest tree species expanded its range since the end of the last glacial maximum, it evolved rapidly in response to geographically variable selection.” It is likely to do so again if circumstances warrant; as they conclude, “balsam poplar is both highly variable and capable of a broad range of adaptive physiological responses to a changing climate.”

Niu *et al.* (2012) write, “it is well documented that plants (Mooney *et al.*, 1978; Berry and Bjorkman, 1980; Atkin and Tjoelker, 2003), animals (Parmesan, 2006), and microbes (Bradford *et al.*, 2008) acclimate and/or adapt to prevailing environmental conditions in a way that can optimize their functioning under varying temperatures, which is collectively termed optimality (Parker and Maynard Smith, 1990).” They hypothesize “the integrated response of an ecosystem, as an assemblage of interacting organisms, might also demonstrate thermal optimality under temperature change,” citing Loreau (2010).

Niu *et al.* “compiled data from 169 globally distributed sites of eddy covariance and quantified the temperature response functions of net ecosystem exchange (NEE), an ecosystem-level property, to determine whether NEE shows thermal optimality and to explore the underlying mechanisms.”

The team of 68 researchers from 19 countries writes, “the temperature response of NEE followed a peak curve, with the optimum temperature (corresponding to the maximum magnitude of NEE) being positively correlated with annual mean temperature over years and across sites.” They state, “shifts of the optimum temperature of NEE were mostly a result of temperature acclimation of gross primary productivity (upward shift of optimum temperature) rather than changes in the temperature sensitivity of ecosystem respiration.” They report, “extended growing seasons,

increased nitrogen mineralization, and enhanced root growth (Peñuelas and Filella, 2001; Churkina *et al.*, 2005; Luo *et al.*, 2009) may also have contributed to the increased CO₂ uptake under higher temperatures, leading to the upward shift in the optimum temperature of gross primary productivity in warmer years.”

Pluess and Weber (2012) write, “with increasing temperatures and dryer summers [as predicted by various climate models], areas nowadays covered by beech forests are expected to shrink tremendously,” but “if individuals at the dry distribution limits [of the species: *Fagus sylvatica* L.] are adapted to lower moisture availability, *F. sylvatica* might contain the genetic variation for the continuation of beech forests under climate change,” even in areas predicted to become devoid of the trees.

The two researchers used an AFLP (amplified fragment length polymorphism) genome scan approach designed to explore the “neutral and potentially adaptive genetic variation in *Fagus sylvatica* in three regions [in the lowland forests of Switzerland] containing a dry and mesic site each,” after which they “linked this dataset with dendro-chronological growth measures and local moisture availabilities based on precipitation and soil characteristics.” They found a “potential for adaptation to water availability” reflected in observed outlier alleles that “indicated micro-evolutionary changes between mesic and dry stands.” They also note, “while Rose *et al.* (2009) found adaptation to drought in a common garden experiment with seedlings originating from provenances which were more than 1000 km apart,” their own work found genetic differentiation in relation to water availability in neighboring stands. Pluess and Weber conclude “dispersal across large distances is thereby not needed for the spread of ‘pre-adapted’ genes in *F. sylvatica*,” for the trees apparently have the genetic material needed for “the continuation of beech forests under climate change,” even in areas that have been predicted to become too dry for *F. sylvatica* trees to survive.

Hahn *et al.* (2012) note “altitudinal gradients comprise an assemblage of environmental, especially climatic, variables which influence the distribution of plant species and, potentially, population genetic variation.” They also note some scientists argue climate change may alter species distributions such that, locally, certain species “might become extinct,” citing Sala *et al.* (2000) and Thomas *et al.* (2004). The basis for this prediction, the six scientists write, are the observations, “habitat suitability typically decreases at the upper edge of the altitudinal range

where population size might decline,” and “in small populations genetic diversity is often reduced and inbreeding may increase (Lynch *et al.*, 1995; Young *et al.*, 1996),” with the result that “low genetic diversity and high inbreeding potentially cause loss of fitness due to fixation of deleterious alleles and inbreeding depression (Ouborg *et al.*, 1991; Lynch *et al.*, 1995; Young *et al.*, 2002), which could affect future population persistence.”

Hahn *et al.* investigated patterns of population genetic variation in three common plants of semi-dry grasslands—*Briza media*, a wind-pollinated grass, and *Trifolium montanum* and *Ranunculus bulbosus*, two insect-pollinated herbs—at upper peripheral and lower more central altitudes in the Swiss Alps using the AFLP technique. The Swiss researchers determined, contrary to what many had long supposed, altitude had not affected genetic diversity in the grassland species they studied. They report their results indicate “populations at the upper periphery are not genetically depauperate or isolated” and thus may be “important populations for migration under climate change.” Hahn *et al.* conclude what they call the “potentially pre-adapted genes” of the three plant species might “spread easily across altitudes,” which would help to prevent their local extinction in a warming world.

Thompson *et al.* (2013) write, “in addition to changes in distribution and plasticity, an evolutionary response to climate change may occur if species evolve a genetically-based adaptation to climate change,” citing Chevin *et al.* (2010) and Hoffmann and Sgro (2011). They note “it is important to distinguish this genetic response from a plastic response of individuals if we are to fully understand the evolutionary potential of species to evolve with climate change,” as has been described by Gienapp *et al.* (2008).

To test the hypothesis that phenolic chemotypes (thymol and carvacrol) of Mediterranean wild thyme (*Thymus vulgaris*) now occur in sites where they were previously absent or have increased their frequency in transitional sites due to a relaxation of selection normally associated with extreme early winter freezing, the team of eight researchers compared the chemotype composition of populations observed in the early 1970s (Vernet *et al.*, 1977) to that found in 2009–2010 for 36 populations sampled along six transects in and around the Saint Martin-de-Londres basin, which covers an area of about 80 km² with southern limits about 20 km north of Montpellier in the Mediterranean climate region of southern France.

The eight French researchers discovered “a rapid

and probably ongoing spatial reorganization of a genetic polymorphism that is closely associated with a warming of extreme winter freezing events on a highly localized spatial scale,” observing “both a significant appearance of freezing-sensitive phenolic chemotypes in sites where they were historically absent and an increase in their frequency in previously mixed populations.” Thompson *et al.* conclude their study, “done over a similar time span as work reporting ecological changes in plant species distribution, illustrates that a rapid evolutionary response to temperature modifications can occur where genetic variation is combined with a change in a previously strong selection pressure, even for a perennial woody plant.”

Matter *et al.* (2013) write, “gene flow connects populations, maintains genetic diversity, prevents inbreeding and facilitates the spread of adaptive genes across a species range,” citing Slatkin (1985, 1987) and Ellstrand and Elam (1993). They further state, “understanding how plant populations are connected by gene flow, particularly across altitudinal gradients in mountain regions, will improve our understanding of how they will respond to future environmental change.” The four Swiss scientists studied patterns of historic gene flow, flowering phenology, and contemporary pollen flow in two common herbs (*Ranunculus bulbosus* and *Trifolium montanum*) along an altitudinal gradient of 1200–1,800 meters a.s.l. over a distance of 1 km among five alpine meadows in Switzerland.

“Historic gene flow was extensive,” they write, with their data suggesting “contemporary pollen flow is not limited across altitudes in either species.” They conclude “high levels of pollen flow among altitudes in both *R. bulbosus* and *T. montanum* should facilitate exchange of genes which may enhance adaptive responses to rapid climate change.”

The observations discussed above suggest plants may be much better prepared to meet upcoming climatic challenges than most scientists once believed.

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4.5.4 Drought-Induced

- Evidence continues to accumulate for substantial heritable variation of ecologically important plant traits, including root allocation, drought tolerance, and nutrient plasticity, which suggests plants should be capable of rapid evolution based on epigenetic variation alone.

One generally thinks of evolution as acting over very long spans of time. This section explores whether evolution can occur more quickly to help plants cope with the rapid climatic changes IPCC predicts will be caused by continued increases in the atmosphere's CO₂ content.

Franks *et al.* (2007) compared “phenotypic and fitness values of ancestral, descendant, and ancestral x descendant hybrid genotypes [of field mustard (*Brassica rapa*)] grown simultaneously” under conditions that mimicked those before and after a real-world switch from above-average to below-average precipitation in southern California (USA), which led to abbreviated growing seasons from 2000 to 2004. They had “collected *B. rapa* seed in 1997, before the drought, and then again in 2004 from two populations,” a dry site and a wet site. Hence they could grow—at the same time and under the same circumstances, in a new set of experiments—plants that had experienced extended drought conditions (descendants) and plants that had not experienced such conditions (ancestors), as well as hybrids of the two, and thus could see whether flowering times (FT) differed, as is likely from life history theory, which “predicts that the optimal FT in annual plants will be shorter with shorter growing seasons,” such as those that were imposed by the extended drought that occurred between the two times of their seed collecting.

The three researchers found, as predicted, “the abbreviated growing seasons caused by drought led to the evolution of earlier onset of flowering,” as plant descendants “bloomed earlier than ancestors, advancing first flowering by 1.9 days in one study population and 8.6 days in another.” They state, “the intermediate flowering time of ancestor x descendant hybrids supports an additive genetic basis for divergence.” They conclude, “natural selection for drought escape thus appears to have caused adaptive evolution in just a few generations,” further noting, “abundant evidence has accumulated over the past several decades showing that natural selection can cause evolutionary change in just a few generations (Kinnison and Hendry, 2001; Reznick and Ghalambor, 2001).”

Franks *et al.* write their findings “provide evidence for a rapid, adaptive evolutionary shift in flowering phenology after a climatic fluctuation,” which “adds to the growing evidence that evolution is not always a slow, gradual process but can occur on contemporary time scales in natural populations” and in response to real-world climatic changes.

In a follow-up study conducted with the same plant material, Franks and Weis (2008) report several life-history traits “differed between the ancestral genotypes collected before and descendant genotypes collected after the natural drought,” stating “this shows directly that an evolutionary change in the life-history traits has occurred during a 5-year drought.”

They also report “the evolutionary changes in trait levels following the drought are consistent with predictions from life-history theory” because “the drought selected for individuals that flowered earlier, continued to flower for longer given sufficient resources, and produced a more consistent, evenly distributed pattern of flowering over time.” These changes, they write, constitute “a true genetically based evolutionary change rather than an expression of phenotypic plasticity.”

Jump *et al.* (2008) studied *Fumana thymifolia* (a small shrub that occurs around the Mediterranean Basin) at Spain’s Garraf Natural Park, seeking to determine whether reduced seedling establishment observed as a consequence of climate manipulation is a random or selective process, in an attempt to answer what they called “the key question”: Does climate change provoke evolutionary change within natural populations?

As an unaltered control treatment, the seven scientists’ study had a drought treatment that employed automatically activated transparent plastic shields that covered a third of the plots in response to rainfall and retreated when rainfall stopped (which decreased soil moisture by approximately 20%), and a warming treatment employing reflective covers that reduced nighttime re-radiation of energy received from the Sun during the prior daylight hours from another one-third of the plots (which increased temperature by about 1°C).

Over the seven-year period 1999–2005, Jump *et al.* report, mean yearly seedling density per treatment was significantly reduced in the drought and warming treatments compared with the control treatment, and “when compared against control samples, high single-locus genetic divergence occurred in drought and warming treatment samples, with genetic differentiation up to 37 times higher than background (mean neutral locus) genetic differentiation.”

The researchers say the significant reduction in seedling survival in the drought and warming treatments “results from an episode of selection for individuals tolerant of the modified climatic conditions and is not due simply to a random reduction in plant establishment.” This implication, they write, “reinforces results reported by other authors that show that genetic variability for climate-related traits exists within natural plant populations (Hamrick and Holden, 1979; Cobb *et al.*, 1994; Kelly *et al.*, 2003; Mitton and Duran, 2004; Franks *et al.*, 2007).”

Jump *et al.* conclude contemporary climate change “is driving changes in gene frequency within

natural plant populations,” and these changes “are occurring on the same time scale as current climatic changes, based on preexisting genetic variability within populations,” citing Jump and Peñuelas (2005), Thomas (2005), Jump *et al.* (2006), and Reusch and Wood (2007). They state this ability to adapt rapidly to rapid climate change may increase the persistence of species “beyond that predicted under a species-based climate envelope approach,” such as IPCC typically uses to justify predictions of impending extinctions of species.

In a conclusion that clearly repudiates the catastrophic extinction scenario, Jump *et al.* state their results demonstrate “that rapid evolution in response to climate change may be widespread in natural populations, based on genetic variation already present within the population.” The accumulating evidence suggests plants are likely to be much more resilient to rising temperatures and reductions in precipitation than people have long been led to believe.

Franks and Weis (2009) write, “one rigorous way to determine if evolution has occurred in a natural population is to collect propagules before and after an environmental change and raise them under common conditions,” noting “this approach was used previously to show that *Brassica rapa* [a self-incompatible weedy winter annual] evolved drought escape through earlier flowering following a series of recent dry years in Southern California, and that early flowering results in higher fitness under drought conditions (Franks *et al.*, 2007),” and “a related study showed that multiple phenological traits and their interactions evolved in response to the drought (Franks and Weis, 2008).”

Working with the same pre- and post-drought collection lines as were used in the Franks *et al.* (2007) experiment, the two researchers set out to estimate the amount of assortative mating within, and the degree of phenological isolation between, two *B. rapa* populations. They found “climate change can alter plant phenology, which can change patterns of assortative mating within populations,” and “this assortative mating can directly change genotype frequencies and can also increase the rate of evolution by interacting with selection.” Their work demonstrates “climatically driven changes in phenology can potentially influence gene flow among populations due to changes in overlap in flowering schedules,” and “these changes in gene flow can also influence both the rate and pattern of evolutionary change.”

The two scientists conclude “the high degree of

interdependence of flowering time, assortative mating, selection and gene flow make predicting evolutionary responses to changes in climate particularly complex and challenging.” This great degree of complexity suggests that among the multiplicity of outcomes there is a good chance one or more will be just what plants need to respond successfully to the climate change that elicited the changes.

Vigouroux *et al.* (2001) write, “one important phenomenon that is often overlooked and is poorly documented is the ability of agro-systems to rapidly adapt to environmental variations.” Such adaptations, they note, can occur by the adoption of new varieties or by the adaptation of existent varieties to a changing environment. Working in “one of the driest agro-ecosystems in Africa, the Sahel,” they “analyzed samples of pearl millet landraces collected in the same villages in 1976 and 2003 throughout the entire cultivated area of Niger,” to see how the agro-system had responded to recurrent drought over that time. They studied “phenological and morphological differences in the 1976 and 2003 collections by comparing them over three cropping seasons in a common garden experiment.”

The 15 researchers write, “compared to the 1976 samples, samples collected in 2003 displayed a shorter lifecycle and a reduction in plant and spike size.” They also report an early flowering allele “increased in frequency between 1976 and 2003,” and this increase “exceeded the effect of drift and sampling, suggesting a direct effect of selection for earliness on this gene.” Vigouroux *et al.* conclude “recurrent drought can lead to selection for earlier flowering in a major Sahelian crop,” reinforcing the earlier findings of Franks *et al.* (2007), Franks and Weis (2008, 2009), and Jump *et al.* (2008).

Pluess and Weber (2012) note, “with increasing temperatures and dryer summers [as predicted by various climate models], areas nowadays covered by beech forests are expected to shrink tremendously,” but “if individuals at the dry distribution limits [of the species: *Fagus sylvatica* L.] are adapted to lower moisture availability, *F. sylvatica* might contain the genetic variation for the continuation of beech forests under climate change,” even in areas predicted to become devoid of the trees.

Pluess and Weber employed an AFLP genome scan approach designed to explore the “neutral and potentially adaptive genetic variation in *Fagus sylvatica* in three regions [within the lowland forests of Switzerland] containing a dry and mesic site each.” They “linked this dataset with dendrochronological

growth measures and local moisture availabilities based on precipitation and soil characteristics.”

The two Swiss scientists report a “potential for adaptation to water availability” was reflected in observed outlier alleles that “indicated micro-evolutionary changes between mesic and dry stands.” They note, “while Rose *et al.* (2009) found adaptation to drought in a common garden experiment with seedlings originating from provenances which were more than 1000 km apart,” Pluess and Weber found genetic differentiation in relation to water availability in neighboring stands. They conclude, “dispersal across large distances is thereby not needed for the spread of ‘preadapted’ genes in *F. sylvatica*,” for the trees apparently contain the genetic material needed for “the continuation of beech forests under climate change,” even in areas predicted to become too dry for *F. sylvatica* trees to survive.

Zhang *et al.* (2012) note “a key question in ecology and evolution is to what degree variation in ecologically important traits is heritable, because heritability determines the potential for evolutionary change of traits (Fisher, 1930; Falconer and MacKay, 1996),” and this phenomenon significantly enhances the ability of a species “to adapt to changing environments (Visser, 2008; Hoffmann and Sgro, 2011).” Zhang *et al.* conducted a glasshouse experiment in which they tested the response of a large number of epigenetic recombinant inbred lines, or epiRILs (lines that are nearly isogenic but highly variable at the level of DNA methylation, which can stably alter the gene expression pattern in cells) of *Arabidopsis thaliana* to drought and increased nutrient conditions.

The four researchers found “significant heritable variation among epiRILs both in the means of several ecologically important plant traits and in their plasticities to drought and nutrients.” They state the significant selection gradients of the several mean traits and plasticities they discovered “suggest that selection could act on this epigenetically based phenotypic variation.” They conclude their study “provides evidence that variation in DNA methylation can cause substantial heritable variation of ecologically important plant traits, including root allocation, drought tolerance and nutrient plasticity, and that rapid evolution based on epigenetic variation alone should thus be possible.”

These findings bode well for the future of terrestrial plants, even if a significant degree of global warming resumes after its ongoing decade-and-a-half hiatus.

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5

Terrestrial Animals

Key Findings

Introduction

5.1 The Extinction Hypothesis

- 5.1.1 Model Shortcomings
- 5.1.2 Paleoecological Records
- 5.1.3 Other Studies

5.2 Amphibians

5.3 Arthropods

5.4 Birds

- 5.4.1 Population Dynamics
- 5.4.2 Range Expansion
- 5.4.3 Adaptation, Evolution, and Phenotypic Responses

5.5 Insects

- 5.5.1 Aphids
- 5.5.2 Moths
- 5.5.3 Other Herbivores
- 5.5.4 Butterflies
- 5.5.5 Other Insects

5.6 Mammals

5.7 Parasites and Other Diseases

5.8 Polar Bears

- 5.8.1 Population
- 5.8.2 Life History
- 5.8.3 Nutrition and Reproductive Success
- 5.8.4 Effects of More Open Water

5.9 Reptiles

5.10 Worms

Key Findings

The following bullet points summarize the main findings of this chapter:

- The Intergovernmental Panel on Climate Change's (IPCC's) view 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 used to predict the impact of climate on the health and distributions of animal species. Assumptions and limitations make those models unreliable in projecting the future in this regard.
- As in past species extinctions, future species losses are unlikely to be directly attributable to climate changes that act over long terms and to which species are well adapted. Species losses in the future are more likely to be attributable to the novel, relatively rapid twentieth and twenty-first century anthropogenic processes of habitat loss and the transportation-mediated dispersal of pathogens and predators (including man) into previously isolated populations.
- The planet's animal species have inherent abilities enabling them to cope with climate changes over a period of a few generations, a single generation, or even in real time.
- Research suggests amphibian populations will

Climate Change Reconsidered II: Biological Impacts

suffer little, if any, harm from projected CO₂-induced global warming, and they may even benefit from it.

- Enhanced plant productivity driven by elevated levels of atmospheric CO₂ tends to support greater abundance of soil microarthropods.
- 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.
- Published research indicates rising temperatures will not likely 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.
- Global warming is creating opportunities for butterflies to expand their populations and ranges, just the opposite of alarmist projections of range contractions and butterfly species demise in response to a CO₂-induced warming of Earth.
- The warming-induced extinctions of mammals that have been predicted to occur are highly unlikely to be realized in nature, and warming in fact opens new territories for mammal range expansions. In addition, rising atmospheric CO₂ concentrations may produce changes in the palatability of the trunk and branch tissues of certain trees that may protect them from being killed by hares and rabbits.
- The likely net effect of climate change on the spread of parasitic and vector-borne diseases is complex and at this time difficult to predict. Rising temperatures increase the mortality rates as well as the development rates of many parasites, and temperature is only one of many variables that influence the range of viruses and other sources of diseases.
- 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 commercial hunting by humans, which historically has taken a huge toll on polar bear populations.

- Studies of the effects of rising temperatures on reptiles find they often are able to tolerate a greater range of environmental conditions than they have been exposed to in the recent past, demonstrate abilities to thermo-regulate to achieve body temperatures close to their preferred temperatures, and often benefit from warmer temperatures.
- It appears earthworms and soil nematodes respond to increases in the air's CO₂ content, via a number of plant-mediated phenomena, in ways that further enhance the positive effects of atmospheric CO₂ enrichment on plant growth and development, while helping to sequester more carbon more securely in the soil and thereby reducing the potential for CO₂-induced global warming.

Introduction

The draft Summary for Policymakers from the Intergovernmental Panel on Climate Change's (IPCC) Working Group II contribution to the *Fifth Assessment Report* makes the following claims about the impact of climate change on species:

In response to ongoing climate change, terrestrial and marine species have shifted their ranges, seasonal activities, migration patterns, and abundance, have demonstrated altered species interaction (*high confidence*). Increased tree mortality, observed in many places worldwide, has been attributed to climate change in some regions. While recent warming contributed to the extinction of many species of Central American amphibians (*medium confidence*), most recent observed terrestrial-species extinctions have not been attributed to recent climate change, despite some speculative efforts (*high confidence*). Natural climate change at rates much slower than current anthropogenic change has led to significant ecosystem shifts, including species emergences and extinctions, in the past million years (IPCC-II, 2014, p. 3).

While this language is somewhat more nuanced than

past IPCC reports, the necessary qualifications and uncertainties are missing from this language appearing later in the same draft report:

A large fraction of terrestrial and freshwater species faces increased extinction risk under projected climate change during and beyond the 21st century, especially as climate change interacts with other pressures, such as habitat modification, over-exploitation, pollution, and invasive species (*high confidence*). Extinction risk is increased under all RCP scenarios, with risk increasing with both magnitude and rate of climate change. Many species will be unable to move fast enough during the 21st century to track suitable climates under mid- and high-ranges rates of climate change (i.e., RCP4.5, 6.0, and 8.5) (*medium confidence*). See Figure SPM.5. Management actions can reduce, but not eliminate, risks to ecosystems and can increase ecosystem adaptability, for example through reduction of other stresses and habitat (Ibid., pp. 8–9).

These conclusions are overly alarmist and unsupported by scientific research. The primary error made by IPCC's authors is to ignore the growing anomaly between climate model simulations and real-world observations of global temperature. The world in fact is not warming as fast as IPCC predicts, the twentieth century warming was not as "unprecedented" as IPCC previously thought, transient climate response is likely to be less than once thought, the risk of damaging increases in drought or tropical cyclones is lower, and so on (Idso *et al.*, 2013a; Idso *et al.*, 2013b). All of these concessions and walk-backs have implications for the impacts of climate change on terrestrial animals, all of them seemingly positive, yet Working Group II's Summary for Policymakers makes no concessions. A large body of research thus must be treated with considerable caution because of the resulting exaggeration of species range shifts and erroneous climate projections at regional scales.

Even assuming IPCC climate models were unbiased and reasonably accurate at regional scales, the material presented in this chapter reveals IPCC's view of future species extinction relies on a narrow view of the literature that is highly selective. It is based almost entirely on "climate envelope" model projections that often contradict real-world observations. It is clear the SAR-based (species-area-relationship) extinction estimates pioneered by Thomas *et al.* (2005) exaggerate future extinction rates due to the inherent bias of structural errors (He and Hubbell, 2012) and by systematically disregard-

ing any species that benefit from climate change (Stockwell, 2004). IPCC also improperly characterizes the adaptive responses (e.g., range shifts, phenotypic or genetic adaptations) of many species as supporting its model-based extinction claims. In reality such adaptive responses provide documentary evidence of species *resilience*, proving their ability to cope with present and future climate changes as they have so often done throughout the historic and geologic past.

The findings cited in this chapter make it clear that when confronted with climate change or other challenges, terrestrial animals ranging from amphibians and arthropods to insects, polar bears, and worms exhibit opportunistic and highly adaptive behaviors. Ranges do not suddenly shrink as wildlife passively endures changes to its habitat, as is often projected in model-based studies. Instead, the species fortify themselves against the possibility of extinction, behaving as resilient evolutionary survivors and colonizing new habitat as it becomes available, strengthening their populations against the myriad challenges associated with environmental change.

This chapter begins with a review and analysis of the IPCC-based species extinction claim, highlighting many of the problems inherent in the models on which such claims are based and examples from the paleoecological record where species responded to and survived climate changes similar to or greater than those forecast by IPCC. Model projections are then evaluated against real-world observations of how various animal species responded to what IPCC has called the unprecedented rise in atmospheric CO₂ and temperature of the twentieth and twenty-first centuries. Although there likely will be some changes in species population dynamics in the decades and centuries ahead, few if any species are likely to be driven even close to extinction by global warming. In several 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 in its reports such positive externalities of rising temperature and atmospheric CO₂.

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5.1 The Extinction Hypothesis

- IPCC's view 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.

5.1.1 Model Shortcomings

The species extinction hypothesis began to appear in the discussion of potential impacts of CO₂-induced global warming in the late twentieth and early twenty-first centuries. Thomas *et al.* (2004), for example, developed projections of future habitat distributions for more than a thousand plant and animal species. Using those projections, they produced estimates of extinction probabilities associated with climate change scenarios for the year 2050 promoted by IPCC (IPCC, 2007). Their ominous projections (the extinction of more than a million species if anthropogenic CO₂ emissions were not quickly and dramatically reduced) were widely disseminated to the popular media even before the research was published. The projections were typically portrayed as well-founded scientific predictions of what was bound to occur.

The 19 authors first determined the "climate envelopes" of 1,103 species, each envelope representing the current climatic conditions under which a given species was found in nature. Then, after selecting those species where the habitat area would be expected to decrease in response to an increase in temperature, they used an empirical power-law relationship that relates species number to habitat area size to determine extinction probability calculations.

At first blush, their procedure seems reasonable enough, all else being equal. But all else is rarely equal when something changes in the real world. Stockwell (2004) provided an entirely different analysis of the available data, noting most climate change effects research accentuates the "losers" while deprecating the "winners." Stockwell notes Thomas *et al.*'s approach to the issue "ignores species that are currently threatened with extinction by non-climatic factors, and which could therefore benefit from an expanded potential habitat and so escape extinction in the new CO₂/climate regime." As Stockwell describes it, "a CO₂- or climate-driven range expansion would clearly help species that are threatened with extinction due to increasing habitat loss attributable to expanding urbanization and agricultural activities; while it may help other species that are threatened with extinction by habitat fragmentation to cross geographical barriers that were previously insurmountable obstacles to them." Consequently, he continues, "by neglecting the many species that fall into these and other like categories, no decrease in extinctions is possible under Thomas *et al.*'s approach to the problem, even under [a] free dispersal scenario, with the result that a massive increase in extinctions is a foregone conclusion."

Stockwell further notes, "the no dispersal scenario also forces an unrealistic decrease in range with any climatic change that shifts habitat area without reducing it; while 'overfitting' reduces ranges even more, producing systematic errors on the order of 10–20%, particularly with smaller data sets, deficiencies in data sampling and modeling methods, and the inclusion of irrelevant variables (Stockwell and Peterson 2002a; 2002b; 2003)."

With respect to Bakkenes *et al.* (2002), one of the studies relied on by Thomas *et al.*, for example, Stockwell writes, "two independent climate variables adequately explain 93% of the variation in their dependent variable; while the use of more climate variables ends up incorporating more random variation than it does actual signal, leading to a contraction of the climate envelope and a systematic bias towards smaller predicted ranges." It should come as no surprise, therefore, as Stockwell continues, "that in this study and that of Peterson *et al.* (2002)—which comprise two of the six major studies on which the analysis of Thomas *et al.* is based—the use of only two climate variables by the two studies yields extinction percentages of 7% and 9%, while the four additional studies upon which Thomas *et al.* rely (which use from 3 to 36 independent variables) yield extinction percentages

ranging from 20% to 34%, consistent with what would be expected from errors associated with statistical over-fitting.”

Because these ecological models are so unreliable, the common-sense response should be to attempt to verify model-based projections with independent data. However, Stockwell notes, “their single attempt to do so with a real-world extinction supposedly caused by global warming (Pounds *et al.*, 1999) has been satisfactorily explained by changes in local weather patterns due to upwind deforestation of adjacent lowlands (Lawton *et al.*, 2001).” Stockwell concludes, “Thomas *et al.* have a dearth of pertinent hard data to support their contentions; and while the absence of evidence does not necessarily disprove a claim, the lack of any real extinction data to support the results of their analysis certainly suggests that the models they are using are not ‘tried and true’.”

Stockwell concludes, “Thomas *et al.* (2004) seek to create the impression of impending ecological disaster due to CO₂-induced global warming, claiming their results justify mandating reductions of greenhouse gas emissions,” but their findings “are forced by the calculations, confounded with statistical bias, lack supporting real-world evidence, and are perforated with speculation.” Stockwell concludes “their doctrine of ‘massive extinction’ is actually a case of ‘massive extinction bias’.”

It may be argued Thomas *et al.* provide a service to conservation by raising awareness of the potential for species extinction due to climate change, but promoting biased methods that are poorly developed and unsupported by evidence is not scientifically responsible. The discrepancy between the forecasts of future impacts that include large-scale range reduction has yet to be reconciled with the relatively few extinctions from quite large and rapid climate changes in the past (Moritz and Agudo, 2013).

Botkin *et al.* (2007) are highly critical of the application of such methods, particularly when the results are at variance with the evidence provided by the fossil record. And in another critique of the Thomas *et al.* paper, Dormann (2007) found it important to “review the main shortcomings of species distribution models and species distribution projections” such as those employed and derived by Thomas *et al.* He carefully analyzed three aspects of what he described as “problems associated with species distribution models.”

The first of these aspects is general species distribution model issues, under which Dormann listed four major problems. The second is extrapolation issues, where he found five major problems; and

the third is statistical issues, where he listed six major problems. The methods employed and findings claimed by studies such as Thomas *et al.*, Dormann writes, “have been challenged for conceptual and statistical reasons” by many other researchers, including Buckley and Roughgarden (2004), Harte *et al.* (2004), Thuiller *et al.* (2004), Lewis (2006), and Botkin *et al.* (2007). Dormann thus concludes, “projections of species distributions are not merely generating hypotheses to be tested by later data” but instead are being presented as “predictions of tomorrow’s diversity, and policy makers and the public will interpret them as forecasts, similar to forecasts about tomorrow’s weather,” which he clearly believes is unwarranted and unwise.

Detailed intercomparative studies have borne out these concerns about the quality of species’ distribution models. Forecasts of the future geographic distribution of six species of *Falco* from northern Europe ranged from a contraction in 80% of the species to no net loss in any species, seriously hampering their efficacy in conservation practices (Rodriguez-Castaneda *et al.* 2012).

The most effective criticism has been of the method used to estimate extinction rates by reversing the species-area accumulation curve, a species-area relationship (SAR) used to estimate extinction rates before they are actually observed, the so-called “extinction debt” owing to reduction in habitat and population size during a climate change. Researchers He and Hubbell (2011) show Thomas *et al.* (2005) overestimate the extinction debt from habitat loss largely due to a sampling artifact.

Pereira *et al.* (2012) responded by claiming He and Hubbell’s SAR estimates are themselves biased. Thomas and Williamson (2012) report extinction is caused by many factors, not just habitat loss, and species already have responded to climate change in a manner consistent with high future extinction risks. In reply, He and Hubbell (2012) show the Pereira *et al.* (2012) claims are not substantiated and the SAR method of Thomas *et al.* (2005) is not appropriate for estimating extinction rates caused by habitat loss of any kind, concluding, “this so-called backward SAR method is a method for estimating endemic species, not ‘extinction debt.’ The backward SAR method has nothing to do with, and does not measure, extinction debt.” Subsequent debate has clarified the proofs and results are general and explain the widely recognized overestimation of extinction by the backward SAR method, which should not be used to estimate species extinction in practice (He and Hubbell, 2013).

Despite the multitude of problems associated with

Climate Change Reconsidered II: Biological Impacts

the Thomas *et al.* paper, the extinction hypothesis was revived by Parmesan (2006). In reviewing 866 papers addressing the subject of ecological and evolutionary responses to the global warming of the prior few decades, Parmesan raised new concerns about the ability of Earth's many species of plants and animals to maintain a viable foothold on the planet if temperatures continue to rise. But much of the evidence cited by Parmesan actually weighs *against* this concern.

Parmesan notes "most observations of climate-change responses have involved alterations of species' phenologies." She reports, for example, many species had exhibited "advancement of spring events," such that there was "a lengthening of vegetative growing season in the Northern Hemisphere," which is something most would consider a positive phenomenon. She also reports "summer photosynthetic activity increased from 1981–1991"—another positive response—and the growing season throughout the United States "was unusually long during the warm period of the 1940s," but "since 1996, growing season length has increased only in four of the coldest, most-northerly zones (42°–45° N latitude), not in the three warmest zones (32°–37° N latitude)."

The negativity Parmesan associates with these mostly positive warming-induced phenological changes arises from the possibility there may be "mismatches" across different trophic levels in natural ecosystems, such as between the time each year's new crop of herbivores appears and the time of appearance of the plants they depend on for food. Eleven plant-animal associations were studied intensively in this regard, and in seven of them, Parmesan states, "they are more out of synchrony now than at the start of the studies."

Of course there always will be winners and losers (some big and some small) in such animal-plant matchups during periods of climate change, and probably many "draws." In addition, the paucity of pertinent data at the time of the Parmesan study precluded a valid determination of which of the three alternatives is the most likely to predominate. As one example of a "big loser" in the face of recent global warming, Parmesan reports, "field studies have documented that butterfly-host asynchrony has resulted directly in population crashes and extinctions." But population extinctions are not species extinctions, and she acknowledges the local extinctions to which she referred merely resulted in "shifting [the] mean location of extant populations northward [in the Northern Hemisphere] and

upward." Newer research conducted since the publication of Parmesan's study suggests there could be many more wins and draws than losses as species cope with and adapt to such trophic mismatches.

A second major biological response to global warming addressed by Parmesan is species migration, often said to lead to range restrictions that make it difficult for species to maintain the minimum viable population size required for their continued existence. For example, it is often claimed global warming will be so fast and furious that many species will not be able to migrate poleward in latitude or upward in altitude rapidly enough to avoid extinction, or if located on mountaintops they will run out of suitable new habitat to which they can flee when faced with rising temperatures. On this subject, Parmesan essentially rehashed the earlier findings of the meta-analyses of Root *et al.* (2003) and Parmesan and Yohe (2003), which predominantly portrayed species ranges as expanding in the face of rising temperatures, since warming provides an opportunity for species to expand their ranges at their cold-limited boundaries while often providing a much reduced impetus for them to retreat at the heat-limited boundaries of their ranges. An example of this phenomenon cited by Parmesan occurred in the Netherlands between 1979 and 2001, where she reports "77 new epiphytic lichens colonized from the south, nearly doubling the total number of species for that community."

Parmesan also reports "increasing numbers of researchers use analyses of current intraspecific genetic variation for climate tolerance to argue for a substantive role of evolution in mitigating negative impacts of future climate change," additionally noting the fossil record contains "a plethora of data indicating local adaptation to climate change at specific sites." In addition, she states, there is evidence many existing species during earlier periods of dramatic climate change "appeared to shift their geographical distributions as though tracking the changing climate." In both of these situations the outcomes were clearly positive.

The greatest push by Parmesan for a decisively negative consequence of global warming is her claim that "documented rapid loss of habitable climate space makes it no surprise that the first extinctions of entire species attributed to global warming are mountain-restricted species," "many cloud-forest-dependent amphibians have declined or gone extinct on a mountain in Costa Rica (Pounds *et al.*, 1999, 2005)," and "among harlequin frogs in Central and South American tropics, an astounding 67% have

disappeared over the past 20–30 years,” citing Pounds *et al.* (2006) regarding the latter. Such claims subsequently were shown by several researchers to be incorrect (see Amphibians, Section 5.2), as all the extinctions and disappearances of the amphibian species to which Parmesan referred had nothing at all to do with “rapid loss of habitable climate space” at the tops of mountains. As Pounds *et al.* (2006) note, the loss of these species “is largest at middle elevations, even though higher-elevation species generally have smaller ranges.” In addition, as noted in an earlier review of the subject by Stuart *et al.* (2004), many of the amphibian species declines “took place in seemingly pristine habitats,” which had not been lost to global warming nor even modestly altered. The extinctions and species disappearances appeared not to have been due to rising temperatures *per se*, but to the fungal disease chytridiomycosis, which is caused by *Batrachochytrium dendrobatidis*, as noted by both Stuart *et al.* (2004) and Pounds *et al.* (2006).

The fallacy of the montane range restriction assumption was shown by Tingley *et al.* (2012) in a study of breeding ranges of birds across three elevational transects in the Sierra Nevada Mountains (USA). While rising temperature over the past century pushed species upslope, they found increased precipitation pulled them downslope, resulting in range shifts that were heterogeneous within species and among regions. Thus despite increasing temperature in montane environments, the highly variable precipitation regimes create highly heterogeneous responses by species at range margins.

Other studies have poked further holes in the model-based animal extinction hypothesis, some for similar reasons, others for new ones.

Noting “climate envelopes (or the climatic niche concept) are the current methods of choice for prediction of species distributions under climate change,” Beale *et al.* (2008) state, “climate envelope methods and assumptions have been criticized as ecologically and statistically naive (Pearson and Dawson, 2003; Hampe, 2004),” and “there are many reasons why species distributions may not match climate, including biotic interactions (Davis *et al.*, 1998), adaptive evolution (Thomas *et al.*, 2001), dispersal limitation (Svenning and Skov, 2007), and historical chance (Cotgreave and Harvey, 1994).”

Beale *et al.* evaluated the degree of matchup of species distributions to environment by generating synthetic distributions that retained the spatial structure of observed distributions but were randomly placed with respect to climate. They report, “using

data on the European distribution of 100 bird species, we generated 99 synthetic distribution patterns for each species,” and “for each of the 100 species, we fitted climate envelope models to both the true distribution and the 99 simulated distributions by using standard climate variables.” They determined the goodness-of-fit of the many distribution patterns, because, as they note, “there has been no attempt to quantify how often high goodness-of-fit scores, and hence ostensibly good matches between distribution and climate, can occur by chance alone.”

The three U.K. researchers determined “species-climate associations found by climate envelope methods are no better than chance for 68 of 100 European bird species.” And, they write, “because birds are perceived to be equally strongly associated with climate as other species groups and trophic levels (Huntley *et al.*, 2004),” their results “cast doubt on the predictions of climate envelope models for all taxa.” They further state, “many, if not most, published climate envelopes may be no better than expected from chance associations alone, questioning the implications of many published studies.” The researchers conclude, “scientific studies and climate change adaptation policies based on the indiscriminate use of climate envelope methods irrespective of species sensitivity to climate may be misleading and in need of revision.”

These results are not so surprising in view of the well-known ecological principle that critical life-history events and interspecies relationships often can be the major factor limiting the spread of a species. Correspondingly, seasonal climate and ecosystem productivity variables have been found to be more statistically significant determinants of range than the broader annual climate variables typically used in ecological niche models (Stockwell, 2006).

Nogues-Bravo (2009) states climate envelope models “are sensitive to theoretical assumptions, to model classes and to projections in non-analogous climates, among other issues.” He reviewed the pertinent scientific literature to determine how appropriate existing models were for determining whether a species will be driven to extinction by hypothesized planetary warming. He explains, “the studies reviewed: (1) rarely test the theoretical assumptions behind niche modeling such as the stability of species climatic niches through time and the equilibrium of species with climate; (2) they only use one model class (72% of the studies) and one paleoclimatic reconstruction (62.5%) to calibrate their models; (3) they do not check for the occurrence of non-analogous climates (97%); and (4) they do not

use independent data to validate the models (72%).”

Nogues-Bravo notes, “ignoring the theoretical assumptions behind niche modeling and using inadequate methods for hindcasting” may produce “a cascade of errors and naïve ecological and evolutionary inferences.” He concludes, “there are a wide variety of challenges that [climate envelope models] must overcome in order to improve the reliability of their predictions through time.”

Randin *et al.* (2009) focused their attention on the quality of species distribution models (SDMs). They note, “the mean temperature interpolated from local stations at a 20-meter resolution contains more variability than expressed by the mean temperature within a 50-km x 50-km grid cell in which variation in elevation is poorly represented.” Or, as they describe elsewhere in their paper, “climatic differences along elevation gradients, as apparent at 25-m x 25-m resolution, allow plant species to find suitable climatic conditions at higher elevation under climate change,” whereas “models at a 10’ x 10’ resolution [10 minutes of latitude x 10 minutes of longitude, which correspond to 16-km x 16-km cells in the Swiss Alps, where they carried out their analyses] reflect the mean climatic conditions within the cell, and thus provide imprecise values of the probability of occurrence of species along a thermal gradient.”

In testing this “local high-elevation habitat persistence hypothesis,” Randin *et al.* assessed “whether climate change-induced habitat losses predicted at the European scale (10 x 10’ grid cells) are also predicted from local-scale data and modeling (25-m x 25-m grid cells).” For 78 mountain species modeled at both European and local scales, they found the “local-scale models predict persistence of suitable habitats in up to 100% of species that were predicted by a European-scale model to lose all their suitable habitats in the area.”

Randin *et al.* suggest the vastly different results they obtained when using fine and coarse grid scales might help explain what they call the Quaternary Conundrum: “why fewer species than expected went extinct during glacial periods when models predict so many extinctions with similar amplitude of climate change (Botkin *et al.*, 2007).” In addition, they note, “coarse-resolution predictions based on SDMs are commonly used in the preparation of reports by the Intergovernmental Panel on Climate Change,” which are then used by “conservation planners, managers, and other decision makers to anticipate biodiversity losses in alpine and other systems across local, regional, and larger scales.”

Willis and Bhagwat (2009) discuss other problems that arise from coarse model scales. In a “perspective” published in *Science* the two raised a warning flag, stating, “coarse spatial scales fail to capture topography or ‘microclimatic buffering’ and they often do not consider the full acclimation capacity of plants and animals,” citing Botkin *et al.* (2007).

As an example of this model-based deficiency, Willis and Bhagwat cite Randin *et al.* (2009), noting for alpine plant species growing in the Swiss Alps, “a coarse European-scale model (with 16 km by 16 km grid cells) predicted a loss of all suitable habitats during the 21st century, whereas a model run using local-scale data (25 m by 25 m grid cells) predicted persistence of suitable habitats for up to 100% of plant species.” The two Europeans note Luoto and Heikkinen (2008) “reached a similar conclusion in their study of the predictive accuracy of bioclimatic envelope models on the future distribution of 100 European butterfly species,” finding “a model that included climate and topographical heterogeneity (such as elevational range) predicted only half of the species losses in mountainous areas for the period from 2051 to 2080 in comparison to a climate-only model.”

Another problem was the models’ failure to consider the capacity of plants and animals to acclimatize to warmer temperatures. Willis and Bhagwat note “many studies have indicated that increased atmospheric CO₂ affects photosynthesis rates and enhances net primary productivity—more so in tropical than in temperate regions—yet previous climate-vegetation simulations did not take this into account.” They cite Lapola *et al.* (2009), who developed a new vegetation model for tropical South America, the results of which indicate “when the CO₂ fertilization effects are considered, they overwhelm the impacts arising from temperature,” so “rather than the large-scale die-back predicted previously, tropical rainforest biomes remain the same or [are] substituted by wetter and more productive biomes.”

“Another complexity,” note Willis and Bhagwat, is the fact that “over 75% of the Earth’s terrestrial biomes now show evidence of alteration as a result of human residence and land use,” which has resulted in “a highly fragmented landscape” that has been hypothesized to make it especially difficult for the preservation of species. Nevertheless, they report Prugh *et al.* (2008) have “compiled and analyzed raw data from previous research on the occurrence of 785 animal species in >12,000 discrete habitat fragments on six continents,” and “in many cases, fragment size

Terrestrial Animals

and isolation were poor predictors of occupancy.” They further note “this ability of species to persist in what would appear to be a highly undesirable and fragmented landscape has also been recently demonstrated in West Africa,” where “in a census on the presence of 972 forest butterflies over the past 16 years, Larsen [2008] found that despite an 87% reduction in forest cover, 97% of all species ever recorded in the area are still present.”

Suggitt *et al.* (2011) note “most multi-cellular terrestrial organisms experience climate at scales of millimeters to meters,” yet “most species-climate associations are analyzed at resolutions of kilometers or more,” in what is “commonly known as the ‘bioclimate approach’ or ‘climate envelope’ modeling.” They write, “because individuals experience heterogeneous microclimates in the landscape, species sometimes survive where the average background climate appears unsuitable,” which the vast majority of bioclimate studies do not consider in their analyses.

Suggitt *et al.* recorded temperatures in numerous microsites at two locations where the vegetation was relatively homogenous (the Lake Vyrnwy Royal Society for the Protection of Birds reserve in Wales, and High Peak in the Peak District National Park in England) in September 2007 and January 2008, and in numerous microsites within three habitat types (woodland, heathland, and grassland) in Skipwith Common in North Yorkshire, UK, in September 2008 and January 2009. The seven scientists report, “thermal differences between habitats, and slope and aspects, were of the same order of magnitude as projected increases in global average surface temperatures,” and in some cases, microclimate temperature variations exceeded estimates of warming under all of IPCC’s emissions scenarios, “which range from 1.1 to a 6.4°C rise in global mean temperatures (IPCC, 2007).”

Suggitt *et al.* add, “these large temperature differences provide opportunities for individual organisms that are able to move short distances to escape unfavorable microclimates,” and, hence, “populations may shift microhabitats (slopes, aspects and vegetation density) in response to inter-annual variation in the climate.” They state their results indicate “the incorporation of habitat and topographical information is essential for species that (a) have some level of flexibility in their habitat associations, and (b) are at least partially limited by temperature extremes.” In the real world of nature, the “bioclimate approach” and “climate envelope” modeling are not adequate for describing how species will respond to future changes in climate.

Sears *et al.* (2011) analyzed how spatial heterogeneity can impact biological responses to thermal landscapes at scales more relevant to organisms than the (much larger) scales typically employed by standard climate envelopes. They examined the effects of topographic relief on the range of operative temperatures available for behavioral thermoregulation of animals within various parts of an area described by a given climate envelope. Their results indicated “empirical studies alone suggest that the operative temperatures of many organisms vary by as much as 10–20°C on a local scale, depending on vegetation, geology, and topography,” and even this variation in abiotic factors “ignores thermoregulatory behaviors that many animals use to balance heat loads.” Through a set of simulations of these phenomena, they “demonstrate how variability in elevational topography can attenuate the effects of warming climates.” They found “identical climates can produce very different microclimates at the spatial scales experienced by organisms”; “greater topographic relief should decrease selective pressure on thermal physiology for organisms that use behavior to avoid thermal extremes in heterogeneous environments,” citing Huey *et al.* (2003); and “topographic diversity should buffer the impacts of climate change by facilitating behavioral thermoregulation.”

Sears *et al.* say well-known relationships in biophysical ecology show “no two organisms experience the same climate in the same way,” and “changing climates do not always impact organisms negatively.” They conclude, “when coupled with thermoregulatory behavior, variation in topographic features can mask the acute effect of climate change in many cases,” rendering the climate envelope approach to assessing species responses to climate change rather useless if not downright deceptive.

Dobrowski (2011) writes, “the response of biota to climate change of the past is pertinent to understanding present day biotic response to anthropogenic warming,” and “one such adaptive response garnering increased attention is the purported utilization of climatic refugia by biota.” Historically, these refugia were “typically thought of as large regions in which organisms took refuge during glacial advances and retreats during the Pleistocene, which then acted as sources for colonization during more favorable climatic periods.” But “in addition to these large-scale refugia,” he writes, “there is compelling evidence that climatic refugia occurred at local scales during the Last Glacial Maximum and were also utilized during

interglacial warm periods, including the current interglacial (Willis and Van Andel, 2004; Birks and Willis, 2008)."

Dobrowski notes, "modeling using global climate models (GCMs) and regional climate models (RCMs) is done at scales of tens to hundreds of kilometers, whereas research suggests that temperature varies at scales of < 1 km in areas of complex terrain (Urban *et al.*, 2000; Fridley, 2009)." He reports, "Hijmans *et al.* (2005) showed that there can be temperature variation of up to 33°C within one 18-km raster cell." In addition, "GCMs and RCMs can simulate free-air conditions but fail to accurately estimate surface climate due to terrain features that decouple upper atmospheric conditions from boundary layer effects (Grotch and Maccracken, 1991; Pepin and Seidel, 2005)."

Dobrowski points out many researchers "have recently commented on the potential of topographically driven meso- or micro-climatic variation in mountain environments for providing refugia habitats for populations of species threatened by climate warming," citing Luoto and Heikkinen (2008), Randin *et al.* (2009), and Seo *et al.* (2009). And he notes these researchers "point to lower rates of predicted habitat loss and lower predicted extinction probabilities from species distribution models when using finely resolved climate data as compared with coarse scaled data," stating, "they suggest that this is evidence of 'local scale refugia' (Randin *et al.*, 2009) or 'reserves to shelter species' (Seo *et al.*, 2009)."

Dobrowski concludes, "microrefugia are likely to be found in terrain positions that promote the consistent decoupling of the boundary layer from the free-atmosphere," and "these terrain positions are likely to have climate states and trends that are decoupled from regional averages," which is "a requisite for microrefugia to persist through time." Thus, he concludes, "convergent environments (local depressions, valley bottoms, sinks, and basins) are primary candidates for microrefugia based on these criteria," which bodes well for the once-considered-impossible survival of many species of plants and animals in a possible further warming of the planet.

Lande (2009) writes, "the primary mechanisms of phenotypic adaptation are Darwinian evolution by natural selection on genetic variation, and phenotypic plasticity through environmental influence on individual development," further stating, "rapid phenotypic adaptation may be necessary to prevent [the] extinction of modern species subject to anthropogenic global warming, especially those

[species] with long generations such as large-bodied vertebrates and perennial plants." Against this backdrop and while noting "genetic variance in plasticity within and/or among populations has commonly been observed (Scheiner, 1993, 2002)," Lande employed "quantitative genetic models of phenotypic plasticity to analyze the dynamics of phenotypic adaptation to a sudden extreme environmental change" that is "beyond the usual range of background environmental fluctuations."

Lande's model suggests, "during the first generation in the new environment the mean fitness suddenly drops and the mean phenotype jumps towards the new optimum phenotype by plasticity," after which "adaptation occurs in two phases." First, "rapid evolution of increased plasticity allows the mean phenotype to closely approach the new optimum," after which the new phenotype "undergoes slow genetic assimilation, with reduction in plasticity compensated by genetic evolution of reaction norm elevation in the original environment." Such findings suggest there is a sound observational and mechanistic basis for concluding Earth's flora and fauna are genetically capable of coping with the type of rapid CO₂-induced global warming IPCC contends will drive innumerable plant and animal species to extinction.

5.1.2 Paleoeological Records

- As in past species extinctions, future species losses are unlikely to be directly attributable to climate changes that act over long terms and to which species are well adapted. Species losses in the future are more likely to be attributable to the novel, relatively rapid twentieth and twenty-first century anthropogenic processes of habitat loss and the transportation-mediated dispersal of pathogens and predators (including man) into previously isolated populations.

Most of the world's major species "body types" were laid down during the Cambrian period 600 million years ago (Levinton, 1992). These species have dealt successfully through the ages with new pest enemies, new diseases, ice ages, and global temperature swings greater than that predicted to result from CO₂-induced global warming.

During the Paleocene-Eocene Thermal Maximum (PETM), some 56 million years ago, it is believed, large amounts of carbon were released to the ocean-atmosphere system and global temperatures

may have risen by 5–8°C, although more recent climate modelling indicates changes in cloud properties and an increase in shortwave radiation played a much greater role in the warm PETM period than previously believed (Kiehl and Shields, 2013).

McInerney and Wing (2011) reviewed much of the scientific literature on the insights being sought by biologists concerned about potential species extinctions due to CO₂-induced global warming, and they give their assessment of the current status of the grand enterprise in which many scientists have been involved since the early 1990s, when the PETM and its significance first began to be recognized (Kennett and Stott, 1991; Koch *et al.*, 1992).

Although there was a major extinction of benthic foraminifera in the world's oceans, the two researchers write, “most groups of organisms did not suffer mass extinction.” In fact, they say, “it is surprising that cool-adapted species already living at higher latitudes before the onset of the PETM are not known to have experienced major extinctions,” and “this absence of significant extinction in most groups is particularly interesting in light of the predictions of substantial future extinction with anthropogenic global warming.” In addition, “low levels of extinction in the face of rapid environmental change during the Quaternary pose a similar challenge to modeled extinctions under future greenhouse warming,” citing Botkin *et al.* (2007). Finally, they observe, “rapid morphological change occurred in both marine and terrestrial lineages, suggesting that organisms adjusted to climate change through evolution as well as dispersal.”

McInerney and Wing conclude by noting “research on the PETM and other intervals of rapid global change has been driven by the idea that they provide geological parallels to future anthropogenic warming.” The many research results they review seem to suggest Earth's plants and animals, both on land and in the sea, may be much better equipped to deal with the environmental changes that may occur in response to anthropogenic CO₂ emissions than what many students of the subject have long believed.

Hof *et al.* (2011) present evidence demonstrating “recent geophysical studies challenge the view that the speed of current and projected climate change is unprecedented.” In one such study, for example, they report Steffensen *et al.* (2008) showed temperatures in Greenland warmed by up to 4°C/year near the end of the last glacial period. They state this change and other rapid climate changes during the Quaternary (the last 2.5 million years) did not cause a noticeable level of broad-scale, continent-wide extinctions of

species. Instead, these rapid changes appeared to “primarily affect a few specific groups, mainly large mammals (Koch and Barnosky, 2006) and European trees (Svenning, 2003),” so “few taxa became extinct during the Quaternary (Botkin *et al.*, 2007).”

How were the bulk of Earth's species able to survive a climatic change that many today believe is unsurvivable? Hof *et al.* suggest “species may have used strategies other than shifting their geographical distributions or changing their genetic make-up.” They note, for example, “intraspecific variation in physiological, phenological, behavioral or morphological traits may have allowed species to cope with rapid climatic changes within their ranges (Davis and Shaw, 2001; Nussey *et al.*, 2005; Skelly *et al.*, 2007),” based on “preexisting genetic variation within and among different populations, which is an important prerequisite for adaptive responses,” noting “both intraspecific phenotypic variability and individual phenotypic plasticity may allow for rapid adaptation without actual microevolutionary changes.” Hof *et al.* conclude, “species are probably more resilient to climatic changes than anticipated in most model assessments of the effect of contemporary climate change.”

Indeed, as shown in the subsections below, model-based projections of animal extinctions in response to rising temperature and atmospheric CO₂ suffer a major loss of credibility when tested against real-world data. Although there likely will be some changes in species population dynamics, few if any species will be driven to extinction. In contrast, a number of studies indicate many animal species will benefit from a warming climate and rising atmospheric CO₂ concentrations, resulting in a proliferation, as opposed to extinction, of species.

Vegas-Vilarrubia *et al.* (2011) contend “current extinction estimates for the near-future should be revised in light of palaeoecological information, which shows that spatial reorganizations and persistence in suitable microrefugia have been more common than extinction during the Quaternary.” As a result, they say, “an interesting consequence is the possibility of new unknown species combinations with no modern analogues.”

The two phenomena that come into play in these ecosystem transformations are acclimation and adaptation, “with the first relying on phenotypic plasticity and the second involving genetic changes of potential evolutionary significance.” Vegas-Vilarrubia *et al.* note “some authors propose that spatial reorganizations without extinction will be the dominant biotic response to the near-future global

changes.” But “it is also possible that ecosystems never attain equilibrium,” they write, and “transient states perpetuate because of the recurrent action of environmental change.” They note “one of the main lessons from this is that ecosystems may express their resilience when confronted with environmental shifts by attaining several possible equilibrium states, as manifested in changes in biodiversity and/or composition, without losing their ecological functions.”

Vegas-Vilarrubia *et al.* cite the global warming that occurred at the end of the Younger Dryas (~13,000 to 11,500 years ago), which serves as one of the more powerful analogs of projected global warming “because both magnitude and rates of change parallel those predicted for the present century.” This prior real-world transformation “seems to have consisted of ecological reorganizations and changes in community composition because of differential species migration patterns and rates,” but they note, “so far, it has not been possible to associate large-scale extinctions to the Younger Dryas climatic reversal.”

Mergeay and Santamaria (2012) continue that line of thinking in an editorial introducing nine papers in a special issue of *Evolutionary Applications*. The two special-issue editors note Shine (2012) opens the issue by “showing how evolution can rapidly modify ecologically relevant traits in invading as well as native species.” Bijlsma and Loeschke (2012) then “tackle the interaction of drift, inbreeding and environmental stress,” and Angeloni *et al.* (2012) “provide a conceptual tool-box for genomic research in conservation biology and highlight some of its possibilities for the mechanistic study of functional variation, adaptation and inbreeding.”

Van Dyck (2012) shows “an organism’s perception of its environment is subject to selection, a mechanism that could reduce the initial impact of environmental degradation or alleviate it over the longer run.” Urban *et al.* (2012) argue “certain consequences of global change can only be accounted for by interactions between ecological and evolutionary processes.” And Lemaire *et al.* (2012) highlight “the important role of evolution in predator-prey interactions.”

Focusing on eco-evolutionary interactions, Palkovacs *et al.* (2012) “review studies on phenotypic change in response to human activities” and “show that phenotypic change can sometimes cascade across populations, communities and even entire ecosystems.” Bonduriansky *et al.* (2012) examine “non-genetic inheritance and its role in adaptation,”

dissecting “the diversity of epigenetic and other transgenerational effects.” Finally, Santamaria and Mendez (2012) “build on the information reviewed in all previous papers to identify recent advances in evolutionary knowledge of particular importance to improve or complement current biodiversity policy.”

“Overall,” Mergeay and Santamaria (2012) conclude, “these nine papers offer compelling evidence for the role of evolutionary processes in the maintenance of biodiversity and the adaptation to global change.”

Meylan *et al.* (2012) focused on “the role of hormonally mediated maternal effects in inducing phenotypic plasticity as a response to rising temperatures and extreme climatic events,” citing Marquis *et al.* (2008) on lizards. The three researchers describe how the discovery of maternal androgens and glucocorticoids in egg yolks, together with the intra-clutch variation of these hormones (Groothuis and Schwabl, 2008), make it possible for the offspring phenotype to be “manipulated in response to environmental conditions experienced by the female (Weaver *et al.*, 2004).” This maternal effect can be considered a form of “intergenerational phenotypic (developmental) plasticity,” which could prove crucial “in coping with unpredictable environments.” They suggest “hormones are a critical link between the environment and the genome” because they “may mediate the expression of phenotypic variation, generate trait integration, shape multivariate trade-offs (Sinervo *et al.*, 2008) and either directly or indirectly shape phenotypic plasticity during ontogeny and later into adulthood (Lessells, 2008).”

Meylan *et al.* further state, “the hormonal cascades involved in organizational effects during development may be modulated by environmental stressors and the maternal response as given by the duration and magnitude of elevated glucocorticoids.” They discuss “the phenotypic and population dynamic consequences of prenatal exposure to steroid hormones resulting in context-dependent expression of traits by the offspring,” ultimately describing “how hormone-mediated maternal effects may enhance rapid adaptation to changing environmental conditions.” Finally, the three ecologists write, “females exposed to abiotic stressors during reproduction may alter the phenotypes by manipulation of hormones to the embryos,” and they conclude, “hormone-mediated maternal effects, which generate phenotypic plasticity, may be one avenue for coping with global change.”

Clearly, Earth’s life forms are well-endowed with complex change-management strategies, either

through behavior or otherwise. More recent developments have sought to correct or augment the limitation of static, deterministic paradigms such as niche modeling and species area curves with more dynamic and stochastic paradigms—particularly exploring the consequences of “niche assembly” vs. “dispersal assembly” on extinction risk and biodiversity management (Stockwell, 2013). It is well-known that the composition of many communities is not ruled consistently by species’ ecological niches or functional roles, and that they also incorporate stochastic processes (e.g. coastal fish metacommunities, see Moullot, 2007). Recent work is beginning to redress the incomplete “niche-based” frameworks that have produced unrealistic and counterfactual estimates of extinction loss.

The most potent of the tools has been “unified neutral theory” (UNT, Hubbell, 2001), which provides a simple yet rigorous evaluation of the role of “dispersal assembly” in communities’ richness and has provided deeper insights into extinction estimates than “niche assembly” alone might offer. It is clear the SAR-based extinction estimates pioneered by Thomas *et al.* (2005) exaggerate the extinction rates, due to the inherent bias of structural errors (He and Hubbell, 2012) and through disregarding the species that benefit from climate change (Stockwell, 2004). However, it is hypothesized that habitat reductions from any cause will increase the probability of extinction, as rarity usually precedes extinction, even if the effect is not immediately apparent. This is the basis for the notion of “extinction debt.” This is a dilemma, for if every environmental change increases extinctions, why haven’t all species gone extinct?

A recent application of the UNT simulations of habitat reductions has identified two distinctive species area curves: imminent extinctions from habitat loss and delayed total extinctions indicative of extinction debt. The lag times for relaxation of the community into a lower species richness following habitat loss are often very large, within the order of thousands of years (Halley and Sgardeli, 2014). This suggests much of the “extinction debt” from a specific climate disruption may be redeemed by environmental or physiological changes in the intervening period between when the extinction debt is incurred and when the population has dwindled to unsustainable levels.

Another UNT simulation of two types of colonizing dispersal events—the “volcanic island” and the “land bridge” (Rosindell and Harmon, 2013) shows the stark difference between the colonization of a virgin habitat that slowly builds up diversity, and

the drastic reduction of biodiversity from the sudden connection of unrelated communities via a transportation corridor. As in past species extinctions, future species losses are unlikely to be directly attributable to climate changes that act over long terms and to which species are well adapted. Species losses in the future are more likely to be attributable to the novel, relatively rapid twentieth and twenty-first century anthropogenic processes of habitat loss and the transportation-mediated dispersal of pathogens and predators (including man) into previously isolated populations.

It is clear niche-model-based projections of extinctions are riddled with assumptions and limitations that make them an unreliable guide to the impact of climate change on species. The vast majority of the predicted extinctions likely will not occur. A significant body of real-world evidence suggests most of Earth’s plants and animals will be able to easily adapt, survive, and even thrive in the face of projected climate change, even under the worst-case scenarios of CO₂-induced global warming predicted by IPCC. As shown hereafter and in Chapter 4 (see Section 4.4 on Extinction), far from being a detriment to the biosphere, the air’s rising CO₂ content is enhancing vegetative productivity and fostering a great proliferation of plant and animal species all around the world, helping to protect them from other anthropogenic forces that might otherwise drive them to extinction, independent of whatever the planet’s climate may do.

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5.1.3 Other Studies

- The planet’s animal species have inherent abilities enabling them to cope with climate changes over a period of a few generations, a single generation, or even in real time.

Results of other studies also suggest the model-based species extinction hypothesis is unlikely to occur. In a review paper published in *Current Biology*, for example, Erwin (2009) explored past epochs and the myriad nooks and crannies of Earth today, searching for the primary trigger of speciation. His conclusion? Warmth is the fire that fuels the process by which species originate, whereas cold tends to destroy what warmth produced.

Headquartered in the Department of Paleobiology at the National Museum of Natural History in Washington, DC (USA), Erwin writes, “some of the best evidence for a link between biodiversity and climate comes from latitudinal gradients in diversity, which provide an avenue to explore the more general relationship between climate and evolution.” In reviewing that evidence, he notes, “among the wide range of biotic hypotheses, those with the greatest empirical support indicate that warmer climates [1] have provided the energetic foundation for increased biodiversity by fostering greater population size and thus increased extinction resistance, [2] have increased metabolic scope, [3] have allowed more species to exploit specialized niches as a result of greater available energy, and [4] have generated faster speciation and/or lower extinction rates.” He states, “in combination with geologic evidence for carbon dioxide levels and changing areas of tropical seas, these observations provide the basis for a simple, first-order model of the relationship between climate through the Phanerozoic and evolutionary patterns and diversity,” and “such a model suggests that we should expect greatest marine diversity during globally warm intervals,” as is typically also found for terrestrial diversity.

Erwin notes “the three best-studied mass extinction events are associated with sharp changes in climate and support the contention that rapid shifts in climate can reduce global diversity,” which sounds much like the mantra of IPCC regarding global warming. However, the climate shifts Erwin cites consist mostly of cooling, and it is not only the shift to cooling but stagnating in a cool state that bodes ill for biodiversity. As Erwin describes it, “the long interval of stagnant evolution during the Permo-Carboniferous glaciation is consistent with studies of

Climate Change Reconsidered II: Biological Impacts

modern-day latitudinal diversity that [indicate] rates of evolutionary innovation and diversification are higher in high-energy climates than in low-energy climates.”

Further explaining this conceptual framework, Erwin notes “contemporary studies suggest a positive relationship between high-energy climates and [1] increased diversification rates, [2] increased number of niches because of increased metabolic scope, and [3] more specialized niches, and possibly because of [4] niche construction.” He writes, “studies showing that the tropics are a cradle of diversity, pumping clade representatives into higher latitudes, as well as evidence of increased ordinal level originations in the tropics, and of the sudden appearance of several mammalian groups during the Paleocene-Eocene Thermal Maximum suggest an asymmetric pattern of innovations associated with high-energy climate regimes.”

Erwin concludes, “there is an intriguing possibility that diversity does not track climate, but rather builds up during warm intervals but without falling by proportional amounts when climates turn cooler,” with the result that “warmer climates may serve as an evolutionary diversification pump with higher diversity persisting [throughout following cooler periods], at least for a time.”

Two generalizations clearly can be made: warmth typically begets speciation, and cold tends to lead to species extinctions.

Independent support for this thesis was provided in papers by Jaramillo *et al.* (2010) and Willis *et al.* (2010). Jaramillo *et al.* (2010) examined the Paleocene-Eocene Thermal Maximum (PETM), which occurred some 56.3 million years ago, at sites in Venezuela and Columbia. The PETM provides an interesting analog to the Current Warm Period, and it is postulated carbon dioxide rose rapidly in that era over a period of 10,000 to 20,000 years and global temperatures were elevated approximately 5 °C for 100,000 to 200,000 years.

The PETM was clearly identifiable in terms of temperature, where it was between 31 and 34 °C during the peak of global warmth. Using pollen and other organic materials, the authors were able to identify various plant species that existed during this period. In spite of the high temperatures and possibly less-moist conditions, the number of drought-tolerant plants did not increase, nor were moisture-requiring plants shown to decrease during the PETM. These facts lead the authors to speculate either rainfall or water use efficiency increased because of higher levels of atmospheric carbon dioxide, thereby

compensating for the higher temperatures.

They also note the PETM brought a radical increase in diversity, measured in both absolute terms (number of species/taxa) and in evenness (relatively more even species percentages). This was achieved by addition of new taxa. The origination rate for new taxa during the PETM was two to six times higher than during the periods before and after, but extinction rates were not unusual. The species/taxa that originated, and the overall diversity, continued after the PETM. Thus the gains in plant species richness during the PETM were relatively persistent rather than transient.

It is believed tropical forests of today are currently growing in climates near the maximum temperature the plants can tolerate (~27.5 °C), and thus future global warming in tropical zones may stress plants and cause a reduction in forest growth, perhaps driving some species to extinction. However, Jaramillo *et al.* show temperatures of 31 to 34 °C seem not only to have been tolerated but to have caused a burst of speciation in the PETM, including major taxa that persist today. The high temperatures of the PETM were not detrimental to the tropical moist forests examined in this study.

Willis *et al.* (2010) identified past historical periods when climate was similar to that projected by global climate models for the next century or so, or in which the rate of temperature change was unusually rapid. These periods were examined for any climate-related extinctions.

The first period they examined was the Eocene Climatic Optimum (53–51 million years ago), when the atmosphere’s CO₂ concentration exceeded 1,200 ppm and tropical temperatures were 5–10°C warmer than current values. Far from causing extinctions of the tropical flora (where the data are best), the four researchers report, “all the evidence from low-latitude records indicates that, at least in the plant fossil record, this was one of the most biodiverse intervals of time in the Neotropics.” They also note “ancestors of many of our modern tropical and temperate plants evolved ... when global temperatures and CO₂ were much higher than present, ... indicating that they have much wider ecological tolerances than are predicted based on present-day climates alone.”

The second period they examined consisted of two rapid-change climatic events in the Holocene—one at 14,700 years ago and one at 11,600 years ago—when temperatures increased in the mid- to high-latitudes of the Northern Hemisphere by up to 10°C over periods of less than 60 years. Many sites

show evidence of rapid plant responses to rapid warming during these events. The authors note, “at no site yet studied, anywhere in the world, is there evidence in the fossil record for large-scale climate-driven extinction during these intervals of rapid warming.” They report extinctions did occur due to the cold temperatures of the glacial epoch, when subtropical species in southern Europe were driven out of their ecological tolerance zone.

Willis *et al.* also make use of recent historical data, such as the 3°C rise in temperature at Yosemite Park over the past 100 years. Comparing surveys of mammal fauna conducted near the beginning and end of this period, they detected some changes but no local extinctions. Thus they determined for all the periods they studied, there were no detectable extinctions during very warm temperatures or very rapid warming.

D’Odorico *et al.* (2008) write, “recent climate change predictions indicate that, in addition to trends in the mean values of climate variables, an increase in interannual variability is expected to occur in the near future.” Also noting “environmental fluctuations are usually believed to play a ‘destructive role’ in ecosystem dynamics,” they explore the validity of this latter assumption in the context of current climate model predictions, asking, “Can environmental variability have only ‘negative’ effects on ecosystem dynamics?”

After lengthy mathematical analysis, D’Odorico *et al.* determined “opportunities for species existence/coexistence are found to increase with ‘moderate’ values of the variance of environmental fluctuations, while they decrease when these fluctuations are relatively strong.” This outcome constitutes what has come to be known as the “intermediate disturbance hypothesis,” which grew out of the work of Connell (1978), who, in the words of D’Odorico *et al.*, suggested “coral reefs and rain forests maintain high levels of diversity only in a non-equilibrium state,” and Huston (1979), who noted “most communities have relatively high levels of diversity because environmental variability maintains them in a non-equilibrium state.”

Noting numerous real-world indications (Chapin *et al.*, 1997; Steneck *et al.*, 2002; Bengtsson *et al.*, 2003; Elmqvist *et al.*, 2003; Bellwood *et al.*, 2004; Folke *et al.*, 2004) that “biodiversity may enhance ecosystem resilience,” the four researchers provide a theoretical basis for this phenomenon, demonstrating the validity of the ecological equivalent of the common dictum of physical exercise gurus: no pain, no gain. This evidence suggests what IPCC considers

unfavorable may in fact be just what is needed to increase the diversity and resilience of myriad terrestrial and aquatic ecosystems and propel them to higher levels of activity in the brave new world of our CO₂-enriched future.

In an overview of a symposium titled “Molecules to Migration: Pressures of Life,” held in Africa on the Maasai Mara National Reserve of Kenya, Fuller *et al.* (2010) note the theoretical approach most commonly used to predict future species distributions in a CO₂-enriched and warmer world (the “climate envelope” approach) assumes “animals and plants can persist only in areas with an environment similar to the one they currently inhabit.” This approach, they point out, “typically ignores the potential physiological capacity of animals to respond to climate change.” They explain how “behavioral, autonomic, and morphological modifications such as nocturnal activity, selective brain cooling, and body color may potentially serve as buffers to the consequences of climate change.”

The six scientists note all organisms “have the capacity to adapt to changing environmental conditions both by phenotypic plasticity within a life span and by microevolution over a few life spans.” They note, “there is evidence that microevolution—that is, heritable shifts in allele frequencies in a population (without speciation)—has occurred in response to climate warming,” citing Bradshaw and Holzapfel (2006, 2008). They also point out phenotypic plasticity “is likely to represent the first response of individual organisms.” They report “adaptive changes in phenotype induced by climate change have been documented, for example, in the morphology and phenology of birds (Charmanier *et al.*, 2008) and mammals (Reale *et al.*, 2003; Linnen *et al.*, 2009; Maloney *et al.*, 2009; Ozgul *et al.*, 2009).”

Fuller *et al.* cite Pincebourde *et al.* (2009), who “showed that intertidal sea stars can behaviorally regulate their thermal inertia by increasing their rate of water uptake during high tide on hot days,” which is “a response that affords protection against extreme aerial temperatures during subsequent low tides.” Next they note “exposure of humans to hot conditions on successive days induces an increase in sweat capacity (Nielsen *et al.*, 1993).” They state, “other adaptations also ensue, including plasma volume expansion and decreased electrolyte content of sweat,” and thus “a typical unacclimatized male, who can produce about 600 ml of sweat per hour, can double that output with heat acclimatization (Henane and Valatx, 1973).” This “phenotypic adaptation (in this case, heat acclimatization) can alter physiological

Climate Change Reconsidered II: Biological Impacts

tolerance (the risk of heat illness),” they note.

The Australian, South African, and U.S. scientists also cite several studies—Zervanos and Hadley (1973), Belovsky and Jordan (1978), Grenot (1992), Hayes and Krausman (1993), Berger *et al.* (1999), Dussault *et al.* (2004), Maloney *et al.* (2005), and Hetem *et al.* (2010)—of large herbivores that “increase nocturnal activity in the face of high diurnal heat loads.” They state “another adaptation that may enhance plasticity in response to aridity that is available to oryx and other artiodactyls, as well as members of the cat family (Mitchell *et al.*, 1987), is selective brain cooling,” in which cooling of the hypothalamus and the temperature sensors that drive evaporative heat loss “inhibits evaporative heat loss and conserves body water (Kuhnen, 1997; Fuller *et al.*, 2007),” which “is likely to be particularly valuable to animals under concurrent heat stress and dehydration.” Finally, they suggest maintaining genetic diversity for a trait such as fur or feather color that adapts various organisms to different thermal environments “may provide important plasticity for future climate change,” citing Millien *et al.* (2006), and “there is already evidence that, over the past 30 years as the climate has warmed, the proportion of dark-colored to light-colored Soay sheep has decreased on islands in the outer Hebrides,” citing Maloney *et al.* (2009).

Clearly, the planet’s animal species have inherent abilities enabling them to cope with climate changes over a period of a few generations, a single generation, or even in real time.

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Terrestrial Animals

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5.2 Amphibians

- Research suggests amphibian populations will suffer little, if any, harm from projected CO₂-induced global warming, and they may even benefit from it.

Still *et al.* (1999) and Pounds *et al.* (1999) published a pair of papers in *Nature* dealing with the cause of major decreases in frog and toad populations in the highland forests of Monteverde, Costa Rica. Those diebacks—in which 20 of 50 local species went extinct locally, or were extirpated—had occurred over the prior two decades, a period described by IPCC as having experienced unprecedented warming. Holmes (1999), in a popular science article describing the mystery’s putative solution, wrote the authors of the two reports made “a convincing case blaming global climate change for these ecological events.” Then came the study of Lawton *et al.* (2001), who challenged this hypothesis, presenting “an alternative mechanism [of] upwind deforestation of lowlands” as the cause of the amphibian decline.

Lawton *et al.* began their analysis by noting the trade winds that reach the Monteverde cloud-forest ecosystem flow across approximately 100 km of lowlands in the Rio San Juan basin, and that deforestation proceeded rapidly in the Costa Rican part of the basin over the past century. By 1992, only 18 percent of the original lowland forest remained. The four scientists noted this conversion of forest to

pasture and farmland altered the properties of the air flowing across the landscape. The reduced evapotranspiration that followed deforestation, for example, decreased the moisture content of the air mass, and regional atmospheric model simulations suggested there should be reduced cloud formation and higher cloud bases over such deforested areas, which would cause there to be fewer and higher-based clouds than otherwise would have been the case when the surface-modified air moved into the higher Monteverde region.

Thus there were two competing theories from which to choose a candidate mechanism for the environmental changes that had altered the Monteverde cloud-forest ecosystem: one that was global in nature (CO₂-induced warming) and one that was local (upwind lowland deforestation). Lawton *et al.* resolved the matter. Noting the lowland forests north of the San Juan River in southeastern Nicaragua had remained largely intact—providing a striking contrast to the mostly deforested lands in neighboring Costa Rica—they used satellite imagery to show “deforested areas of Costa Rica’s Caribbean lowlands remain relatively cloud-free when forested regions have well-developed dry season cumulus cloud fields,” noting further the prominent zone of reduced cumulus cloudiness in Costa Rica “lies directly upwind of the Monteverde tropical montane cloud forest.” Consequently, they demonstrated by direct observation the effects predicted by the theory they espoused did indeed occur in the real world, alongside a “control” area identical in all respects but for the deforestation that produced the cloud effects.

Two years later, Nair *et al.* (2003) demonstrated the reduced evapotranspiration that followed prior and ongoing deforestation upwind of the Monteverde cloud forest decreased the moisture contents of the air masses that ultimately reached the tropical preserve, and regional atmospheric model simulations they conducted indicated there also should have been reduced cloud formation and higher cloud bases over these areas than there were before the deforestation began. Three years later, Ray *et al.* (2006) extended the work of Lawton *et al.* and Nair *et al.* while exploring in more detail the impact of deforestation in Costa Rican lowland and premontane regions on orographic cloud formation during the dry season month of March.

Ray *et al.* used the mesoscale numerical model of Colorado State University’s Regional Atmospheric Modeling System to derive high-spatial-resolution simulations “constrained by a variety of ground based and remotely sensed observations,” in order to

“examine the sensitivity of orographic cloud formation in the Monteverde region to three different land use scenarios in the adjacent lowland and premontane regions,” namely, “pristine forests, current conditions and future deforestation.”

This observation-constrained modeling work revealed historic “deforestation has decreased the cloud forest area covered with fog in the montane regions by around 5–13% and raised the orographic cloud bases by about 25–75 meters in the afternoon.” In addition, they write, their work suggests “further deforestation in the lowland and premontane regions would lead to around [a] 15% decrease in the cloud forest area covered with fog and also raise the orographic cloud base heights by up to 125 meters in the afternoon.”

As additional cases of amphibian mass mortality were reported throughout the world, Parmesan (2006) and Pounds *et al.* (2006) pointed accusing fingers at atmospheric CO₂, this time claiming global warming was promoting the spread of *Batrachochytrium dendrobatidis* (Bd), a non-hyphal zoospore fungus that was the immediate cause of the amphibian declines and triggering outbreaks of chytridiomycosis via what came to be known as the climate-linked epidemic hypothesis (CLEH).

Investigating this concept in the Penalara Natural Park in the Sierra de Guadarrama of Central Spain, Bosch *et al.* (2007) looked for relationships between 20 meteorological variables and the development of chytridiomycosis infection in the area’s amphibian populations, focusing on “two time periods according to the lack (1976–1996) or presence (1997–2003) of observed chytrid-related mortalities.” This work revealed “a significant association between change in local climatic variables and the occurrence of chytridiomycosis,” leading them to conclude, “rising temperature is linked to the occurrence of chytrid-related disease.”

Being careful not to be too adamant about what their data implied, however, Bosch *et al.* note “associations between climate and disease do not necessarily imply causation.” They also state, “chytrid-related declines are probably the result of a complex web of interaction, and the effects of climate will be conditional on other factors such as host density, amphibian community composition, microbial competitors and zooplankton predators, to name but a few.” To disentangle this network and break it down into its key components, they say it will be necessary “to collect seasonal data on amphibian densities, contemporary and historical measurements of the prevalence and intensity of infection, seasonal

mortalities, and fine-scale meteorological conditions from a range of sites that represent altitudinal clines,” and conduct “molecular epidemiological analyses.”

Lips *et al.* (2008) evaluated data pertaining to population declines of frogs of the genus *Atelopus*, as well as similar data from other amphibian species, in Lower Central America and Andean South America, based on their own work and that of others recorded in the scientific literature. They sought to determine whether the documented population declines were more indicative of an emerging infectious disease or a climate-change-driven infectious disease, noting in this regard, “both field studies on amphibians (Briggs *et al.*, 2005; Lips *et al.*, 2006) and on fungal population genetics (Morehouse *et al.*, 2003; Morgan *et al.*, 2007) strongly suggest that *Bd* is a newly introduced invasive pathogen.”

Lips *et al.* say their findings reveal “a classical pattern of disease spread across native populations, at odds with the CLEH proposed by Pounds *et al.* (2006).” Emphasizing the latter’s “analyses and re-analyses of data related to the CLEH all fail to support that hypothesis,” Lips *et al.* conclude their own analyses support “a hypothesis that *Bd* is an introduced pathogen that spreads from its point of origin in a pattern typical of many emerging infectious diseases,” reemphasizing that “the available data simply do not support the hypothesis that climate change has driven the spread of *Bd* in our study area.”

Although the four U.S. scientists make it clear disease dynamics are “affected by micro- and macro-climatic variables,” and “such synergistic effects likely act on *Bd* and amphibians,” their work clearly shows the simplistic scenario represented by the CLEH—which posits, in their words, that “outbreaks of chytridiomycosis are triggered by a shrinking thermal envelope”—paints an unrealistic picture of the role of global climate change in the much-more-complicated setting of real-world biology, where many additional factors may play even greater roles in determining amphibians’ well-being.

Laurance (2008) tested the hypothesis, put forward by Pounds *et al.* (2006), that “the dramatic, fungal pathogen-linked extinctions of numerous harlequin frogs (*Atelopus* spp.) in upland rainforests of South America mostly occurred immediately following exceptionally warm years, implicating global warming as a likely trigger for these extinctions.” He used “temperature data for eastern Australia, where at least 14 upland-rainforest frog species [had] also experienced extinctions or striking population declines attributed to the same fungal

pathogen, and where temperatures [had] also risen significantly in recent decades.” This work provided “little direct support for the warm-year hypothesis of Pounds *et al.*” Instead, Laurance “found stronger support for a modified version of the warm-year hypothesis,” where frog declines were likely to occur only following three consecutive years of unusually warm weather; and these declines were observed “only at tropical latitudes, where rising minimum temperatures were greatest.”

Laurance states many researchers “remain unconvinced that ongoing disease-linked amphibian declines are being widely instigated by rising global temperatures or associated climatic variables, as proposed by Pounds *et al.*” He notes, for example, “chytrid-linked amphibian declines have been documented on several continents and at varying times” and to date, “no single environmental stressor has been identified that can easily account for these numerous population crashes.” He continues, “it stretches plausibility to argue that the chytrid pathogen is simply an opportunistic, endemic micro-parasite that has suddenly begun causing catastrophic species declines as a consequence of contemporary global warming.”

Rohr *et al.* (2008) provided a rigorous test of the two competing hypotheses by evaluating “(1) whether cloud cover, temperature convergence, and predicted temperature-dependent *Bd* growth are significant positive predictors of amphibian extinctions in the genus *Atelopus* and (2) whether spatial structure in the timing of these extinctions can be detected without making assumptions about the location, timing, or number of *Bd* emergences.” The five scientists report, “almost all of our findings are contrary to the predictions of the chytrid-thermal-optimum hypothesis,” even noting “not all of the data presented by Pounds *et al.* (2006) are consistent with the chytrid-thermal-optimum hypothesis.” They write, “there was no regional temperature convergence in the 1980s when extinctions were increasing, and that convergence only occurred in the 1990s when *Atelopus* spp. extinctions were decreasing, opposite to the conclusions of Pounds *et al.* (2006) and the chytrid-thermal-optimum hypothesis.” On the other hand, they report, “there is a spatial structure to the timing of *Atelopus* spp. extinctions but that the cause of this structure remains equivocal, emphasizing the need for further molecular characterization of *Bd*.”

Alford *et al.* (2009) quantified four movement characteristics of three groups of radio-tracked cane toads (*Bufo marinus*) at three places in Australia: a location where the toads had been established for

some 50 years at the time of their sampling; a location where the first toads arrived about six months before sampling began in 1992 and 1993; and a location where sampling occurred for a period of 13 months, starting at the time of the toads' initial arrival in 2005. For all of the movement parameters they studied, "toads from the current invasion front differed dramatically from animals in the long-established population, while toads from the earlier invasion front were intermediate between these extremes."

The five researchers report "cane toads are now spreading through tropical Australia about 5-fold faster than in the early years of toad invasion." They state "the current invasion-front animals achieved these [high invasion speeds] by rarely reusing the same retreat site two days in succession, by travelling further each night when they did move, and by moving along straighter paths." Therefore, as they describe it, the toad invasion front "advances much more rapidly than would occur if the toads retained ancestral behaviors (less frequent relocation, with shorter movements, and fewer toads using straight paths)." And because "invasion-front toads in 1992 were more dispersive than origin-population toads in the same year, but ... invasion-front toads have continued to evolve heightened dispersal ability and dispersed even more effectively in 2005 than they did in 1992," these observations suggest "as long as toads continue to invade suitable new habitat, dispersal ability will be selected upwards."

Alford *et al.* write the rapidity and magnitude of the shifts in cane toads "are truly remarkable," having been accomplished in only 50 generations (about 70 years), and they state "such a major shift over such a brief period testifies to the intense selective pressure exerted on frontal populations of range-shifting species." This development, in their words, "not only has implications for our understanding of the rates of invasion by non-native species, but also for the rate of range-shift in native taxa affected by climate change." The capacity for species to respond to changing environments may be underestimated when it is based on observations of individuals at the core of their range.

Further exploring this issue, Bustamante *et al.* (2010) exposed groups of Panamanian golden frogs (*Atelopus zeteki*) to varying dosages of zoospores of *Bd* and different temperatures and hydric environments to ascertain whether the frogs were susceptible to the pathogen and, if so, how environmental factors might affect the frogs' survival. These operations indicated "frogs exposed to a dosage of 100 *Bd* zoospores survived significantly longer than those

that had been exposed to 10^4 or 10^6 zoospores." They also found "exposed frogs housed at 23°C survived significantly longer than those that were housed at 17°C," and "exposed frogs held in dry conditions survived significantly longer than those in wet conditions."

Since their study was conducted in a laboratory, Bustamante *et al.* acknowledge their results "do not directly test hypotheses about the relation between climate change and the decline of the frogs in the field," but they note their data nevertheless "do not support the contention that rising global temperatures are necessary to cause the death of amphibians infected with this pathogen, because the pathogen was just as lethal at 17°C as at 23°C, and frogs at the warmer temperature lived significantly longer than those at the cooler one." This result is inconsistent with the climate-linked epidemic hypothesis of Pounds *et al.* (2006)—and Bustamante was a coauthor of that paper.

Anchukaitis and Evans (2010) state "widespread amphibian extinctions in the mountains of the American tropics have been blamed on the interaction of anthropogenic climate change and a lethal pathogen." However, they note, "limited meteorological records make it difficult to conclude whether current climate conditions at these sites are actually exceptional in the context of natural variability," casting doubt once again on the contention modern global warming was the primary culprit in the demise of the Monteverde golden toad (*Bufo periglenes*).

Anchukaitis and Evans developed annual proxy records of hydroclimatic variability over the past century within the Monteverde Cloud Forest of Costa Rica, based on measurements of the stable oxygen isotope ratio ($\delta^{18}\text{O}$) made on trees lacking annual rings, as described in the papers of Evans and Schrag (2004) and Anchukaitis *et al.* (2008). That work revealed, "contrary to interpretations of the short instrumental record (Pounds *et al.*, 1999), no long-term trend in dry season hydroclimatology can be inferred from our $\delta^{18}\text{O}$ time series at Monteverde (1900–2002)." Instead, they found, "variability at the interannual scale dominates the isotope signal, particularly during the period of increased ENSO variance since the late 1960s," and they add, "there is no evidence of a trend associated with global warming." They emphasize "the extinction of the Monteverde golden toad appears to have coincided with an exceptionally dry interval caused by the 1986–1987 El Niño event," which they describe as "one of the longest driest periods in the last 100 years," based on their $\delta^{18}\text{O}$ chronology. In

addition, they report, there is currently no consensus on how anthropogenic climate change might influence the El Niño Southern Oscillation, and “ENSO anomalies in the most recent decades are not beyond the range of natural variability during the instrumental period (Rajagopalan *et al.*, 1997).”

Anchukaitis and Evans conclude their analysis suggests “the cause of the specific and well-documented extinction of the Monteverde golden toad was the combination of the abnormally strong ENSO-forced dryness and the lethality of the introduced chytrid fungus, but was not directly mediated by anthropogenic temperature trends, a finding from paleoclimatology that is in agreement with statistical reanalysis (Rohr *et al.*, 2008; Lips *et al.*, 2008) of the ‘climate-linked epidemic hypothesis’.” The latter two analyses also had revealed the chytrid-thermal-optimum hypothesis, as it alternatively has been described, to be devoid of merit. Consequently, even in the case of struggling amphibians, there are no real-world data indicating global warming is, or ever will be, responsible for driving them to extinction.

Noting “phenotypic plasticity, the capacity of a genotype to produce distinct phenotypes under different environmental conditions, is a common and powerful method of adaptation in nature,” Orizaola and Laurila (2009) investigated variations in temperature-induced plasticity in larval life-history traits among populations of an isolated “meta-population” of pool frogs (*Rana lessonae*) in Central Sweden. They exposed larvae from three closely located populations to two temperatures (20 and 25°C) in the laboratory and then documented their growth and development responses at the two different temperatures. According to the two Swedish researchers, the results indicated “in general, larvae exposed to warmer temperature experienced higher survival and metamorphosed faster.” They also found “differences among the populations in both trait mean values and in the plastic responses,” and “among-family variation within populations was found in growth rate and time to metamorphosis, as well as in plasticity, suggesting that these traits have a capacity to evolve.”

Orizaola and Laurila also report finding “strong population differentiation at a microgeographic scale in life-history characteristics and temperature-induced plasticity in [the] isolated amphibian meta-population.” They report, in spite of “the near absence of molecular genetic variation within [the] meta-population, our study detected strong variation in trait means and plastic responses both among and within populations, possibly suggesting that natural selection

is shaping life-history traits of the local populations.” This phenomenon may be preparing pool frogs for still further temperature increases by providing them “ample phenotypic variation” to deal with a potentially warming environment.

Skelly *et al.* (2007) critique the use of the “climate-envelope approach” to predict extinctions, citing as their primary reason for doing so the fact that this approach “implicitly assumes that species cannot evolve in response to changing climate,” when in numerous cases they can do so effectively. Noting “many examples of contemporary evolution in response to climate change exist,” the group of seven scientists from the United States, Canada, and Australia report, “in less than 40 years, populations of the frog *Rana sylvatica* have undergone localized evolution in thermal tolerance (Skelly and Freidenburg, 2000), temperature-specific development rate (Skelly, 2004), and thermal preference (Freidenburg and Skelly, 2004),” and “laboratory studies of insects show that thermal tolerance can change markedly after as few as 10 generations (Good, 1993).” Since “studies of microevolution in plants show substantial trait evolution in response to climate manipulations (Bone and Farres, 2001),” they state, “collectively, these findings show that genetic variation for traits related to thermal performance is common and evolutionary response to changing climate has been the typical finding in experimental and observational studies (Hendry and Kinnison, 1999; Kinnison and Hendry, 2001).”

Although evolution obviously will be slower among long-lived trees and large mammals, where long generation times are the norm, Skelly *et al.* say the case for rapid evolutionary responses among many other species “has grown much stronger (e.g., Stockwell *et al.*, 2003; Berteaux *et al.*, 2004; Hariston *et al.*, 2005; Bradshaw and Holzapfel, 2006; Schwartz *et al.*, 2006; Urban *et al.*, 2007).” They write, “on the basis of the present knowledge of genetic variation in performance traits and species’ capacity for evolutionary response, it can be concluded that evolutionary change will often occur concomitantly with changes in climate as well as [with] other environmental changes (e.g., Grant and Grant, 2002; Stockwell *et al.*, 2003; Balanya *et al.*, 2006; Jump *et al.*, 2006; Pelletier *et al.*, 2007).” Frogs, as noted above, are no exception to this general rule.

Catenazzi *et al.* (2010) write, “climate change has been proposed as a driver of amphibian declines,” but they note this hypothesis has been largely displaced by a competing theory built around the observation that the pathogen *Bd* has been “associated with

amphibian declines throughout the world (Berger *et al.*, 1998; Briggs *et al.*, 2005; Lips *et al.*, 2006)” in a manner indicating an introduced and subsequently spreading epidemic disease. They studied the recent collapse in anuran species richness and abundance in the Upper Manu National Park of Southeastern Peru.

Catenazzi *et al.* surveyed frogs in the Peruvian Andes in montane forests along a steep elevation gradient (1,200–3,700 m), using visual encounter surveys to sample stream-dwelling and arboreal species and leaf-litter plots to sample terrestrial-breeding species, in order to compare species richness and abundance among the wet seasons of 1999, 2008, and 2009. The U.S. and Peruvian researchers found there had been “a dramatic decline in species richness of amphibians”—a mean decline of 38% in the area of their study over the 10-year period—with stream-breeding species being “disproportionally represented among the missing taxa in 2008 and 2009.” They state this result “is consistent with observations in other Neotropical (Lips, 1998) and Australian (Laurance *et al.*, 1996; Williams and Hero, 1998) sites where the species richness and abundance of frogs have declined or frogs have been extirpated,” noting “declines in these other areas are unequivocally linked to the introduction of *Bd* to naïve amphibian populations (Berger *et al.*, 1998; Lips *et al.*, 2006).”

Their results show “the geographic and elevational distribution of *Bd* extends to southern Peru,” noting this extent is consistent with Lips *et al.*’s (2008) hypothesis of *Bd* spreading southward in a wave from a *Bd* introduction site in southwestern Ecuador. Alternatively, they suggest the *Bd* introduction site could be Cusco, which “receives more visitors than any other tourist destination in Peru.” And, noting “frogs originating from many streams, ponds and lakes of the Bolivian-Peruvian Altiplano are sold live in the city for human consumption,” they suggest this frog trade “could facilitate the spread of *Bd* over large areas in southern Peru.”

Given the above observations, plus the fact that “*Bd* occurs in a wide range of land-cover types and microclimates,” Catenazzi *et al.* say “it is unclear how climate change would increase the rate of spread or the virulence of such an opportunistic pathogen in frog populations.” They conclude it hasn’t. Despite decades of research and a general belief that the link between *Bd* arrival and population decline is well-resolved in regions such as Australia, there is no evidence the arrival of *Bd* coincided with amphibian population decline, because the present data are not adequate to determine whether *Bd* was present prior

to initial sampling (Phillips *et al.*, 2012). Phillips *et al.* (2012) conclude, “more generally, our discovery of a complete lack of evidence linking the arrival of *Bd* and the timing of population declines in north-eastern Australia points to the alarming ease with which paradigms can become established even in the absence of critical tests of those paradigms.” An alternative explanation for the upturn in recorded fungal infections is not global warming, but human-mediated intensification of fungal disease dispersal, caused by transportation and modification of natural environments (Fisher *et al.*, 2012).

In a nine-year study conducted in the Little Rock Creek Basin, located within the Selway-Bitterroot Wilderness just south of Hamilton, Montana (USA), McCaffery and Maxell (2010) “evaluated relationships among local climate variables, annual survival and fecundity, and population growth rates” in “a high-elevation population of a temperate pond-breeding frog species, the Columbia spotted frog (*Rana luteiventris*).” They monitored all life stages of the species and related the resulting demographic data to climate data collected at a nearby weather station. The two University of Montana biologists report “parameters that describe winter severity were negatively correlated with survival, transition, and breeding probabilities in this high-elevation *R. luteiventris* population,” and there was “an increase in survival and breeding probability as severity of winter decreased.”

“Contrary to much of what has been discussed in the literature,” McCaffery and Maxell write, “these results suggest that under certain circumstances, a warming climate may be helpful to some amphibian populations, particularly those that live in harsh conditions at the edge of their thermal tolerances.” As a case in point, they state their results “unambiguously demonstrate that earlier ending winters with lower snowpack in this system lead to higher survival rates, higher probabilities of breeding, and higher population viability.” Thus, they conclude, “more generally, amphibians and other ectotherms inhabiting alpine or boreal habitats at or near their thermal ecological limits may benefit from the milder winters provided by a warming climate.”

Additional studies show other real-world data that refute the contention global warming is driving amphibians to extinction. Berger *et al.* (2004), for example, found lower temperatures enhanced the development of chytridiomycosis in a study of eastern Australian frogs, and Seimon *et al.* (2007) determined glacial recession in the Peruvian Andes has been creating new amphibian habitats at recently

deglaciated sites. Woodhams *et al.* (2010) note “amphibian skin peptides are one important defense against chytridiomycosis,” and examining “the population-level variation in this innate immune defense [is important] to understand its relationship with disease dynamics.” Briggs *et al.* (2010) note some amphibians with chytridiomycosis “develop only minor infections and suffer little or no negative effects.” And Zukerman (2010) reports some of the most devastated populations of Australia’s barred river frogs (*Mixophyes esiteratus*), tusked-frogs (*Adelotus sp.*), and several tree frog species (*Litoria sp.*), once thought to have been wiped out by the fungus, are now showing strong signs of recovery.

All in all, the above studies suggest amphibian populations will suffer little, if any, harm from projected CO₂-induced global warming, and they may even benefit from it.

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5.3 Arthropods

- Enhanced plant productivity driven by elevated levels of atmospheric CO₂ tends to support greater abundance of soil microarthropods.

Arthropods are invertebrate animals composed of a segmented body, jointed appendages, and an exoskeleton. A handful of studies have examined how these animals may be affected by Earth's rising

atmospheric CO₂ concentration. One of the early emerging hypotheses is that if the productivity of the plants at the base of a food chain is enhanced by the aerial fertilization effect of extra CO₂, they could be expected to support greater animal populations at the other end, including arthropods.

Siemann (1998) studied the effects of both short- and long-term nitrogen fertilization on plant productivity and arthropod communities in an upland grass ecosystem in Minnesota. In both situations, plant productivity was enhanced; arthropods responded by increasing both their numbers and the number of their species, suggesting if atmospheric CO₂ enrichment tends to enhance plant productivity, it also will increase arthropod numbers and ecosystem species richness.

Rillig *et al.* (1999) confirmed this conclusion. In serpentine and sandstone grasslands in California, they found an approximate doubling of the air's CO₂ content significantly enhanced the masses of fungi living in the soil, resulting in large increases in the numbers of fungal-feeding microarthropods (108 and 39% increases in the sandstone and serpentine grasslands, respectively). Likewise, in a study of poplar tree cuttings in Michigan, Lussenhop *et al.* (1998) observed the fine roots of the trees in their approximately doubled CO₂ treatment supported twice as many microarthropods as the fine roots of the trees growing in ambient air. And in a multiple-microcosm study of mini-terrestrial ecosystems conducted in the United Kingdom, Jones *et al.* (1998) found a 53% increase in atmospheric CO₂ concentration produced an enhanced soil fungal population that supported 52% more soil microarthropods.

Sanders *et al.* (2004) studied effects of atmospheric CO₂ enrichment on the plant and arthropod communities of the understory of a closed-canopy sweetgum plantation (which reduces the light available to the understory between 70 and 95% during the growing season) in a study where the air's CO₂ content was increased by approximately 48%. They report total arthropod abundance did not differ between ambient and elevated CO₂ plots, nor did the abundances of detritivores, omnivores, or parasitoids. They conclude, "changes in plant community composition did not translate into differences in arthropod communities."

Sticht *et al.* (2006) investigated how elevated atmospheric CO₂ concentration (550 ppm as opposed to the ambient concentration of about 380 ppm) delivered via free-air CO₂ enrichment (FACE) technology interacted with two levels of nitrogen (N) fertilization (normal N and half-normal N) to

Climate Change Reconsidered II: Biological Impacts

influence the abundance and diversity of collembolans in a field planted to winter wheat at the Federal Agricultural Research Centre in Braunschweig, Lower Saxony, Germany, where the 45% increase in the air's CO₂ content increased aboveground wheat biomass production by approximately 14%. Invertebrate communities in general, and collembolans in particular, play an important role in maintaining soil fertility, as the authors say they “participate in organic matter decomposition and can stimulate nutrient mobilization and plant nutrient uptake (e.g. Wardle *et al.*, 2004).”

The German researchers found “CO₂ enrichment enhanced the collembolan abundance by 58% under conventional N fertilization and by 100% under restricted N supply,” and “under FACE conditions the collembolan diversity was higher (28 species) compared to ambient air conditions (23 species).” Sticht *et al.* conclude, “an increase in collembolan abundance and diversity can be expected as a result of enhanced quantity and changed quality of organic matter input into the soil associated with elevated atmospheric CO₂.” And since this phenomenon “can stimulate nutrient mobilization and plant nutrient uptake,” as they note, it is especially encouraging that its relative strength was greatest when nitrogen was most limiting in their experiment.

Enhanced plant productivity driven by elevated levels of atmospheric CO₂ tends to support greater abundance of soil microarthropods.

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5.4 Birds

- 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.

One of the great concerns associated with predictions of CO₂-induced global warming is the claim that the number of birds and their habitat areas will decline. Some estimates go so far as to suggest global warming could result in the extinction of several bird species. In the following subsections, such claims are examined through peer-reviewed studies conducted on birds in an effort to see how they have responded to what IPCC has called the unprecedented rise in atmospheric CO₂ and temperature of the late-twentieth and early twenty-first century.

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.

5.4.1 Population Dynamics

How has modern warming impacted bird population dynamics? Several researchers have addressed this question for various bird species in many locations across the planet. This section summarizes what they have learned.

Schmidt *et al.* (2009) employed Bayesian hierarchical models to estimate the population size of trumpeter swans (*Cygnus buccinator*) based on aerial survey data collected by the U.S. Fish and Wildlife

Terrestrial Animals

Service throughout all known nesting habitats in the state of Alaska. These data collections were first made in 1968 and subsequently in 1975 and every five years thereafter through 2005. The results indicated “adult swan populations in Alaska increased at an average rate of 5.9% annually and cygnet production increased at 5.3% annually.” The authors also found “cygnet production exhibited higher rates of increase at higher latitudes in later years,” which they opine was “a response to warmer spring temperatures.” The five researchers conclude, “trumpeter swan populations are increasing in Alaska, especially at northern latitudes,” stating their study “represents one of the first to demonstrate a shift in breeding range of a bird possibly due to climate change.” Hence, “for trumpeter swans, it appears that breeding range limits in Alaska have expanded” in response to the warming experienced there between 1968 and 2005.

White *et al.* (2011) analyzed how Great Cormorant numbers varied over the years in response to changes in sea surface temperature (SST) in the vicinity of Greenland’s Disko Bay, using data obtained from the U.S. National Climate Data Center plus data for the number of breeding pairs of Great Cormorants in Disko Bay and adjacent areas they obtained from aerial and boat-based surveys described by Boertmann *et al.* (1996) and Boertmann (2006) for the period 1946–2005. According to the six scientists, population change rates of Great Cormorant colonies in the vicinity of Disko Bay “were significantly positively correlated with mean winter SST,” adding, “populations increased during relatively warm years and decreased during relatively cold years,” while also noting “the highest rates of population change correspond with periods of relatively high SST in recent years and during the 1960s.” White *et al.* conclude, “taken together, the positive relationship between rates of population change in Cormorants and SST, the likely positive impact of Arctic warming on the preferred prey species of Cormorants, and the flexible food preferences and foraging strategies of Cormorants suggest that Cormorants are likely to benefit from a warming Arctic.”

Grandgeorge *et al.* (2008) analyzed population sizes and phylogenetic and spatial structures of British and Irish seabirds based on “(1) presence or absence of the seabird species in the different counties of Britain and Ireland between 1875 to 1900 and 1968 to 1972, (2) seabird breeding censuses of Britain and Ireland from 1969 to 1970, 1985 to 1988 and 1998 to 2002, (3) at-sea abundance and

distribution surveys of seabirds in the North Sea from 1980 to 1985 and 1990 to 1995, and (4) a bioenergetics model to estimate energy expenditures for 40 seabird species.” With respect to population dynamics, their work revealed total seabird numbers “increased at an average rate of 1% per annum between 1969 and 2002, with a related increase of 115% in predicted total seabird predation.” Also, “between 1875 and 1972 no seabird species was lost and there was an overall expansion in breeding range of the seabird population of Britain and Ireland, with the number of counties occupied increasing from 31 to 47.”

The six scientists conclude, “the seabird community of Britain and Ireland has been remarkably resilient to environmental change in the 20th century.” In fact, it “prospered during the 20th century” and “significantly raised ocean temperatures in the North Sea (Beaugrand, 2004)” may even have “created more favorable environmental conditions for some seabird species,” citing Thompson (2006).

Lemoine *et al.* (2007) used data from the *Breeding Bird Atlas* of Lake Constance, which borders Germany, Switzerland, and Austria, to analyze the impact of land-use and climate changes on the region’s abundance of Central European birds between the periods 1980–1981 and 1990–1992, and between 1990–1992 and 2000–2002. They found “the total number of [bird] species in the Lake Constance region increased from 141 species in 1980 to 146 species in 1990 and to 154 species in 2000,” and “winter temperatures increased by 2.71°C and spring temperatures increased by 2.12°C over the 23 years from the first to the last census.” These and other data led them to conclude, “increases in temperature appear to have allowed increases in abundance of species whose range centers were located in southern Europe and that may have been limited by low winter or spring temperature.” In addition, they report “the impact of climate change on bird populations increased in importance between 1990 and 2000 and is now more significant than any other tested factor.”

Seoane and Carrascal (2008) write, “it has been hypothesized that species preferring low environmental temperatures, which inhabit cooler habitats or areas, would be negatively affected by global warming as a consequence of the widely accepted increase of temperature during the last two decades.” They note “this effect is assumed to be more intense at higher latitudes and altitudes because these areas seem to be changing more rapidly.” They devised a study “to assess whether population changes agree with what could be expected under

global warming (a decrease in species typical of cooler environments),” focusing on birds. Working in the Spanish portion of the Iberian Peninsula in the southwestern part of the Mediterranean Basin, the two researchers determined breeding population changes for 57 species of common passerine birds between 1996 and 2004 in areas without any apparent land-use changes. This work revealed, “one-half of the study species showed significant increasing recent trends despite the public concern that bird populations are generally decreasing,” and “only one-tenth showed a significant decrease.”

Seoane and Carrascal state, “the coherent pattern in population trends we found disagrees with the proposed detrimental effect of global warming on bird populations of western Europe.” They are not the only ones to have reached this conclusion. They note, for example, “one-half of terrestrial passerine birds in the United Kingdom exhibited increasing recent trends in a very similar time period (1994–2004),” citing Raven *et al.* (2005), and they explain, “there is also a marked consistency between the observed increasing trends for forest and open woodland species in the Iberian Peninsula and at more northern European latitudes in the same recent years,” citing Gregory *et al.* (2005). Likewise, they write, “Julliard *et al.* (2004a), working with 77 common bird species in France, found that species with large ecological breadth showed a tendency to increase their numbers throughout the analyzed period.”

Seoane and Carrascal state, “bird species that inhabit dense wooded habitats show striking patterns of population increase throughout time.” Noting “this is also the case with those bird species mainly distributed across central and northern Europe that reach their southern boundary limits in the north of the Iberian Peninsula,” they theorize “these short- to medium-term population increases may be due to concomitant increases in productivity.” In support of this notion they cite Julliard *et al.* (2004b) and the empirical observations of Myneni *et al.* (1997), Tucker *et al.* (2001), Zhou *et al.* (2001), Fang *et al.* (2003), and Slayback *et al.* (2003), whose work figured prominently in establishing the reality of the late twentieth-century warming- and CO₂-induced greening of the Earth phenomenon (see Section 4.2 on Biospheric Productivity), which has produced, in the words of the Spanish scientists, “an increase in plant growth or terrestrial net primary production in middle latitudes of the Northern Hemisphere since the 1980s, particularly in forest environments.” It is clear the supposedly unprecedented warmth of the past two decades has not led to what Seoane and Carrascal call

“the proposed detrimental effect of global warming on bird populations of western Europe.”

Qian *et al.* (2009) compiled a comprehensive dataset of bird species richness in China based on pertinent scientific literature published over the past three decades for 207 localities, the vast majority of which were national nature reserves with a mean area of 3270 km², which dataset they analyzed for their relationships to 13 environmental variables. The authors observe, “of all environmental variables examined, normalized difference vegetation index [NDVI], a measure of plant productivity, is the best variable to explain the variance in breeding bird richness.” Four of the 13 variables they tested explained 45.3% of the total species richness variance, with 21.2% being accounted for by NDVI, 12.5% by elevation range, and 11.6% by annual potential evapotranspiration and mean annual temperature together. They note the two most important predictors of their study (NDVI and elevation range) “have been found to be major predictors for breeding bird richness in other regions and the whole of the globe, indicating that the finding of [their] study at a smaller scale is to a large degree consistent with those of previous studies of breeding birds at larger scales.”

In a major review of plant-animal interactions in 51 terrestrial ecosystems conducted 20 years earlier, McNaughton *et al.* (1989) found the biomass of plant-eating animals is a strongly increasing function of aboveground primary production, and in a subsequent review of 22 aquatic ecosystems, Cyr and Pace (1993) found the herbivore biomass of watery habitats also increases in response to increases in vegetative productivity. Thus it is abundantly clear greater plant productivity—both terrestrial and aquatic—leads to greater populations of plants and the animals that feed upon them, which should lead to greater ecosystem biodiversity and a reduced risk of extinction. Atmospheric CO₂ enrichment increases plant productivity (see Chapter 1), which supports more animal life, which leads to greater animal biodiversity, which is good for the planet and good for mankind.

A warmer climate has benefited birds on Australia’s Heard Island, some 4,000 kilometers southwest of Perth. Over the last five decades of the twentieth century, as this sub-Antarctic island experienced a local warming of approximately 1°C, there were rapid increases in flora and fauna. The population of the King penguin, for example, “exploded from only three breeding pairs in 1947 to 25,000,” and the Heard Island cormorant, listed

Terrestrial Animals

previously as “vulnerable,” increased to 1,200 pairs. Recovering from near extinction, fur seals now number 28,000 adults and 1,000 pups (Pockely, 2001).

Penguins in Antarctica also have fared well in warmer times. In response to dramatic warming observed on the western Antarctic Peninsula over the past several decades, the penguin population has become more diverse as chinstrap and gentoo penguins have begun to take up residence among the long-inhabiting Adelie penguin population (Smith *et al.*, 1999). A study of penguin populations on the Ardley Peninsula of maritime Antarctica by Sun *et al.* (2000) found over the past 3,000 years the penguin population was lowest at 1,800–2,300 years BP, during a period of low temperature.

Huang *et al.* (2009) reported similar findings after evaluating paleo-evidence for penguin populations at Gardner Island in East Antarctica. According to the five researchers, penguins colonized the site shortly after it became ice-free 8,500 years ago. A pronounced population peak is evident in the data from about 4,700 to 2,400 BP, which corresponds closely to a substantially warmer period at this site. The authors document four other studies showing a penguin optimum roughly 3,000 to 4,000 years ago and coinciding with notably warm conditions. Together, these five studies encompass East Antarctica, the Ross Sea region, and the West Antarctic Peninsula. With all data currently available pointing to penguins having been most abundant during the warmest period of the Holocene several thousand years ago, it would seem reasonable to believe penguins will respond positively, not negatively, to any future warming.

Although global warming, regardless of its cause (natural or anthropogenic), appears to favor the population of many bird species, other human-related factors may offset such benefits and induce harm. For example, studies on the population dynamics of King penguins, *Aptenodytes patagonicus*, have been ongoing for many years. Recently, these fish-eating, top-of-the-food-chain predators have been used as indicator species for studies on the impacts of climate change in the southern hemisphere (Croxall *et al.*, 2002; Tynan 1998). In many respects, penguins have become “polar bear equivalents” of the Antarctic ecosystem. It appears something other than global warming has had a major influence on their population in recent years.

Saraux *et al.* (2011) note “in 2007, the Intergovernmental Panel on Climate Change highlighted an urgent need to assess the responses of

marine ecosystems to climate change. Because they lie in a high-latitude region, the Southern Ocean ecosystems are expected to be strongly affected by global warming. Using top predators of this highly productive ocean (such as penguins) as integrative indicators may help us assess the impacts of climate change on marine ecosystems.”

Following that charge from IPCC, several reports have used data collected from penguins marked with flipper bands (Barbraud and Weimerskirch 2001; Jenouvrier *et al.*, 2009) to predict impacts on the entire population from climate change scenarios modeled for the future. Flipper bands are metal markers attached to the upper part of the front flipper, where they are easily visible on land or in the water. Since penguins are birds that fly through the water, these “flippers” are actually wings and thus the sole source of a penguin’s swimming power. Banding involves a single loop slipped over the upper, muscular section of one wing (equivalent to the human upper arm) and is meant to remain there for the life of the bird. These bands themselves, however, might have an influence on the data being collected on these penguins.

Research was conducted over a decade, in part to test the assumption that birds would adapt within a year at most to any negative effects of the metal flipper band (Barbraud and Weimerskirch 2001). Saraux *et al.* (2011) analyzed differences in reproduction and survival on 50 banded and 50 unbanded penguins over 10 years. The researchers evaluated annual and overall survival, arrival time at the breeding colony, laying dates, breeding success, success in chick rearing, duration of feeding trips (“foraging”) and population growth.

They found the “banding of free-ranging king penguins (*Aptenodytes patagonicus*) impairs both survival and reproduction, ultimately affecting population growth rate.” Over the 10-year period, banded birds were found to produce 39% fewer chicks and had a survival rate 16% lower than non-banded birds. Much of this effect appeared to be due to an increased time banded birds required to find sufficient food (both before and during the summer breeding season) and to their relatively late arrival at the breeding colony.

Saraux and colleagues write “one of our major findings is that responses of flipper-banded penguins to climate variability (that is, changes in sea surface temperature and in the Southern Oscillation index) differ from those of non-banded birds. We show that only long-term investigations may allow an evaluation of the impact of flipper bands and that every

major life-history trait can be affected, calling into question the banding schemes still going on. In addition, our understanding of the effects of climate change on marine ecosystems based on flipper-band data should be reconsidered.”

Another human-related activity with a significant impact on bird populations is the construction of wind farms. Pearce-Higgins *et al.* (2009) note “the displacement of birds away from turbines can result in individuals abandoning otherwise suitable habitat,” and this “has been found to occur in a number of individual wind farm studies,” citing Leddy *et al.* (1999), Larsen and Madsen (2000), Kowallik and Borbach-Jaene (2001), Hotker (2006), Hotker *et al.* (2006), and Larsen and Guillemette (2007). Pearce-Higgins *et al.* report, “some poorly sited wind farms have resulted in sufficient deaths to produce a population-level effect,” citing Barrios and Rodriguez (2004, 2007), Everaert and Stienen (2006), Smallwood and Thelander (2007), Sterner *et al.* (2007), and Thelander and Smallwood (2007).

Pearce-Higgins *et al.* assessed the degree of occurrence of 12 widely distributed species of breeding birds within the vicinity of wind farm infrastructure (turbines, access tracks, and overhead transmission lines) on 12 wind farms located within unenclosed upland habitats (moorland, rough grassland, and blanket bog) in the United Kingdom, including most of the existing large upland wind farms in Scotland and northern England. The five UK scientists obtained “considerable evidence for localized reduction in breeding bird density on upland wind farms.” After accounting for habitat variation, they report, “seven of the twelve species studied exhibited significantly lower frequencies of occurrence close to the turbines,” and there was “equivocal evidence of turbine avoidance in a further two,” and “no species were more likely to occur close to the turbines.” Access tracks proved much less of a nuisance than turbines, and there was no evidence for consistent avoidance of overhead transmission lines. They conclude, “levels of turbine avoidance suggest breeding bird densities may be reduced within a 500-m buffer of the turbines by 15–52%, with buzzard (*Buteo buteo*), hen harrier (*Circus cyaneus*), golden plover (*Pluvialis apricaria*), snipe (*Gallinago gallinago*), curlew (*Numenius arquata*) and wheatear (*Oenanthe oenanthe*) most affected.”

Pearce-Higgins *et al.* say their findings emphasize the need for a “strategic approach” to ensure wind farm development avoids areas with high densities of potentially vulnerable species, not only in the UK but also “across other similar windy semi-natural habitats

in northwest Europe, southern South America, and central North America.” Efforts should be made to “avoid high densities of potentially vulnerable open country species such as waders and raptors,” they write. Their findings augment those of many others who have raised serious questions about the constructing of wind farms in inappropriate locations.

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5.4.2 Range Expansion

IPCC claims the increase in temperature predicted to result from the ongoing rise in the air's CO₂ content will be of such magnitude and speed that many species of plants and animals will not be able to migrate poleward in latitude or upward in elevation rapidly enough to avoid extinction as they are forced to seek cooler living conditions. There are many reasons for rejecting this contention, one of the most powerful being that increases in the air's CO₂ content generally enable plants to endure warmer weather, and as a result there is little or no need for them to shift the heat-limiting warm-temperature boundaries of their ranges as temperatures rise (see Section 3.13 and Section 4.2.3). At the cold-limiting cool-temperature boundaries of their ranges, warming provides opportunities for plants to push poleward and upward, resulting in expansions of their ranges and reductions in their risk of extinction.

This section reviews studies that suggest birds

may respond in like manner, mimicking the respective shifts and non-shifts of the cold- and heat-limited boundaries of the ranges of the plants and associated herbivore life forms on which they depend for food.

Thomas and Lennon (1999) helped initiate extinction concerns about birds when they analyzed temporal trends in the spatial distributions of British birds over a 20-year period of global warming, looking for climate-induced changes in their breeding ranges. They found the northern margins of southerly species' breeding ranges shifted northward by an average of 19 km from 1970 to 1990, while the southern margins of northerly species' breeding ranges did not shift at all, in the mean. British birds thus expanded their ranges in the face of global warming, clearly a positive response that makes extinction less likely than it was before the warming.

Norment *et al.* (1999) analyzed bird surveys conducted along the Thelon River and its tributaries in the Canadian Northwest Territories from the 1920s through much of the 1990s, finding three bird species had expanded their breeding ranges southward, nine northward, and 16 were new to the area. The authors note the primarily northward range expansions may be explained by “a recent warming trend at the northern treeline during the 1970s and 1980s.” Alternatively, they note the influx of new species may result from “increasing populations in more southerly areas.” In either case, the birds appear to be faring quite well—even thriving—in the face of increasing temperatures in this forest-tundra landscape, which also appears to be the case in Norway (Saether *et al.*, 2000).

Research suggests seabirds of Greenland are also likely to benefit from global warming. According to Wagner and Melles (2001), a significant number of seabirds inhabited the area around Liverpool Land, on the east coast of Greenland, during the Medieval Warm Period (900–1300 AD), yet there was little or no (inferred) bird presence for a several-hundred-year period prior to this time (Dark Ages Cold Period) and another significant absence of birds thereafter during the Little Ice Age, which marked “the coldest period since the early Holocene in East Greenland.” As temperatures have risen over the past 100 years, seabirds once again have expanded their range to inhabit the area.

Kinzelbach (2004) explored the range history of the serin, a bird that “was a topic of particular interest to ornithologists of the 19th and 20th century” due to “the rapid expansion of its range in historical times.” The author reexamined “all the sources of records of

the serin in 16th century Europe, ... both those already known and some that have been newly discovered.” The data confirmed the findings of Mayr (1926), that “north of 48°N there were no free-living populations of *Serinus serinus* in the 16th century.” During that period, the serin’s range was constrained, Kinzelbach reports, as it “was halted by colder periods of the Little Ice Age after 1585, only resuming a rapid expansion at the beginning of the 19th century,” after which it was “able to expand its range from the Mediterranean region throughout large areas of Central Europe within a mere 200 years.”

Brommer (2004) categorized birds of Finland as either northerly (34 species) or southerly (116 species) and quantified changes in their range margins and distributions from two atlases of breeding birds, one covering the period 1974–1979 and one for 1986–1989, to determine how the two groups of species responded to what he called “the period of the Earth’s most rapid climate warming in the last 10,000 years,” citing McCarthy *et al.* (2001). Southern species experienced a mean poleward advancement of their northern range boundaries of 18.8 km over the 12-year period, while the southern-range boundaries of the northern species remained essentially unaltered. Noting similar results had been obtained for birds in the United Kingdom (Thomas and Lennon, 1999) and other animals (primarily butterflies) elsewhere (Parmesan, 1996; Parmesan *et al.*, 1999), Brommer concludes, “in general, for Northern Hemisphere species, southerly range margins of species are less responsive to climate change than the northerly margins.” This demonstrates once again the ranges of birds (and possibly other animals) in a warming world likely will increase, as their northern range boundaries expand poleward and upward while their southern range boundaries remain largely unaltered, which should render them less subject to extinction than they are currently or have been in the past.

For the portion of the United States east of the Rocky Mountains, Hitch and Leberg (2007) used data from the North American Breeding Bird Survey to evaluate shifts in the northern range boundaries of 26 species of birds with southern distributions and the southern range boundaries of 29 species of birds with northern distributions between the periods 1967–1971 and 1998–2002. They found the northern margins of the southern group of birds showed significant northward shifts that averaged 2.35 km per year for all species studied, which they describe as being “consistent with the results of Thomas and Lennon (1999) from Great Britain.” Also in agreement with the observations on British birds, they determined

“levels of warming do not appear to be so great [that] they are forcing birds to abandon the southernmost portions of their distributions.”

Grandgeorge *et al.* (2008) analyzed population sizes and phylogenetic and spatial structures of British and Irish seabirds based on “(1) presence or absence of the seabird species in the different counties of Britain and Ireland between 1875 to 1900 and 1968 to 1972, (2) seabird breeding censuses of Britain and Ireland from 1969 to 1970, 1985 to 1988 and 1998 to 2002, (3) at-sea abundance and distribution surveys of seabirds in the North Sea from 1980 to 1985 and 1990 to 1995, and (4) a bioenergetics model to estimate energy expenditures for 40 seabird species.” They found “a marked expansion in the breeding range of seabirds in Britain and Ireland between 1875 and 1972.” In addition, they report total seabird numbers “increased at an average rate of 1% per annum between 1969 and 2002, with a related increase of 115% in predicted total seabird predation.” Also, they state, “between 1875 and 1972 no seabird species was lost and there was an overall expansion in breeding range of the seabird population of Britain and Ireland, with the number of counties occupied increasing from 31 to 47.”

The six scientists conclude, “the seabird community of Britain and Ireland has been remarkably resilient to environmental change in the 20th century.” In fact, it “prospered during the 20th century,” and “significantly raised ocean temperatures in the North Sea (Beaugrand, 2004)” may have “created more favorable environmental conditions for some seabird species,” citing Thompson (2006).

Brommer (2008) notes a “population-level change expected under a climate-warming scenario is a poleward shift in the distribution of organisms,” and he states many believe birds that “do not shift their range margin consist of species that are declining, and would therefore be of particular management concern.” A few years earlier, Brommer (2004) had measured the range sizes and northern range margin locations of 116 bird species with a predominantly southern distribution in Finland, and of those species “the trend slope describing the change in their abundance for the period 1983–2005 was calculated for 53 species by Vaisanen (2006).” This, he notes, resulted in “the largest dataset available of the long-term trends in population numbers of Finnish birds that is comparable across species, because it has both been gathered and analyzed using the same procedures.” Brommer (2008) determined the concomitant changes in the northern range margins of

the 53 species.

The Finnish bird specialist found “species foraging in wet habitats had experienced strong range margin shifts as compared with other feeding ecologies.” However, he found “no evidence that those feeding ecological groups that showed a relatively small shift in range margin had experienced low population growth or a population decline.” Therefore, in discussing “the lack of correlation between the shift in range margin of the different feeding ecologies and the change in their mean abundance,” Brommer states this real-world finding “is contrary to expected under a climate-change scenario, because, all else being equal, a clear range-margin shift should indicate a good capacity to track climatic change, which should result in a more positive trend in abundance if climate change is indeed the main driver of population-level change.”

Maclean *et al.* (2008) analyzed counts of seven wading bird species—the Eurasian oystercatcher, grey plover, red knot, dunlin, bar-tailed godwit, Eurasian curlew, and common redshank—made at approximately 3,500 sites in Belgium, Denmark, France, Germany, Ireland, the Netherlands, and the United Kingdom on at least an annual basis since the late 1970s. They did this in order to determine what range adjustments the waders may have made in response to regional warming, calculating the weighted geographical centroids of the bird populations for all sites with complete coverage for every year between 1981 and 2000. They found “the weighted geographical centroid of the overwintering population of the majority of species has shifted in a northeasterly direction, perpendicular to winter isotherms,” with overall 20-year shifts ranging from 30 to 119 km. In addition, they report, “when the dataset for each species was split into 10 parts, according to the mean temperature of the sites, responses are much stronger at the colder extremities of species ranges.” They found, “at warmer sites, there was no palpable relationship between changes in bird numbers and changes in temperature.” They conclude, “range expansions rather than shifts are occurring” as the planet warms.

Maclean *et al.* note the commonly used climate-envelope approach to predicting warming-induced species migrations “essentially assumes that as climate alters, changes at one margin of a species’ range are mirrored by those at the other, such that approximately the same ‘climate space’ is occupied regardless of actual climate,” whereas the evidence suggests “that this may not be the case: climate space can also change.”

Maclean *et al.* further write, “it is actually not surprising that responses to temperature appear only to be occurring at the colder extremities of species ranges,” for “it has long been known that it is common for species to be limited by environmental factors at one extremity, but by biological interactions at the other,” citing Connell (1983) and Begon *et al.* (2005). They conclude it is likely “the warmer extremities of the species ranges examined in this study are controlled primarily by biotic interactions, whereas the colder margins are dependent on temperature.”

In a model-based study, Jensen *et al.* (2008) state “global climate change is expected to shift species ranges polewards, with a risk of range contractions and population declines of especially high-Arctic species,” citing the Arctic Climate Impact Assessment (ACIA, 2005). To evaluate this claim, they constructed species distribution models for the Svalbard-nesting pink-footed goose (*Anser brachyrhynchus*), in order to “relate their occurrence to environmental and climatic variables.” They used the most parsimonious of the models to “predict their distribution under a warmer climate scenario,” based on “mean May temperature, the number of frost-free months and the proportion of moist and wet moss-dominated vegetation in the area,” the latter being “an indicator of suitable feeding conditions.”

They found global warming “will have a positive effect on the suitability of Svalbard for nesting geese in terms of range expansion into the northern and eastern parts of Svalbard which are currently unsuitable.” They also note this result does not even consider whether glaciers will decrease in size and expose still more potential nest sites. Thus they conclude by stating increased temperatures could help the population of pink-footed geese, as “elongation of the frost-free season in Svalbard may relax their dependence on the acquisition of body stores before arrival (so-called ‘capital’ breeding, *sensu* Drent and Daan, 1980), so that geese will have more time to acquire the necessary resources upon arrival and still breed successfully,” noting “both factors are likely to have a positive effect on the population growth.”

Zuckerberg *et al.* (2009) “used the New York State Breeding Birds Atlas, a statewide survey of 5,332 25-km² blocks surveyed in 1980–1985 and 2000–2005, to test several predictions that the birds of New York State are responding to climate change.” They found “all bird species (n = 129) included in this analysis showed an average northward range shift in their mean latitude of 3.58 km.” Citing a number of other studies, the researchers conclude, “the repeated

pattern of a predicted northward shift in bird ranges in various geographic regions of the [Northern Hemisphere] provides compelling evidence that climate change is driving range shifts.” This provides compelling evidence Earth’s birds did precisely what they should have done, over the period of Zuckerberg *et al.*’s study, in order to maintain a strong presence on the planet in the face of the rising temperatures (natural or anthropogenic) of that period.

Hockey and Midgley (2009) write, “in the influential fourth assessment report of the Intergovernmental Panel on Climate Change, Rosenzweig *et al.* (2007) tested several thousand time-series data sets for changes in species behavior and geographic range consistent with climate change, reaching the conclusion that it is very likely that climate change is driving changes in natural biological systems.” They note, “the use of such large data sets in meta-analyses may discourage the close inspection of observations and result in naively misattributing observed shifts to climate when other explanations may be more parsimonious.”

To test this hypothesis, Hockey and Midgley “collated information about recent range changes in South African birds, specifically indigenous species that have colonized the Cape Peninsula, at the southwestern tip of Africa in the Western Cape province, since the 1940s,” where they state there have been “widespread anthropogenic changes of many kinds to the landscape, including urbanization, commercial afforestation and the introduction and spread of invasive alien trees, most of which occurred before climate change accelerated in the 1970s.”

The two researchers found the colonization events “concur with a ‘climate change’ explanation, assuming extrapolation of Northern Hemisphere results and simplistic application of theory,” but “on individual inspection, all but one may be more parsimoniously explained by direct anthropogenic changes to the landscape than by the indirect effects of climate change.” Also, “no *a priori* predictions relating to climate change, such as colonizers being small and/or originating in nearby arid shrub-lands, were upheld.”

The South African scientists state their work suggests “observed climate changes have not yet been sufficient to trigger extensive shifts in the ranges of indigenous birds in this region, or that *a priori* assumptions are incorrect.” Either way, they continue, “this study highlights the danger of naive attribution of range changes to climate change, even if those range changes accord with the predictions of climate-change models,” because “misattribution could

distract conservationists from addressing pressing issues involving other drivers of biodiversity change such as habitat transformation, and obscure important lessons that might be learned from the dynamics that pertain to such changes.”

Tyrberg (2010) compared fossil avifaunas of the Last Interglacial (LIG), about 130,000 to 117,000 years ago from multiple sites around the world to the modern avifaunas found in those locations. During much of this time interval, the globe was about 2°C warmer than it is today, and it was up to 10°C warmer in much of the Arctic. For fossil faunas, only species that still exist were included in the comparisons, because during the cold period of the last glacial, which followed the LIG, many species went extinct due to the cold, and climate tolerance can be determined reliably only for living species.

Based on the areal distributions of fossil avifaunas in different parts of the world, regions were delineated in which many of the identified species coexisted. If it was found the same sets of species share the same common ranges today, it was concluded the avifauna, as a whole, did not respond to any significant degree to the warmer temperatures of the LIG.

For sites that were about 2°C warmer during the LIG—including four sites in Florida, one in Alaska, two in Germany, and one in New Zealand—species present during the LIG were found to be the same as those that inhabit those regions today. At a site in Wales, however, where LIG temperatures were a full 4°C warmer than today, the fossil avifauna was similar to the current avifauna of Spain and Portugal, indicating the fossil avifauna had located themselves further northward during the LIG in response to the much greater warmth of that period. And in another exception to the study’s primary findings of similar faunal structures, the LIG avifauna at a site in North Africa (which is now desert, with no birds present) was similar to that of the area south of the desert today, indicating—in light of the fact that during the LIG the Sahara desert received much more rainfall than it does currently—precipitation was the overriding factor determining both the current and fossil avifauna choice of territories.

Tyrberg concludes, “as for the effect of the generally warmer climate during the LIG it seems clear that differences on the order of 2°C or less, both on land and in sea-surface temperatures, are barely, if at all, detectable in the avifaunas.”

Popy *et al.* (2010) employed data from two bird atlas surveys performed on a 1 km by 1 km grid (the first in 1992–1994 and the second in 2003–2005) in

Climate Change Reconsidered II: Biological Impacts

an alpine valley in the Italian Piedmont in search of evidence for an upward shift in the ranges of 75 bird species (68 of which were detected in both surveys) over this period, during which time the region's mean air temperature rose by 1.0°C. They found "the number of species whose mean elevation increased ($n = 42$) was higher than the number whose mean elevation decreased ($n = 19$), but the overall upward shift [29 m] was not significantly different from zero." In addition, they state even the 29-m increase was "smaller than would be expected from 'climatic envelope' models," as the "1.0°C increase in temperature would be equivalent to c. 200 m in elevation, based on an average gradient of -0.5°C per 100 m." In addition, they write, "at the European scale, no overall expansion or contraction of the distributions of the studied species was detected." Popy *et al.* conclude, "until a better understanding of the underlying mechanisms is achieved, predictions based only on 'climate envelope' models should be either validated or considered cautiously."

Using the same sampling techniques employed by Terborgh and Weske (1975) in 1969, and working at five of the nine localities studied by those earlier investigators, Forero-Medina *et al.* (2011) resampled bird communities at five elevations (690, 1310, 1570, 1970, and 2220 meters) within the Reserva Comunal El Sira on the Cerros del Sira massif in Peru some 41 years later, in 2010. They sought to determine what changes might have occurred in the elevations of the several species encountered at the two sampling times. Of the 55 species encountered in both sampling periods, 36 had moved up in elevation, 12 had moved down, and seven had not moved in either direction, resulting in an average upward shift of 49 meters for the 55 bird species over the 41-year period. They describe this change in elevation as being "significantly smaller" than the 152-meter increase one would have expected from the amount of warming experienced throughout the region between the times of the two studies.

In an attempt to determine to what extent tropical and subtropical birds from lower latitudes may have been making their way northwards in response to regional warming since the mid-1970s, Rappole *et al.* (2011) conducted a three-year field study on ranch land of the Welder Wildlife Refuge along a 30-km stretch of the Aransas River in southeastern Texas, which they say is located "at the northern end of the New World subtropics." Their findings indicate "range change is occurring at a rapid rate for tropical, subtropical, and warm desert birds in Texas." They report, "comparisons between former (1974) and

current avian distributions for the region show significant breeding range extension of 40–220 km to the north, northeast or east for at least 68 species, many of which cross major biogeographic boundaries." They conclude "change in key parameters of habitat, e.g. seasonal food availability, as affected by factors related to climate change, e.g. mean annual precipitation, temporal distribution of precipitation (monthly means), or monthly means for nighttime-low temperatures during the breeding season, provide the most likely explanations for observed range extensions."

As for the single overriding "environmental factor associated with avian range shift in South Texas," Rappole *et al.* identify "change in mean annual temperature," as documented by Norwine and John (2007). They report the movement of this "large segment of the subtropical avian community into temperate habitats has not been met with a corresponding shift of temperate species as had been predicted by a number of models." Quite to the contrary, they continue, "the communities now overlap, creating, in effect, novel communities." These new communities possess a greater biodiversity than the ones that existed there prior to the arrival of the many new tropical and subtropical bird species.

The findings cited in this section make it clear that where confirmed regional warming over the time periods has been investigated, the vast majority of studies of bird range adjustments have revealed opportunistic poleward expansions of their cold-limited boundaries with little or no change in the locations of their (supposedly) heat-limited boundaries. This behavior is not a matter of massive range reductions or of bird species rushing, or even inching, toward extinction, as is often projected in model-based studies. Instead, the species are fortifying themselves against the possibility of extinction, behaving as resilient evolutionary survivors and colonizing new habitat as it becomes available, strengthening their populations against the myriad challenges associated with environmental change.

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Terrestrial Animals

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5.4.3 Adaptation, Evolution, and Phenotypic Responses

Amid concerns of species extinctions in response to rising temperatures, observational data indicate birds are effectively coping with and adapting to various challenges to their existence, real or perceived, arising from global warming. This section examines adaptive responses pertaining to reproductive success, timing of spring arrival, and trophic mismatches. In brief, the findings discussed here provide ample reason to conclude birds likely will benefit from future global warming.

5.4.3.1 Reproductive Success

Concerns have been expressed that global warming may upset certain reproductive traits in birds, leading to downward trends in the populations of many species. However, as discussed below, birds are well-equipped to respond to warming, often adapting their breeding habits so their reproductive success is frequently higher at warmer temperatures.

Brown *et al.* (1999) studied a population of individually recognizable, color-banded Mexican jays in the Chiricahua Mountains of Arizona (USA) over the period 1971–1998 for trends in egg-laying dates and monthly minimum air temperatures. Over this 29-year period, they determined the date of first nest construction occurred 10.8 days earlier, and the date of first clutch came 10.1 days earlier. These changes were associated with significant upward trends in monthly minimum temperature in the study area; in many bird species “breeding is timed so as to have young in the nest when the principal food of the nestlings is at its peak.” With warmer minimum temperatures occurring earlier over their study period, they suggest this climatic trend could be producing an earlier abundance of such food, which would help explain the earlier egg-laying date.

The researchers also identified a second way in which earlier-occurring warmer night temperatures might lead to earlier breeding dates in birds: by

alleviating thermal stresses on females on cold nights. Citing several studies that had revealed similar breeding trends in European birds, they suggest the “recognition of similar trends on both continents in very different environments is consistent with the interpretation that some avian populations are already responding to climate changes in the last 29 years or so.” These widespread changes are positive in nature, for not only are bird ranges increasing in size as air temperatures rise, the temporal availability of food needed to sustain important life processes is advancing in synchrony with the timing of egg-laying.

Visser *et al.* (2003) examined laying dates for 24 populations of great and blue tits (*Parus major* and *Parus caeruleus*, respectively) in six European countries from 1979 to 1998, during which time several (but not all) of the locations studied exhibited increases in near-surface air temperature. Results indicated “the phenological response to large-scale changes in spring temperature varies across a species’ range, even between populations situated close to each other.” They also report “this variation cannot be fully explained by variation in the temperature change during the pre- and post-laying periods.” Their results “show the value of replicating population studies across parts of a species’ range, as the effects of climate change may differ, even within a single species, on a small geographical scale.”

Halupka *et al.* (2008) documented various breeding parameters of reed warblers (long-lived passerine birds that winter in Africa but breed in the reed beds of marshlands in the Palaearctic) during 12 breeding seasons (1970–1973, 1980–1983, 1994, 2003, and 2005–2006) and compared trends in what they measured with concomitant trends in mean monthly temperatures. They found temperatures in the mean breeding season (April–August) increased significantly between 1970 and 2006, as did the mean temperature of each individual month of the breeding season, with the average temperature for the May–July period rising by 2°C. Egg-laying started three weeks earlier in 2005 and 2006 than in 1970 (as assessed by the first-egg date of the earliest pair of breeding birds), and the median first-egg date shifted forward by 18 days.

The end of egg-laying, however, did not change significantly in either direction, so there was a corresponding increase in the length of the egg-laying period, and with this longer laying period available to them, more birds were able to rear second broods. In the 1970s and 1980s, for example, the Polish researchers report, “only about 0–15% of individuals

laid second clutches,” but “between 1994 and 2006 up to 35% of birds reared second broods.” In addition, they report, “during seasons with warm springs, early nests were better protected by being hidden in newly emerged reeds,” and “as a result, these nests suffered fewer losses from predation.” They conclude, “the studied population of reed warblers benefits from climate warming.”

Based on bird-ringing records spanning 41 years (1964–2004), Husek and Adamik (2008) “documented shifts in the timing of breeding and brood size in a long-distance migrant, the red-backed shrike (*Lanius collurio*) from a central European population.” They compared their results with the climatic history of the region over the same period. They determined temperatures in May increased significantly over the period of their study, and “in line with this increasing May temperature” there was “a 3- to 4-day shift towards earlier breeding.” This pattern, they write, “is consistent with the results of similar studies on other long-distance migrating songbirds (e.g., Dunn, 2004).” In addition, they report, there was “an increase in brood size by approximately 0.3 nestlings since 1964.” They state, “given that early broods are usually larger (Lack, 1968; this study) and that they have a higher nest success (Muller *et al.*, 2005), this may have a positive effect on future population increases as the temperature continues to rise.”

After observing two second clutches in a newly established population of tree swallows in the Shenandoah Valley of Virginia (USA), Monroe *et al.* (2008) monitored all late nests in the following two breeding seasons to see what they could learn about the phenomenon. This revealed, “among all females nesting in the early breeding rounds of 2006 and 2007, 5% of birds with successful first clutches later laid second clutches.” The mean productivity for double-brooded females for 2006–2007 was 4.4 ± 1.3 fledglings from first clutches and 3.4 ± 0.8 from second clutches, so “double-brooded females significantly increased their total annual productivity compared to birds nesting only in the early rounds of breeding.” The productivity of the double-brooded females was approximately 75 percent greater than that of the single-brooded females. Monroe *et al.* conclude, “in general, late summer and fall nesting among North American birds is underappreciated and may be increasing due to global warming,” citing Koenig and Stahl (2007).

Dyrce and Halupka (2009) examined long-term responses in the breeding performance of Great Reed Warblers living on fish ponds near Milicz in

southwest Poland during various years from 1970 to 2007 (1970–1974, 1981–1984, 1997, and 2004–2007), over which period mean temperatures during the egg-laying months of the species (May–July) rose by 2.2°C, from 15.3 to 17.5°C. The two researchers found a “significant advancement in both earliest and annual median first-egg-laying dates” that “correlated with temperature increases early in the season.” Latest first-egg-laying dates remained unchanged, as did several other breeding statistics, including clutch size, nest losses, and number of young per nest. Consequently—and contrary to a Bavarian population of Great Reed Warblers that also advanced its latest first-egg-laying date—the Polish bird population expanded its breeding season in response to regional warming, whereas the Bavarian birds merely shifted theirs, as documented by Schaefer *et al.* (2006).

Dyrce and Halupka conclude, “the studied population does not benefit from climate warming (as found in Bavaria), but apparently does not suffer,” reiterating “the Great Reed Warbler has adapted well ... by shifting the timing of breeding.” The results of their study, they state, “do not confirm the prediction of Bairlein and Winkel (2000) that long-distance migrants would suffer due to climate change.” In addition, they write, a comparison of their data with that of the Bavarian population “provides evidence that different populations of the same species can adapt in different ways to climate change,” noting “this was also previously found for woodland species,” citing Visser *et al.* (2002) and Sanz (2003).

Wesolowski and Cholewa (2009) investigated evidence for climate warming in Białowieża National Park of East Poland over the period 1975–2007 to determine “whether local populations of four sedentary birds (*Sitta europaea*, *Poecile palustris*, *Cyanistes caeruleus*, *Parus major*) advanced their breeding phenology during that time, and how breeding phenology was affected by temperature variation during the period preceding egg laying.” According to the authors, “mean yearly temperatures varied strongly across years, with a significant warming ($\sim 1^\circ\text{C}$) trend,” and “in all species the onset of breeding was vary variable across years (up to 30 days), as birds started breeding earlier in springs with higher temperatures in the pre-laying period.” They note the spring of 1990—when February and March were extremely warm with “mean temperatures $+5^\circ\text{C}$ higher than these months’ averages, equivalent to the ‘worst’ IPCC warming scenario”—served as a natural experiment, showing “what would happen when the late winter/early spring period got substantially warmer.” They found “all four species were able to

Climate Change Reconsidered II: Biological Impacts

react to this challenge by advancing the onset of breeding to unusually early dates that are usually found only in the Mediterranean populations.”

The two researchers write, “the ability to react even in these extreme conditions shows that the range of phenotypic plasticity in these birds is far greater than normally observed, and suggests that there is still unexpressed potential in lay date flexibility.” They therefore conclude, “local birds are already prepared to cope with envisaged warming, suggesting that there is no need for new response mechanisms.” In addition, they state this phenomenon is “clearly noticeable among different groups of organisms in Bialowieza National Park (e.g. timing of bud burst in trees, Wesolowski and Rowinski, 2006, 2008; development of herbs on the forest floor, Falinski 2001, Sparks *et al.*, 2009),” and they thus also conclude, “birds, trees and herbs in this primeval forest apparently ‘read’ environmental cues in a similar way and react to them in a comparable fashion,” probably because “they have been exposed to the same vagaries of local climate over ages if not millennia, and there was plenty of time to match phenology of interacting species with one another.”

Thomas *et al.* (2010) note “the timing of annual breeding is a crucial determinant of reproductive success, individual fitness, and population performance, particularly in insectivorous passerine birds,” because “by synchronizing hatching with the narrow time window of maximal food abundance, parents can enhance their reproductive success through an increase in offspring growth rate and body condition, survival to fledging, and subsequent recruitment into the breeding population.” They studied two populations of blue tits in northern Corsica (Muro and Piro) to determine “how laying date is related to spring temperatures and vegetation phenology.” These two factors were assumed to figure highly in determining the peak period of blue tit food abundance (caterpillars). They discovered “Blue Tits use a cue system that is context specific to fine-tune laying dates to match local conditions both on a spatial (habitat) scale and on a temporal (inter-annual) scale,” and their “reliance on both temperature and phenology when breeding late in the season, as occurs in most populations where tits have been intensively studied north of the Mediterranean region, satisfactorily explains how these populations can advance breeding in response to rising spring temperatures while maintaining a relatively large variation in the onset of breeding on a local spatial scale.”

Thomas *et al.* acknowledge, “if a single

environmental feature [such as temperature] were responsible for the timing of breeding, climate change could cause a severe decline in breeding success, with negative demographic consequences.” However, they state they “have not detected any consistent mismatch between Blue Tit breeding dates and caterpillar peak [abundance] dates over the 14 and 21 years for which they have data for Muro and Piro, respectively.” Their findings, they conclude, “offer some hope that breeding populations will respond well to global warming.”

Barnagaud *et al.* (2011) note “deciphering the effects of climatic conditions on population dynamics is of major importance in understanding how organisms are likely to be affected by climate changes.” Toward that end, they “used broad scale annual censuses of adult and young Black Grouse in the French Alps between 1990 and 2007 to test whether the breeding success of the species is affected by inter-annual climatic variation and long-term climate change,” based on “annual counts of Black Grouse hens and chicks carried out by the French Mountain Galliforms Observatory on 58 counting sites,” where “counts were performed on the same sites and areas from one year to another, with the same operators.”

They note “the Alps are currently undergoing a significant global change in climatic conditions, with warmer temperatures and drier conditions, especially in winter, that reflect particularly well such large scale processes as the NAO [North Atlantic Oscillation],” citing Beniston *et al.* (1997), Giorgi *et al.* (1997), and Beniston (2005, 2006). They determined “the [current] optimal weather conditions for the reproduction of the Black Grouse in the French Alps correspond to average winter NAO values for the last 30 years,” which suggests, they write, “the species has adapted to more frequent positive NAO anomalies in the last decades, i.e., to a warmer and drier climate.”

Noting “neither the numbers of hens nor the breeding indexes have declined during the last 18 years,” they further state “this result is consistent with recent reports (Storch, 2007) suggesting that the alpine populations of Black Grouse which declined during most of the twentieth century (Magnani, 1987) have stabilized in the past two decades, despite the climate warming threat.” They point out “this absence of decline agrees with community-level studies showing lower-than-expected effects of climate change on alpine birds (Archaux, 2004).” The seven scientists also say their results indicate “Black Grouse have until now been able to track climatic trends

towards a warmer and drier climate,” and they “appear to be more threatened by declines in the availability of suitable areas and changes in habitat structure than by direct effects of climate warming on [their] reproduction.” Thus, they conclude, “even a highly specialized mountain species can track rapid climate changes without decreasing its productivity, at least within the limits of current climate changes.”

Weimerskirch *et al.* (2012) write, “in marine systems, wind is a major component of the environment, and climate change-induced alterations in oceanic wind regimes and strength have already occurred and are predicted to increase.” With respect to what has “already occurred,” they note “over the past fifty years, Southern Hemisphere westerlies have shifted poleward and increased in intensity,” which could affect “the movement or distribution of wind-dependent species, such as migratory land birds or pelagic seabirds.” The latter, the authors note, “rely extensively on wind to move at low costs between breeding and foraging sites,” citing Weimerskirch *et al.* (2000) and Wakefield *et al.* (2009).

Weimerskirch *et al.* analyzed the possible influence of wind conditions over the Southern Ocean on the foraging ecology and life-history traits of the wandering albatross (*Diomedea exulans*), one of the most wide-ranging pelagic seabirds, employing data on the duration of their foraging trips and breeding success collected over the period 1966–2010, and foraging performance and body mass collected over the period 1989–2010, focusing on breeding birds from the Crozet Islands, which are situated in the windiest area of the Southern Ocean.

Over the period of time characterized by IPCC as having experienced unprecedented global warming, the foraging range of wandering albatrosses shifted poleward, as the wind also “strongly increased and shifted poleward,” the four researchers report. As a result of this change, albatross “rates of travel and flight speeds have increased,” a trend they say also has been found to have occurred in the southwestern Indian Ocean over the past 30 years by Peron *et al.* (2010). One important consequence of this change was a 22% decrease in the duration of albatross foraging trips between 1970 and 2008 (a drop from 12.4 to 9.7 days). And as a consequence of this change, they write, “breeding success has improved, and birds have increased in mass by more than one kilogram,” a 10–12% increase in body weight for males and females alike.

The above-described real-world wind changes of the past half-century, in the words of Weimerskirch *et al.* (2012), “have affected positively the foraging

efficiency and foraging range of wandering albatrosses, ultimately improving breeding success and reducing mortality risks, respectively.” As can be estimated from their graph of the pertinent data, albatross breeding success rose from approximately 65% to 77% over the period studied.

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Climate Change Reconsidered II: Biological Impacts

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5.4.3.2 Spring Arrival Dates

Changes in the date of spring migration arrival date of birds have been viewed by some as a fingerprint of climate change and possibly of species distress. Trends in this parameter should be evaluated with caution before making such a leap.

A case in point is the study of Mills (2005), who used data collected at Long Point Bird Observatory on the north shore of Lake Erie in Ontario, Canada over the period 1975–2000 to investigate whether there had been changes in the timing of spring and autumn migrations of 13 species of birds that might be viewed as ecological responses to global warming. He analyzed for trends in the day of first arrival in the spring, and in the days of first, second, and third quartile arrivals in the spring, as well as like departures in the autumn.

All 13 species exhibited earlier trends in the date

Terrestrial Animals

of first arrival in the spring. When subjected to stringent thresholds of statistical analysis, however, only one species was considered to exhibit a definite trend. Spring quartile analyses were not nearly as universal. Only nine of the 13 species trended toward an earlier arrival date, and four trended toward a later arrival date. Of the nine that trended toward an earlier arrival date, only two were statistically significant, leaving the author to conclude, “most individuals of most species cannot conclusively be said to have migrated in 2000 earlier than their 1975 ancestors.” Analysis of the quartile means revealed no significant phenological change by bird sex. With respect to autumn trends, five species showed delayed migration, two showed advanced migration, and six exhibited no trend.

Mills writes, “caution should be exercised in drawing broad conclusions about changes in migration phenology” with respect to global warming. He notes, for example, using first arrival dates to characterize migration systems “can be problematic because they are data from one tail of a distribution, they comprise a mostly male population and they may not correlate well with the balance of the migration period.” He also notes “changes do not appear to be universal in spring, and change in that season is (a) considerably less than that suggested by [first arrival date] analysis and (b) both less complex and less common than that exhibited during autumn migration.”

For studies that show a more conclusive link between temperature and date of bird migration, rather than considering such observations to be a sign of species in distress, an alternative and perhaps more correct interpretation is that such changes are simply a manifestation of the ability of birds to adapt or evolve in response to an environmental perturbation. Model-based claims of species decline typically do not account for adaptive or evolutionary responses, but because birds are winged creatures, it would be expected that under the threat of global warming they might take flight and migrate to cooler regions of the globe as an adaptive measure. Several studies of bird migration dates suggest they may be doing so.

Gordo and Sanz (2006) analyzed a large database of about 44,000 records they assembled from observations at more than 1,300 sites throughout Spain during the period 1944–2004 in a study of the migratory behavior for five trans-Saharan bird species: *Ciconia ciconia* or white stork, *Cuculus canorus* or cuckoo, *Apus apus* or swift, *Hirundo rustica* or barn swallow, and *Luscinia megarhynchos* or nightingale. This phenomenon previously had been

proposed by the country’s Instituto Nacional de Meteorología as “a potential bioindicator of the timing of seasons,” the current study of which the two Spanish researchers describe as “the most complete and thorough analysis available for the Mediterranean region.”

Gordo and Sanz report “spring arrival dates have tended to advance since the mid-1970s,” and “individuals arrived earlier in warmer years,” noting “the earlier arrivals related to higher temperatures should be due to the advancement of the spring course in the Iberian Peninsula and consequently the presence of ecological suitable conditions for an early colonization of first breeders.” They found “current arrival dates are similar or even seem to be a bit later to those occurring at the beginning of the study period.” According to Gordo and Sanz, “the advance in arrival date recorded over the last few decades should be better interpreted as a trend towards re-establishing the timing of migration after an anomalous period of delayed arrivals during the 1970s–1980s,” which suggests birds have been adapting to temperature changes throughout the Mediterranean region, where temperatures were likely warmer in the mid-1940s than they were throughout the 1990s and during the first years of the twenty-first century.

Studying the skylark (*Alauda arvensis*), which is migratory in Eastern and Northern Europe but resident in areas with milder winters (such as the UK), Askeyev *et al.* (2009) analyzed the dates of their spring arrival in the Volga-Kama region of the Tatarstan Republic of Russia, using “one of the longest extant records of bird migration in the world,” which runs from 1811 to 2008, with sporadic missing years in the first half of the record. They report March temperatures rose about 5.2°C over their study period, but 3.7°C (~70%) of that warming occurred over the final three decades of the nearly two-century-long interval. They also found a corresponding inflection point in the rate-of-advancement of skylark spring arrival-date that was approximately 15 times greater (0.368 day per year) than it was over the study period’s first 17 decades (0.024 day per year).

Plotting arrival-date as a function of temperature, they found the inflection point occurred at a mean March temperature of –3.5°C, suggesting a mean rate of advancement of spring arrival-date of 0.5 day per °C for mean March temperature increases below a negative 3.5°C, and a mean rate of advancement of arrival-date of 3.4 days per °C for mean March temperature increases above –3.5°C. That represents close to a seven-fold increase in the rate of

advancement of spring arrival-date upon exceeding this biological “tipping point” temperature.

Askeyev *et al.* conclude, “the nonlinear nature of the relationship between first arrival and temperature suggests that above a critical temperature threshold a much more rapid change in first arrival date will occur.” This observation suggests regardless of whether “tipping points” occur in the realm of climatology, they do in fact occur, and in some cases already have occurred, to the benefit of certain of Earth’s birds—the hotter it gets, the better they do what they need to do to deal with the evolving situation.

Van Buskirk *et al.* (2012) state, “phenological responses to climate change are well-documented in plants and animals,” and “it is widely assumed that much of the shift in phenology is due to facultative changes in the activities or physiologies of individuals induced by environmental conditions, known as phenotypic plasticity.” However, they write, “phenotypic plasticity is not the only mechanism that can produce population responses to climate change,” noting “gradual or sudden shifts in the selection regime can be triggered by environmental change, and these in turn can alter the genetic composition of populations.” They point out “rapid evolved responses to climate change are widely anticipated by evolutionary biologists (Bradshaw and Holzapfel, 2001; Davis *et al.*, 2005; Gienapp *et al.*, 2008; Hoffman and Willi, 2008; Hoffmann and Sgro, 2011), and already have been observed in a few cases (Umina *et al.*, 2005; Bradshaw and Holzapfel, 2008).”

Between June 1961 and August 2006, Van Buskirk *et al.* operated 35 mist nets for five to six days a week on a 10-ha study area on the Powdermill Nature Reserve in Pennsylvania (USA), in order to obtain the data needed to estimate the magnitude of temperature-induced phenotypic plasticity in spring arrival date of 27 species of birds in eastern North America, by recording the effects of annual variation in spring temperature on the behavior of thousands of individuals. They hypothesized that if phenotypic plasticity could not account for the totality of observed shifts in migration phenology over this period, what remained unaccounted for could be attributed, at least partly, to microevolutionary change.

The three researchers report “for 2441 individuals detected in multiple years, arrival occurred earlier during warm years, especially in species that migrate short distances,” but the change in phenology predicted “under a model of pure phenotypic plasticity” fell far short of the change in arrival date

they observed, explaining only 13–25% of the climate-induced trend in phenology. Although they acknowledge their approach to the problem “probably underestimates the full scope of plasticity,” Van Buskirk *et al.* say their data suggest “part of the response to environmental change [warming] has been caused by microevolution.” They also conclude “the estimated evolutionary rates [0.016 haldanes] are plausible.”

The three scientists write, “rapid genetic response to climate change is widely seen as a critical component of the kind of adaptation that will be required of many organisms,” especially in a world that warms as suggested by the models employed by IPCC. In addition, “the contribution of plasticity will allow individuals to adjust their phenotype to short-term environmental fluctuations, which are projected to increase under most scenarios of climate change.” That’s good news for birds.

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5.4.3.3 Trophic Mismatches

Another concern about the potential effects of global warming is that, as the world warms, mismatches may occur among various life cycle stages of plants, the insects that feed on them, and numerous species of animals, such as birds, that feed on insects and provide them as food for their young, a situation that could spell disaster for some species. This concept has been said by Visser and Both (2005) to constitute an “insufficient adjustment” to climate change. This section investigates the validity of such concerns, finding trophic mismatches are a non-problem in most instances.

Bauer *et al.* (2010) examined the effect of 47 years of warming (1961–2007) on the time of leafing-out of dominant English oak trees (*Quercus robur*) at four research sites in the Czech Republic located in full-grown, multi-aged floodplain forests that had been under no forestry management. The researchers also evaluated 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*).

According to the researchers, “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,” the observational variable they used to characterize the caterpillars’ presence. Last, they determined “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.” Similarly, 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 “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.” In this specific food chain, the common 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.”

Citing Visser *et al.* (1998, 2006) and Visser (2008), Matthysen *et al.* (2011) note “the increasing mismatch between great tit *Parus major* laying dates and their caterpillar food supply in the Netherlands has rapidly become a classic example of a lack of adaptation to climate change.” However, they report, “other populations of the same bird species have subsequently been shown to advance their laying dates much more strongly” in order to match the earlier spring growth of vegetation that typically occurs during periods of extended warming, citing Cresswell and McCleery (2003) and Charmantier *et al.* (2008).

Matthysen *et al.* “studied the breeding cycle of two sympatric and closely related species, the blue tit *Cyanistes caeruleus* and the great tit *Parus major*, in a rich oak-beech forest,” where they had collected data on the breeding biology of the birds from 1979 to 2007 in a 12-hectare plot provided with nest boxes inside the Peerdsbos forest near Antwerp, Belgium. Both bird species were shown to have “advanced their mean first-egg dates by 11–12 days over the last three decades,” and “the time from first egg to fledging has shortened by 2–3 days, through a decrease in laying interruptions, incubation time and nestling development time.” As a consequence, they write, “the average time of fledging has advanced by 15.4 and 18.6 days for blue and great tits, respectively, and variance in fledging dates has decreased by 70–75%.” Most important, they note, “indirect estimates of the food peak suggest that both species have maintained synchronization with the food supply,” and “analyses of within-individual variation show that most of the change can be explained by individual plasticity in laying date, fledging date and nest time.” Matthysen *et al.* emphasize “synchronization of the nestling period with the food supply not only depends on first-egg dates but also on additional reproductive parameters including laying interruptions, incubation time and nestling growth rate.” As a result of adjustments in these several related phenomena, they report, “both of our study species have been able to maintain synchrony with their food supply in the face of global warming.”

Vatka *et al.* (2011) further investigated the possibility global warming may lead to trophic mismatches between the times when birds of temperate and boreal regions require an abundance of food to feed their new hatchlings and the times when that food is available in its greatest abundance, as in the cases of great tits, blue tits, and pied flycatchers in the Netherlands, which require a timely abundance of caterpillars to feed their young (Visser *et al.*, 1998; Visser *et al.*, 2006; Both *et al.*, 2009). Vatka *et al.* note, “the same has not happened with great tits in England (Cresswell and McCleery, 2003) nor with great tits and collared flycatchers in the Czech Republic (Bauer *et al.*, 2010).” They describe yet a third type of food supply-and-demand response to warming they recently observed and documented.

Working with data collected in northern Finland over the period 1975–2009 within coniferous, deciduous, and mixed forests of varying ages—including young stands, swamps, and clear cuttings—the three Finnish scientists studied “changes in the timing of breeding in the willow tit (*Poecile montanus*), and the timing of its caterpillar food resource in relation to warming springs,” using “generalized linear mixed effect models to study the importance of synchrony between the timing of breeding in willow tits and the caterpillar food availability on the breeding success, measured as nestling survival rate and mean nestling weight.” In contrast to prior no change results and poorer synchrony findings, Vatka *et al.* report they not only “found no signs of emerging asynchrony” but that synchrony actually improved during the study, and it had moderate positive effects on breeding success. The observed improvement in synchrony mirrors results from the coal tit in the Netherlands, the authors add, citing Both *et al.* (2009).

Reed *et al.* (2013) studied a wild population of great tits (*Parus major*) in the Netherlands in relation to the phenology of their food supply, noting “great tits rely on caterpillars to feed their chicks and strive to match their breeding time with the pronounced seasonal peak in caterpillar biomass, which enhances offspring survival.” The researchers studied this by “using almost four decades of individual-level life-history data from a great tit population.” They report warmer springs had indeed “generated a mismatch between the annual breeding time and the seasonal food peak, intensifying directional selection for earlier laying dates.” However, they found inter-annual variation in population mismatch had not affected population growth, and they “demonstrated a mechanism contributing to this uncoupling, whereby

fitness losses associated with mismatch are counteracted by fitness gains due to relaxed competition.” The team of Dutch, French, Norwegian, and U.S. scientists states their findings imply “natural populations may be able to tolerate considerable maladaptation driven by shifting climatic conditions without undergoing immediate declines.” They conclude, “our results imply that considerable directional selection might be demographically tolerable on decadal time scales without immediate population declines, effectively buying time for microevolution to restore adaptation.”

Burthe *et al.* (2012) “compared phenological trends for species from four levels of a North Sea food web over 24 years [1983–2006] when sea surface temperature (SST) increased significantly,” starting with primary producers (phytoplankton), primary consumers (zooplankton), and secondary consumers (sandeels), and finally focusing on five seabird predators—the common guillemot (*Uria aalge*), razor bill (*Alca torda*), European shag (*Phalacrocorax aristotelis*), black-legged kittiwake (*Rissa tridactyla*), and Atlantic puffin (*Fratercula arctica*)—all of which are seabirds that prey on current-year sandeels (*Ammodytes marinus*). The nine researchers say they found “little consistency in phenological trends between adjacent trophic levels, no significant relationships with SST, and no significant pairwise correlations between predator and prey phenologies,” which they take as evidence “trophic mismatching is occurring.” Yet in spite of the supposed trophic mismatches discovered over the course of their research, Burthe *et al.* report, “to date, there is no evidence that these changes are impacting on the breeding success of any of the seabird species.”

Although much remains to be learned about this topic, it is clear trophic mismatches, thought to be initiated by global warming, need not produce negative responses from bird populations. Many bird species may not be affected at all, and others may even benefit from such a climate change.

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Terrestrial Animals

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5.4.3.4 Other Responses

Additional adaptive or evolutionary responses to warming, not discussed in the prior subsections, have been identified in the literature for birds, each of which suggests birds are adequately suited to

withstand any of the temperature changes predicted to accompany the future rise in atmospheric CO₂.

In regard to the challenges migratory animals may face due to potential changes in climate, Dias *et al.* (2011) write, “existing phenotypic plasticity *per se* may allow, within certain limits, the persistence of species and populations (even if in suboptimal circumstances), gaining time for selection to act, or for more favorable environmental conditions to be restored,” noting “there is strong evidence that recent climate changes may have already impacted migratory behavior” as it pertains to birds, citing Fiedler (2003) and Newton (2008).

Dias *et al.* evaluated individual flexibility in the migration strategies of a highly pelagic seabird, the Cory’s shearwater (*Calonectris diomedea*). They deployed leg-mounted geolocators weighing approximately 3.6 grams at the end of the breeding seasons of 2006, 2007, and 2008, recovering them in the early stages of the subsequent breeding seasons, to track the migration of 57 of the birds that spent the breeding season at Selvagem Grand Island (30°02’ N, 15°52’ W). The five researchers report 14 birds that were tracked for more than one non-breeding season “showed a remarkable capacity to change winter destinations between years,” with some shifting all the way from the South Atlantic to the North Atlantic, and from the Atlantic Ocean to the Indian Ocean. They found individual birds “also showed flexibility in stopover behavior and migratory schedule.” Dias *et al.* conclude Cory’s shearwaters are in a good position “to face the consequences of a changing environment,” adding, “whether Cory’s shearwaters are unusual in this respect, or whether future analyses will reveal that flexibility in migration strategies is a more general trait of marine migratory fauna is something that repeated tracking of individuals in coming years should clarify.”

According to Forero-Medina *et al.* (2011), “the tropics contain most of the world’s species at risk of extinction (Pimm and Jenkins, 2010), yet few studies evaluate the response of tropical species to climate disruption other than through modeling (Jetz *et al.*, 2007; Marini *et al.*, 2009; La Sorte and Jetz, 2010).” Using the same sampling techniques employed by Terborgh and Weske (1975) in 1969, and working at five of the nine localities studied by those earlier investigators, Forero-Medina *et al.* (2011) resampled bird communities at five elevations (690, 1310, 1570, 1970, and 2220 meters) within the Reserva Comunal El Sira on the Cerros del Sira massif in Peru 41 years later in 2010, seeking to determine what changes might have occurred in the elevations of the several

species encountered at the two sampling times. Of the 55 species encountered in both sampling years, the four researchers report 36 had moved up in elevation, 12 had moved down, and seven had not moved in either direction, resulting in an average upward shift of 49 meters for the 55 bird species over the 41-year period. They describe this change in elevation as “significantly smaller” than the 152-meter increase one would have expected from the amount of warming experienced throughout the region between the times of the two studies.

Forero-Medina *et al.* note more than one mountain had been involved in the initial study of Terborgh and Weske (1975), and “the same bird species exhibited different elevation ranges on different mountains, indicating considerable flexibility in the occupancy of habitat and independence of temperature (Diamond, 1970; Terborgh, 1985).” Therefore, they write, “the limited upward elevational shifts reported here are unlikely to be simple responses to increased temperature *per se*.” Instead, they suggest, “birds are likely responding to gradual changes in the nature of the habitat or availability of food resources through their dependence on long-lived elements of the ecosystem (trees), and how the species’ competitors respond.” They note “the rate of migration of trees is less (45%) than that predicted from the temperature increase of the region,” and “similar lags in the response of trees may be occurring at the Sira, accounting for the lag in response of birds.”

Put another way, Forero-Medina *et al.* conclude, “instead of being directly dependent on temperature, birds may be responding to gradual changes in the nature of their habitat or availability of food resources, and presence of competitors,” so “endothermy [the ability of certain animals to control their body temperature] may provide birds with some flexibility to temperature changes and allow them to move less than expected.”

Van Buskirk *et al.* (2010) write, “recent climate change has caused comparatively rapid shifts in the phenology and geographic distributions of many plants and animals,” but “there is debate over the degree to which populations can meet the challenges of climate change with evolutionary or phenotypic responses in life history and morphology,” which for a warming climate includes a reduction in body size. They devised an experimental strategy to explore the issue further, studying the body sizes of birds captured in mist-nets and traps between June 1961 and November 2006 at the Powdermill Nature Reserve, a field station operated by the Carnegie

Museum of Natural History in Pennsylvania (USA) at a location broadly representative of bird communities in the Appalachian region of eastern North America. At this location, 35 mist nets were operated five to six days per week during spring and autumn migrations. A reduced number of nets was used during summer, and birds for winter banding were caught in wire traps when the temperature was below freezing.

The three researchers report migrating birds captured at the banding station “have steadily decreasing fat-free mass and wing chord since 1961, consistent with a response to a warmer climate” and confirming “phenotypic responses to climate change are currently underway in entire avian assemblages,” where “size was negatively correlated with temperature in the previous year, and long-term trends were associated with the direction of natural selection acting on size over the winter.” In addition, they note, “species undergoing the strongest selection favoring small wing chord showed the most rapid long-term declines in wing [size],” which suggests “phenotypic changes are therefore in line with the prevailing selection regime.” Noting “in summer, 51 of 65 breeding species had negative slopes of mass against year, 20 of 26 wintering species had negative slopes, 60 of 83 spring migrants had negative slopes, and 66 of 75 autumn migrants had negative slopes,” Van Buskirk *et al.* state their results “offer compelling evidence that climate change has already produced observable adaptive shifts in morphology, behavior, and phenology of a great many species,” which suggests these birds have evolved a capacity for rapid phenotypic shifts to optimum body mass in response to climate fluctuations.

Additional support for this thesis comes from Carey (2009), who notes “organisms living today are descended from ancestors that experienced considerable climate change in the past,” and thus suggests, “species that persist into future climates may be able to do so in part owing to the genetic heritage passed down from ancestors who survived climate changes in the past.” She also states, “if climate change were the only new challenge facing birds, one might imagine that many species could become adapted to new conditions and survive with existing population variability and the genetic information that their ancestors used to survive past climate change.”

Karell *et al.* (2011) theorize “global climate warming changes the environment of most organisms and is expected to lead to a change in selection pressures with micro-evolutionary consequences that allow the adaptation of organisms to the new environment and thereby long-term population

persistence.” They further note, “microevolution in response to climate change has been demonstrated in invertebrate populations (Umina *et al.*, 2005; Balanya *et al.*, 2006),” but “these studies lack information on the mechanisms and selective factors linking particular genotypes to climate.”

Karell *et al.* explored “the links between climate change and alteration of the selective regime on a highly heritable phenotypic trait, plumage coloration in the tawny owl (*Strix aluco*), a common bird of prey throughout the temperate regions of Europe.” They used data from 1981 to 2008 in a 250-km² study area in Southern Finland dominated by mixed forests, agricultural areas, and small freshwater courses, where “plumage coloration was scored using a semi-continuous ordinal scale (range from 4 (grey) to 14 reddish-brown)) on all breeding individuals on each encounter ($N = 1116$ records of 491 individuals) using a standardized and repeatable scoring that shows coloration is independent of age and sex.” In addition, they scored museum skin specimens collected between 1915 and 1980; and they extracted the data on all records of adult ringed and recaptured tawny owls in Finland to which color morph (grey or brown) had been assigned during 1961–2008. Finally, they write, “measures of temperature and snow depth from the time window that correlated best with annual tawny owl survival were selected as covariates for further modeling.”

The five Finnish researchers determined “brown individuals had lower survival than grey ones as snow cover became deeper” and there was a “lower survival for brown individuals compared with grey ones in cold temperatures,” as cooler conditions would be expected to promote a deeper snow cover. Thus they report as snow depth decreased over time in response to warming, “there was a time trend in survival of the color morphs from 1981–2008, in which survival of the grey morph was fairly stable across years, whereas survival of brown individuals improved dramatically towards the end of the time series.” They also report this phenotypic change was present on a larger nationwide scale—the increase of the brown morph occurred “all over Finland, involving thousands of individuals,” such that “the survival propensities of the morphs have equalized in recent, mild winters.”

Karell *et al.* remark the phenotypic change they documented “is unlikely to be caused by genetic drift, because drift is only a major force for changing allele frequencies in small populations.” Therefore, “given the strong genetic underpinning of tawny owl morphs,” they say they consider the observed pheno-

typic trend in the proportion of the brown morph as “indicative for a shift in gene frequencies.” Hence, they conclude, to the best of their knowledge, the results of their study constitute “the first empirical evidence of climate-driven change in selection on a heritable trait,” providing a whole new perspective on the potential of Earth’s fauna to withstand the challenges of global warming.

Gremillet *et al.* (2012) state little auks (*Alle alle*) are the most numerous seabirds in the North Atlantic, with an estimated population of 40 to 80 million individuals, citing Stempniewicz (2001), and they consume up to 24% of local plankton production, citing Karnovsky and Hunt (2002). The researchers also note the “little auk field metabolic rate is 70% higher than predicted by body mass, and they have very limited capacity to store fat.” Consequently, they say, little auks “are predicted to be particularly sensitive to altered feeding conditions,” citing Harding *et al.* (2009). More specifically, they write, the recent work of Karnovsky *et al.* (2010) “showed a very strong link between summer SST [sea surface temperature] within the foraging areas of little auks, species composition of local zooplankton communities, and dietary preferences of the birds, whereby colder water contained more larger copepods, which were also preferentially fed upon by little auks,” so “birds had to feed on smaller, less profitable copepod species in warmer water.” As a result of these observations, they hypothesize “higher SSTs would modify little auk diet, foraging effort, provisioning rates, breeding success and adult survival,” which they presume would significantly decline in response to warming.

In an integrative study of the behavior, physiology, and fitness of colonies of little auks at three sites of significantly different temperature—Kap Hoegh, East Greenland (70°43’N, 22°38’W), Hornsund, West Spitsbergen (77°00’N, 15°22’E), and Kongsfjorden, West Spitsbergen (79°01’N, 12°25’E)—Gremillet *et al.* evaluated the effects of ocean warming on little auks across the Greenland Sea over the period 2005–2007. They noted “comparing the ecophysiology of little auks from different colonies subject to contrasting SST regimes at one moment in time” would allow them to “simulate the effect that increasing water temperatures might have on this Arctic species across the 21st century.”

“During the study period,” the researchers write, “little auks maintained their fitness despite contrasting ocean surface temperatures and copepod availability across the Greenland Sea.” Gremillet *et al.* write, “contrary to our hypothesis, the birds

responded to a wide range of sea surface temperatures via plasticity of their foraging behavior, allowing them to maintain their fitness levels,” indicating “they are successful at dealing with the influence of current climate change in the Arctic.” In the concluding sentence of their abstract, the team of nine scientists from eight countries (Canada, Denmark, France, Ireland, Norway, Poland, South Africa, and the United States) writes, “predicted effects of climate change are significantly attenuated by such plasticity, confounding attempts to forecast future effects of climate change using envelope models.”

According to Smit *et al.* (2013), “one of the main predictions of bioclimatic envelope models is that populations near the climatic extremes of species’ distributions, where thermoregulatory costs are presumably high, are performing sub-optimally and are at greater risk of extinction,” citing Thomas *et al.* (2004). However, Smit *et al.* suggest, “if populations are physiologically adapted (genetic variation across generations and/or plastic adjustments) to their respective climates, species may be capable of maintaining high levels of performance throughout their geographic ranges,” citing Chown *et al.* (2010) and Glanville *et al.* (2012).

Smit *et al.* investigated the effects of air temperature (T_A) on body temperature (T_B) and the behavior of an arid-zone endotherm, the White-Browed Sparrow-Weaver (*Plocepasser mahali*) at two sites 100 km apart, in the southern Kalahari Desert of South Africa, over two consecutive summer seasons. The four researchers found a relatively large variation in T_B that occurred both within and between populations, suggesting “an arid-zone passerine responds differently to prevailing weather conditions in two locations over its range, and that it also responds to seasonal changes in weather conditions.” This further suggests “a species’ current range may not be an accurate representation of its climatic tolerance.”

“Taken together with the data of Glanville *et al.* (2012),” Smit *et al.* explain, this result “suggests that the thermal physiology of endotherms is far more flexible than previously thought, and could potentially contribute to the adaptation of populations under changing climatic conditions,” citing Boyles *et al.* (2011).” They conclude, “when predicting species’ responses to climate change, their sensitivity (*sensu* Williams *et al.*, 2008) should be resolved at the population, rather than species, level.”

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Terrestrial Animals

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5.5 Insects

- Published research indicates rising temperatures will not likely 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.

Included among the many animal-related concerns over global warming is the worry there will be an increase in the intensity of herbivore pressure on plants. This section reviews research that has been conducted on this topic, beginning with research regarding aphids and then moths, and then regarding specific kinds of vegetation (herbaceous plants, woody plants, and other plants).

5.5.1 Aphids

We begin our survey of the effects of rising temperature and CO₂ levels on aphids with Ma *et al.* (2004), who conducted detailed experiments on the impacts of high temperature, period of exposure, and developmental stage on the survival of the aphid *Metopolophium dirhodum*, which they say “is the most abundant of the three cereal aphid species in Germany and central European countries.” This protocol revealed “temperatures over 29°C for 8 hours significantly reduced survival, which decreased generally as the temperature increased.” The researchers also determined “exposing aphids to 32.5°C for 4 hours or longer significantly reduced survival,” and “mature aphids had a lower tolerance of high temperatures than nymphs.” Ma *et al.* conclude, “global warming may play a role in the long-term changes in the population abundance of *M. dirhodum*.” Specifically, “an increase in TX [daily average temperature] of 1°C and MaxT [maximum daily temperature] of 1.3°C during the main period of the aphid population increase would result in a 33% reduction in peak population size,” and “an increase in TX of 2°C and MaxT of 2.6°C would result in an

early population collapse (74% reduction of population size)."

Adler *et al.* (2007) examined the effects of long-term experimental warming on an aphid-sagebrush (*Obtusicauda coweni*-*Artemisia tridentata*) interaction out-of-doors in the field at the Rocky Mountain Biological Laboratory, Colorado (USA), where five of ten 3-m x 10-m plots in an ungrazed montane meadow were warmed by overhead infrared heaters that provided a continuous heat flux of 22 W/m² to the plots ever since 1993. Working at this facility for three consecutive years (1996–1998), they determined how warming affected aphid density, and they used additional observations, manipulative experiments, and chemical analyses to explore some of the mechanisms that might mediate potential effects of warming on aphid density.

The four researchers report, "in no year did we find support for the prediction that warming increased aphid abundance or population growth." They found "warming decreased aphid density on sagebrush in one year, tended to decrease aphids in a second year, and had no effect in a third year." In the first of these years (1997), "there were over 3 times as many aphids per stalk in control compared to warmed plots," and "the proportion of stems infested was almost twice as high." Furthermore, "in enclosures that excluded predators, warming decreased aphid population growth by an amount consistent with observed field density differences," and in a separate snow-manipulation experiment in unheated plots, they found "the timing of snowmelt did not affect aphid density." Adler *et al.* conclude, "long-term studies within a natural community context may provide counterexamples to the prediction that warming will increase herbivore pressure on plants."

Much more research has been conducted on the direct and indirect response of aphids to rising atmospheric CO₂. Docherty *et al.* (1997), for example, grew beech and sycamore saplings in glasshouses maintained at atmospheric CO₂ concentrations of 350 and 600 ppm, while groups of three sap-feeding aphid species were allowed to feed on the saplings. Overall, the elevated CO₂ had few significant effects on aphid feeding and performance. There was, however, a non-significant tendency for elevated CO₂ to reduce the individual weights and population sizes of the aphids, suggesting future increases in the air's CO₂ content might reduce aphid feeding pressures on beech and sycamore saplings, and possibly other plants as well.

Whittaker (1999) reviewed the scientific literature on population responses of herbivorous insects to

atmospheric CO₂ enrichment, concentrating on papers resulting from relatively long-term studies. The only herbivorous insects found to exhibit population increases in response to elevated CO₂ exposure were those classified as phloem feeders; specifically, aphids. Although this finding appeared to favor aphids over plants, additional studies came to different conclusions.

Newman *et al.* (1999) grew tall fescue plants for two weeks in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm before inoculating them with aphids (*Rhopalosiphum padi*). After nine additional weeks of differential CO₂ exposure, the plants were harvested and their associated aphids counted. Although elevated CO₂ increased plant dry matter production by 37%, this did not result in similar increases in aphid colonization. The plants grown in air of elevated CO₂ concentration contained far fewer aphids than the plants grown in ambient air.

Percy *et al.* (2002) grew the most widely distributed tree species in all of North America—trembling aspen—in 12 30-m-diameter FACE rings 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 each growing season from 1998 through 2001. Throughout the experiment they assessed a number of the young trees' growth characteristics and the responses of the sap-feeding aphid *Chaitophorus stevensis*, which they say "infests aspen throughout its range." By itself, elevated CO₂ did not affect aphid abundance, but it increased the densities of natural enemies of the aphids, which over the long term would tend to reduce aphid numbers. Also, by itself, elevated O₃ did not affect aphid abundance, but it had a strong negative effect on natural enemies of aphids, which over the long term would tend to increase aphid numbers. When both trace gases were applied together, elevated CO₂ completely counteracted the reduction in the abundance of natural enemies of aphids caused by elevated O₃. Hence, elevated CO₂ tended to reduce the negative impact of aphids on trembling aspen in this study.

Holopainen (2002) reviewed the scientific literature addressing the joint effects of elevated concentrations of atmospheric O₃ and CO₂ on aphid-plant interactions. Compiling the results of 26 pertinent studies, Holopainen found atmospheric CO₂ enrichment increased aphid performance in six studies, decreased it in six studies, and had no significant impact on it in the remaining 14 studies. Similar

results were found for aphid-plant interactions in the presence of elevated O₃ concentrations.

Newman (2003) reviewed the scientific literature on aphid responses to concurrent increases in atmospheric CO₂ and air temperature and also investigated the subject via the aphid population model of Newman *et al.* (2003). He concluded when the air's CO₂ concentration and temperature are both elevated, "aphid population dynamics will be more similar to current ambient conditions than expected from the results of experiments studying either factor alone." The only general conclusion that can be drawn, Newman states, is "insect responses to CO₂ are unlikely to all be in the same direction." Nevertheless, "the lack of a simple common phenomenon does not deny that there is some overriding generality in the responses by the system."

Awmack *et al.* (2004) conducted a two-year study at the Aspen FACE site near Rhinelander, Wisconsin (USA) of the individual and combined effects of elevated CO₂ (+200 ppm) and O₃ (1.5 x ambient) on the performance of *Cepigillettea betulaefoliae* aphids feeding on paper birch trees, in what they call "the first investigation of the long-term effects of elevated CO₂ and O₃ atmospheres on natural insect herbivore populations." At the individual scale, they report, "elevated CO₂ and O₃ did not significantly affect [aphid] growth rates, potential fecundity (embryo number) or offspring quality." At the population scale, "elevated O₃ had a strong positive effect," but "elevated CO₂ did not significantly affect aphid populations."

In comparing their results with those of prior related studies, the three scientists report "the responses of other aphid species to elevated CO₂ or O₃ are also complex." In particular, they note "tree-feeding aphids show few significant responses to elevated CO₂ (Docherty *et al.*, 1997), while crop-feeding species may respond positively (Awmack *et al.*, 1997; Bezemer *et al.*, 1998; Hughes and Bazzaz, 2001; Zhang *et al.*, 2001; Stacey and Fellowes, 2002), negatively (Newman *et al.*, 1999) or not at all (Hughes and Bazzaz, 2001), and the same species may show different responses on different host plant species (Awmack *et al.*, 1997; Bezemer *et al.*, 1999)." In summarizing their observations, they state "aphid individual performance did not predict population responses to CO₂ and O₃," and they conclude, "elevated CO₂ and O₃ atmospheres are unlikely to affect *C. betulaefoliae* populations in the presence of natural enemy communities."

In a study of a different aphid (*Chaitophorus stevensis*) conducted at the same FACE site, Mondor

et al. (2004) focused on pheromones, which they note "are utilized by insects for several purposes, including alarm signaling," and which in the case of phloem-feeding aphids induces high-density groups of them on exposed leaves of trembling aspen trees to disperse and move to areas of lower predation risk. In this experiment the four treatments were: control (367 ppm CO₂, 38 ppb O₃), elevated CO₂ (537 ppm), elevated O₃ (51 ppb), and elevated CO₂ and O₃ (537 ppm CO₂, 51 ppb O₃). Within each treatment, several aspen leaves containing a single aphid colony of 25 ± 2 individuals were treated in one of two ways: (1) an aphid was prodded lightly on the thorax so as to not produce a visible pheromone droplet, or (2) an aphid was prodded more heavily on the thorax and induced to emit a visible pheromone droplet, after which, in the words of the scientists, "aphids exhibiting any dispersal reactions in response to pheromone emission as well as those exhibiting the most extreme dispersal response, walking down the petiole and off the leaf, were recorded over 5 min."

Mondor *et al.*'s observations were striking. They found the aphids they studied "have diminished escape responses in enriched carbon dioxide environments, while those in enriched ozone have augmented escape responses, to alarm pheromone." They report, "0% of adults dispersed from the leaf under elevated CO₂, while 100% dispersed under elevated O₃," indicating the effects of elevated CO₂ and elevated O₃ on aphid response to pheromone alarm signaling are diametrically opposed. Elevated O₃ (which is detrimental to vegetation) helped aphids escape predation and therefore live to do further harm to the leaves they infest, but elevated CO₂ (which is beneficial to vegetation) made it more difficult for aphids to escape predation and thereby provided an additional benefit to plant foliage. Mondor *et al.* state this phenomenon may be of broader scope than what is revealed by their specific study, noting other reports suggest "parasitoids and predators are more abundant and/or efficacious under elevated CO₂ levels (Stiling *et al.*, 1999; Percy *et al.*, 2002), but are negatively affected by elevated O₃ (Gate *et al.*, 1995; Percy *et al.*, 2002)."

Chen *et al.* (2004) grew spring wheat from seed to maturity in high-fertility well-watered pots out-of-doors in open-top chambers (OTCs) maintained at atmospheric CO₂ concentrations of 370, 550, and 750 ppm. Approximately two months after seeding, 20 apterous adult aphids (*Sitobion avenae*) from an adjacent field were placed on the wheat plants of each of 25 pots in each OTC, and 15 pots were left as controls. At subsequent five-day intervals, both

apterous and alate aphids were counted. About one month later, 10 alate morph fourth instar nymphs were introduced onto the plants of each of nine control pots, and for the next two weeks the number of offspring laid on those plants were recorded and removed daily to measure reproductive activity. At the end of the study, the wheat plants were harvested and their various growth responses determined.

The scientists found the introduced aphid populations increased after infestation, peaked during the grain-filling stage, and declined a bit as the wheat matured. On the final day of measurement, aphids in the 550 ppm CO₂ treatment were 32% more numerous than those in ambient air, and aphids in the 750 ppm treatment were 50% more numerous. Alate aphids also produced more offspring on host plants grown in elevated CO₂: 13% more in the 550 ppm treatment, and 19% more in the 750 ppm treatment.

As for the wheat plants, Chen *et al.* report “elevated CO₂ generally enhanced plant height, aboveground biomass, ear length, and number of and dry weight of grains per ear, consistent with most other studies.” With respect to aboveground biomass, for example, the 550 ppm treatment displayed an increase of 36%, and the 750 ppm treatment displayed an increase of 50%, in the case of both aphid-infested and non-infested plants.

Chen *et al.* comment, “aphid infestation caused negative effects on all the plant traits measured ... but the negative effects were smaller than the positive effects of elevated CO₂ on the plant traits.” They conclude, “the increased productivity occurring in plants exposed to higher levels of CO₂ more than compensate for the increased capacity of the aphids to cause damage.” In this experiment, therefore, both the plant and the insect that feeds on it were benefited by the applied increases in atmospheric CO₂ concentration.

Chen *et al.* (2005) grew transgenic cotton plants for 30 days in well-watered and fertilized sand/vermiculite mixtures in pots set in controlled-environment chambers maintained at atmospheric CO₂ concentrations of 370, 700, and 1,050 ppm. A subset of aphid-infected plants was additionally supplied with predatory ladybugs, and three generations of cotton aphids (*Aphis gossypii*) were subsequently allowed to feed on some of the plants. Based on measurements made throughout this complex set of operations, Chen *et al.* found “plant height, biomass, leaf area, and carbon:nitrogen ratios were significantly higher in plants exposed to elevated CO₂ levels,” and “more dry matter and fat content and less soluble protein were found in *A.*

gossypii in elevated CO₂.” They also found “cotton aphid fecundity significantly increased ... through successive generations reared on plants grown under elevated CO₂”; “significantly higher mean relative growth rates were observed in lady beetle larvae under elevated CO₂”; and “the larval and pupal durations of the lady beetle were significantly shorter and [their] consumption rates increased when fed *A. gossypii* from elevated CO₂ treatments.” Chen *et al.* say their study “provides the first empirical evidence that changes in prey quality mediated by elevated CO₂ can alter the prey preference of their natural enemies,” and in this particular case, they found this phenomenon could “enhance the biological control of aphids by lady beetle.”

According to Auad *et al.* (2012), the yellow sugarcane aphid—first called *Chaitophorus flavus*, but later changed to *Sipha flava*—“has an extensive geographic range that includes all the Americas and Hawaii,” and it “is not only a serious pest of sugarcane, but it infests corn, sorghum, wheat, and several other grasses.” They note “plant injury caused by this aphid is often severe and is associated with the release of an unidentified toxin followed by leaf chlorosis (Breen and Teetes, 1986; Webster, 1990).” In Brazil, where Auad *et al.* reside, the four scientists report elephant grass (*Pennisetum purpureum*)—one of the most widely used grasses for dairy cattle forage—“is being compromised by *S. flava* attack.” The four Brazilian researchers investigated the “effects of elevated CO₂ alone and in combination with elevated temperature on the interactions of *S. flava* and one of its hosts,” *P. purpureum*.

Auad *et al.* discovered “the combination of elevated CO₂ and high temperature significantly decreased the duration of nymphal stadia” and “the longevity and reproductive success of *S. flava*,” such that “adults produced fewer nymphs in an environment with elevated CO₂ and high temperature than an environment with elevated CO₂ and lower fluctuating temperatures.”

The four researchers conclude “*S. flava* populations will significantly decrease under future climatic conditions when both the concentration of atmospheric CO₂ and temperature are projected to increase.”

Klaiber *et al.* (2013) “used a model system comprised of Brussels sprout (*Brassica oleraceae* var. *gemmifera*) and a specialized herbivorous insect, the cabbage aphid (*Brevicoryne brassicae*) to test for the effects of various periods of exposure to an elevated (2 x ambient) CO₂ concentration on key plant functional traits and on host plant location behavior

by the insect, assessed as plant colonization rates.” With respect to plant/herbivore interactions, the four Swiss scientists say, “doubling the ambient CO₂ concentration had a marked effect on plant colonization by winged aphids particularly when plants were exposed to CO₂ for longer periods.” After an exposure of only two weeks, for example, there was no difference in colonization rate, whereas after six and 10 weeks “elevated CO₂ led to a respective 15 and 26% reduction of colonization rates” by the cabbage aphid. The authors also note plant volatile emissions, which have been linked to attracting insects, were significantly reduced at the higher CO₂ concentration. Klaiber *et al.* conclude, “in agro-ecosystems, reduced crop plant colonization by an herbivorous pest insect under elevated CO₂ might be advantageous.”

It appears the ongoing rise in the air’s CO₂ content will likely not have a major impact on aphid-plant interactions, although the scales appear to be tipped in favor of plants over aphids. It is also possible both plants and aphids will benefit from atmospheric CO₂ enrichment, but with plants benefiting more.

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Climate Change Reconsidered II: Biological Impacts

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5.5.2 Moths

Among the insects most responsible for herbivore pressure on plants is moths. This section reviews research on how moths are likely to fare in a warmer world with higher levels of CO₂ in the air.

Kerslake *et al.* (1998) collected five-year-old heather plants from a Scottish moor and grew them in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 600 ppm for 20 months, with and without soil nitrogen fertilization. Twice during the study, larvae of *Operophtera brumata*, a voracious winter moth whose outbreaks have caused extensive damage to heather moorland in recent years, were allowed to feed on current-year shoots for up to one month. The survivorship of larvae placed on CO₂-enriched foliage was not significantly different from that of larvae placed on foliage produced in ambient air, regardless of nitrogen treatment. In addition, feeding on CO₂-enriched foliage did not affect larval growth rate, development, or final pupal weight. Consequently, Kerslake *et al.* conclude their study “provides no evidence that increasing atmospheric CO₂ concentrations will affect the potential for outbreak of *Operophtera brumata* on this host.”

Hattenschwiler and Schafellner (1999) grew

seven-year-old spruce trees at atmospheric CO₂ concentrations of 280, 420, and 560 ppm in various nitrogen deposition treatments for three years, after which they performed needle quality assessments and allowed nun moth (*Lymantria monacha*) larvae to feed on current-year needles for 12 days. This moth is an especially voracious defoliator that resides in most parts of Europe and East Asia between 40 and 60° N latitude, and it is commonly regarded as the “coniferous counterpart” of its close relative the gypsy moth, which feeds primarily on deciduous trees.

The two scientists observed elevated CO₂ significantly enhanced needle starch, tannin, and phenolic concentrations, while significantly decreasing needle water and nitrogen contents. Thus, atmospheric CO₂ enrichment reduced overall needle quality from the perspective of this foliage-consuming moth, as nitrogen content is the primary factor associated with leaf quality. Increasing nitrogen deposition, on the other hand, tended to enhance needle quality, for it lowered starch, tannin, and phenolic concentrations while boosting needle nitrogen content. The positive influence of nitrogen deposition on needle quality was not large enough to completely offset the quality reduction caused by elevated CO₂.

Larvae placed on CO₂-enriched foliage consumed less needle biomass than larvae placed on low-CO₂-grown foliage, regardless of nitrogen treatment, and the larvae feeding on CO₂-enriched foliage exhibited reduced relative growth rates and attained an average biomass only two-thirds of that attained by larvae consuming foliage produced at 280 ppm CO₂. Hattenschwiler and Schafellner conclude, “altered needle quality in response to elevated CO₂ will impair the growth and development of *Lymantria monacha* larvae,” which should lead to reductions in the degree of spruce tree destruction caused by this voracious defoliator.

Stiling *et al.* (2002) studied the effects of an approximate doubling of the air’s CO₂ concentration on a number of characteristics of several insect herbivores feeding on plants native to a scrub-oak forest ecosystem at the Kennedy Space Center, Florida (USA) in eight ambient and eight CO₂-enriched open-top chambers. They found 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,” and “the response to elevated CO₂ was the same across all plant species.” Also, “more host-plant

induced mortality was found for all miners on all plants in elevated CO₂ than in ambient CO₂.” These effects were so powerful that 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. It would appear that in a higher CO₂ world of the future, Earth’s natural ecosystems may be able to better withstand the onslaughts of various insect pests, including moths, that have plagued them in the past. Stiling *et al.* note, is “reductions in herbivore loads in elevated CO₂ could boost plant growth beyond what might be expected based on pure plant responses to elevated CO₂.”

In a follow-up study to that of Stiling *et al.*, conducted at the same facilities, Rossi *et al.* (2004), focused on the abundance of a guild of lepidopteran leafminers that attack the leaves of myrtle oak, as well as various leaf chewers. They periodically examined 100 marked leaves in each of 16 open-top chambers 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.” This protocol revealed “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 amount of leaves suffering chewing damage was 37% lower ($P = 0.072$) in the CO₂-enriched air.

Williams *et al.* (2003) bagged first instar gypsy moth larvae on branches of red maple saplings entering their fourth year of growth within open-top chambers maintained at four sets of CO₂/temperature conditions: (1) ambient temperature, ambient CO₂, (2) ambient temperature, elevated CO₂ (ambient + 300 ppm), (3) elevated temperature (ambient + 3.5°C), ambient CO₂, and (4) elevated temperature, elevated CO₂. For these conditions they measured several parameters to test their hypothesis that a CO₂-enriched atmosphere would lead to reductions in foliar nitrogen concentrations and increases in defensive phenolics that would in turn lead to increases in insect mortality.

The results indicated “larvae feeding on CO₂-enriched foliage ate a comparably poorer food source than those feeding on ambient CO₂-grown plants, irrespective of temperature.” Nevertheless, they determined “CO₂-induced reductions in foliage

quality were unrelated to insect mortality, development rate and pupal weight.” They concluded, “phytochemical changes resulted in no negative effects on gypsy moth performance,” but neither did they help them.

Noting increases in the atmosphere’s CO₂ concentration typically lead to greater decreases in the concentrations of nitrogen in the foliage of C₃ as opposed to C₄ grasses, Barbehenn *et al.* (2004) note “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, they grew *Lolium multiflorum* (Italian ryegrass, a common C₃ pasture grass) and *Bouteloua curtipendula* (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 two grasses.

As expected, Barbehenn *et al.* found 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. They write, “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.” However, and “contrary to our expectations,” they add, “neither caterpillar species significantly increased its consumption rate to compensate for the lower concentration of protein in [the] C₃ grass.” They note “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.” They 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.* suggest “there will not be a single pattern that characterizes all grass feeders” with respect to their feeding preferences and developmental responses in a world where certain C₃ plants may experience foliar protein concentrations lower than those they exhibit today, nor will the

changes that may occur necessarily be detrimental to herbivore development or the health and vigor of their host plants. Nevertheless, subsequent studies continue to suggest moth species likely will be negatively impacted by the ongoing rise in the air's CO₂ content.

A case in point is the study of Chen *et al.* (2005), who grew well-watered and fertilized cotton plants of two varieties (one expressing *Bacillus thuringiensis* toxin genes and one a non-transgenic cultivar from the same recurrent parent) in pots placed within open-top chambers maintained at either 376 or 754 ppm CO₂ in Sanhe County, Hebei Province, China, from planting in mid-May to harvest in October. Immature bolls were periodically collected and analyzed for various chemical characteristics, and others were stored under refrigerated conditions for later feeding to larvae of the cotton bollworm. They found the elevated CO₂ treatment increased immature boll concentrations of condensed tannins by approximately 22% and 26% in transgenic and non-transgenic cotton, respectively, and it slightly decreased the body biomass of the cotton bollworm and reduced moth fecundity. The Bt treatment was even more effective in this regard, and in the combined Bt-high-CO₂ treatment the negative cotton bollworm responses were expressed most strongly.

Bidart-Bouzat *et al.* (2005) grew three genotypes of mouse-ear cress (*Arabidopsis thaliana*) from seed in pots within 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 these 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. Then, 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 this herbivory trial, the 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 (Mauricio and Rausher, 1997)—and total glucosinolate production was determined by summation of the individual glucosinolate assays. Influences of elevated CO₂ on moth performance and its association with plant defense-related traits also were evaluated.

Overall, the researchers 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. However, the three scientists 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),” Bidart-Bouzat *et al.* 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).”

In a study of a major crop species, Wu *et al.* (2006) grew spring wheat (*Triticum aestivum* L.) from seed to maturity in pots placed in open-top chambers maintained at either 370 or 750 ppm CO₂ in Sanhe County, Hebei Province, China, after which they reared three generations of cotton bollworms (*Helicoverpa armigera* Hubner) on the milky grains of the wheat while monitoring a number of bollworm developmental characteristics. They report, “significantly lower pupal weights were observed in the first, second and third generations,” and “the fecundity of *H. armigera* decreased by 10% in the first generation, 13% in the second generation and 21% in the third generation,” resulting in a “potential population decrease in cotton bollworm by 9% in the second generation and 24% in the third generation.” In addition, they observe, “population consumption was significantly reduced by 14% in the second generation and 24% in the third generation,” and the efficiency of conversion of ingested food was reduced “by 18% in the first generation, 23% in the second generation and 30% in the third generation.” They conclude, the “net damage of cotton bollworm on wheat will be less under elevated atmospheric CO₂,” while “at the same time, gross wheat production is expected to increase by 63% under elevated CO₂.”

Wu *et al.* (2007) write, “significant decreases in the protein, total amino acid, water and nitrogen content by 15.8%, 17.7%, 9.1% and 20.6% and increases in free fatty acid by 16.1% were observed in cotton bolls grown under elevated CO₂.” When fed with these cotton bolls, the larval survival rate of *H. armigera* “decreased by 7.35% in the first generation, 9.52% in the second generation and 11.48% in the

third generation under elevated CO₂ compared with ambient CO₂.” In addition, “the fecundity of *H. armigera* decreased by 7.74% in the first generation, 14.23% in the second generation and 16.85% in the third generation.” They conclude, “fecundity capacity is likely to be reduced even further in the next generation.”

The synergistic effects of these several phenomena, note Wu *et al.*, “resulted in a potential population decrease in cotton bollworm by 18.1% in the second generation and 52.2% in the third generation under elevated CO₂,” with the result that “the potential population consumption of cotton bollworm decreased by 18.0% in the second generation and 55.6% in the third generation ... under elevated CO₂ compared with ambient CO₂.” They conclude, “the potential population dynamics and potential population consumption of cotton bollworm will alleviate the harm to [cotton] plants in the future rising-CO₂ atmosphere.”

Esper *et al.* (2007) reconstructed an annually resolved history of population cycles of a foliage-feeding Lepidopteran commonly known as the larch budmoth (*Zeiraphera diniana* Gn.)—or LBM for short—in the European Alps in the southern part of Switzerland. As is typical of many such insect pests, they note, “during peak activity, populations may reach very high densities over large areas,” resulting in “episodes of massive defoliation and/or tree mortality” that could be of great ecological and economic significance.

The team of Swiss and U.S. researchers first developed a history of LBM outbreaks over the 1,173-year period AD 832–2004, which they describe as “the longest continuous time period over which any population cycle has ever been documented.” They did so using radiodensitometric techniques to characterize the tree-ring density profiles of 180 larch (*Larix deciduas* Mill.) samples, where “LBM outbreaks were identified based upon characteristic maximum latewood density (MXD) patterns in wood samples, and verified using more traditional techniques of comparison with tree-ring chronologies from non-host species,” i.e., fir and spruce. Then they developed a matching temperature history for the area by combining “a tree-ring width-based reconstruction from AD 951 to 2002 integrating 1527 pine and larch samples (Buntgen *et al.*, 2005) and a MXD-based reconstruction from AD 755 to 2004 based upon the same 180 larch samples used in the current study for LBM signal detection (Buntgen *et al.*, 2006).”

From AD 832 to 1981, there were 123 LBM outbreaks with a mean reoccurrence time of 9.3 years,

and “there was never a gap that lasted longer than two decades.” From 1981 to the end of their study in 2004, however, there were no LBM outbreaks, and since there had never before (within their record) been such a long outbreak hiatus, they conclude, “the absence of mass outbreaks since the 1980s is truly exceptional.”

To what do Esper *et al.* attribute this unprecedented recent development? Noting “conditions during the late twentieth century represent the warmest period of the past millennium”—as per their temperature reconstruction for the region of the Swiss Alps in which they worked—they point to “the role of extraordinary climatic conditions as the cause of outbreak failure,” and they discuss what they refer to as the “probable hypothesis” of Baltensweiler (1993), who described a scenario by which local warmth may lead to reduced LBM populations.

Warmth may indeed explain the lack of LBM outbreaks, but given the results of other studies examined in this section, it should be noted atmospheric CO₂ concentrations since 1980 also have been unprecedented over the 1,173-year period of Esper *et al.*’s study. The suppression of LBM outbreaks over the past quarter-century may have been the result of some synergistic consequence of the two factors (temperature and CO₂) acting in unison, and a third possibility may involve only the increase in the air’s CO₂ content.

Esper *et al.* say their findings highlight the “vulnerability of an otherwise stable ecological system in a warming environment,” in what would appear to be an attempt to attach an undesirable connotation to the observed outcome. This wording seems strange indeed, for it is clear the “recent disruption of a major disturbance regime,” as Esper *et al.* refer to the suppression of LBM outbreaks elsewhere in their paper, would be considered by most people to be a positive outcome, indeed something to be welcomed.

Buntgen *et al.* (2009) analyzed raw measurements of 3,151 tree-ring width (TRW) series and 150 maximum latewood density (MXD) series from 70 larch host sites and 73 spruce non-host sites spread across the European Alps and Tatra Mountains that extended back in time approximately 300 years. Focusing on the European Alps—“because periodic growth depressions caused by LBM outbreaks were not found in the TRW and MXD chronologies from the Tatra Mountains”—Buntgen *et al.* discovered “a distinct periodicity at 8–9 years from sites at elevations between 1750 and 1900 meters above sea level.” In the middle of the twentieth century, for

example, they documented synchronized outbreak pulses at approximately 1936, 1945, 1954, 1963, 1972, and 1981. These outbreaks, the scientists write, “occurred independently of rising temperatures,” all the way from the beginning-of-the-end of “the Little Ice Age until recent warmth.” They report this long stretch of persistent and synchronized Alpine-wide defoliation—which Esper *et al.* (2007) had followed back to AD 832—finally “ceased during recent decades,” when “unprecedented warming in all seasons characterized the post-1980 period.”

Knepp *et al.* (2007) studied two species of oak tree—*Quercus alba* L. (white oak) and *Quercus velutina* Lam. (black oak)—and their susceptibility to *Antheraea polyphemus*, a leaf-chewing generalist lepidopteran herbivore that represents the most abundant feeding guild in the hardwood trees that grow beneath the canopy of the unmanaged loblolly pine plantation that hosts the Forest Atmosphere Carbon Transfer and Storage (FACTS-1) research site in the Piedmont region of North Carolina (USA), where the leaf-chewer can consume 2–15% of the forest’s net primary production in any given year. The researchers examined host plant preference and larval performance of *A. polyphemus* when fed foliage of the two tree species that had been grown in either ambient or CO₂-enriched air (to 200 ppm above ambient) in this long-running FACE experiment. They determined “growth under elevated CO₂ reduced the food quality of oak leaves for caterpillars,” and “consuming leaves of either oak species grown under elevated CO₂ slowed the rate of development of *A. polyphemus* larvae.” In addition, they found feeding on foliage of *Q. velutina* that had been grown under elevated CO₂ led to reduced consumption by the larvae and greater mortality. They conclude, “reduced consumption, slower growth rates, and increased mortality of insect larvae may explain [the] lower total leaf damage observed previously in plots of this forest exposed to elevated CO₂,” as documented by Hamilton *et al.* (2004) and Knepp *et al.* (2005).

Kampichler *et al.* (2008) also worked with oak trees. Noting, however, “systems studied so far have not included mature trees,” they attempted to remedy this situation by determining “the abundance of dominant leaf-galls (spangle-galls induced by the cynipid wasps *Neuroterus quercusbaccarum* and *N. numismalis*) and leaf-mines (caused by the larvae of the moth *Tischeria ekebladella*) on freely colonized large oaks in a mixed forest in Switzerland, which received CO₂ enrichment [540 ppm vs. 375 ppm during daylight hours] from 2001 to 2004” via “the

Swiss Canopy Crane (SCC) and a new CO₂ enrichment technique (web-FACE)” in a forest that they say “is 80–120 years old with a canopy height of 32–38 m, consisting of seven deciduous and four coniferous species.”

The German, Mexican, and Swiss researchers discovered that although elevated CO₂ reduced various leaf parameters (water content, proteins, non-structural carbohydrates, tannins, etc.) at the SCC site, “on the long term, their load with cynipid spangle-galls and leaf-mines of *T. ekebladella* was not distinguishable from that in oaks exposed to ambient CO₂ after 4 years of treatment.” Consequently, although speculation has run rampant over the years about the long-term effects of atmospheric CO₂ enrichment on plant foliage and its subsequent effects on animals of various trophic levels, Kampichler *et al.* conclude in the situation they investigated, “CO₂ enrichment had no lasting effect in all three [animal] taxa, despite the substantial and consistent change in leaf chemistry of oak due to growth in elevated CO₂.”

The results of the studies reviewed above indicate the ongoing rise in the air’s CO₂ content will not cause greater damage to Earth’s vegetation by the larvae of the many moths that inhabit the planet. If anything, it could reduce the damage they cause.

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5.5.3 Other Herbivores

Besides aphids and moths, other herbivores consume vast amounts of foliage, roots, seeds, and other forms of vegetation. Because experiments involving temperatures and CO₂ content of the air often are conducted on specific types of plants, it is useful to sort the research results by the types of plants being studied. This section looks at research on herbaceous plants, woody plants, and finally other plants.

5.5.3.1 Herbaceous Plants

Insect pests have greatly vexed Earth's herbaceous plants in the past and likely will continue to do so in the future. It is possible, however, that the ongoing rise in the atmosphere's CO₂ content may impact this phenomenon, for better or for worse. Several studies have addressed this subject as it applies to herbaceous plant species, and these studies indicate such plants will be able to continue to cope with the periodic assaults of leaf-damaging herbivores as the air's CO₂ content continues to increase.

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, larvae of the destructive winter moth *Operophtera brumata*, outbreaks of which periodically cause extensive damage to heather moorland, were allowed to feed upon 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 authors 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.

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*) that were 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 produced in the ambient-air treatment, suggesting this butterfly species likely will become increasingly robust and plentiful as the air's CO₂ content continues to rise.

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, suggesting this particular insect likely will cause less tissue damage to the plants of this species-poor grassland in a CO₂-enriched world of the future.

Joutei *et al.* (2000) grew bean (*Phaseolus vulgaris*) plants in controlled environments kept at atmospheric CO₂ concentrations of 350 and 700 ppm, to which they introduced the destructive agricultural mite *Tetranychus urticae*. Female mites produced 34% and 49% less offspring in the CO₂-enriched chambers in their first and second generations, respectively. This CO₂-induced reduction in the reproductive success of this invasive insect, which negatively affects more than 150 crop species worldwide, bodes well for mankind's ability to grow the food needed to feed the planet's growing population in the years ahead.

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 toward 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 concentrations of two Mediterranean perennial grasses (*Dactylis glomerata* and *Bromus erectus*) by 15% and 87%, respectively; these compounds tend to enhance plant defensive and resistance mechanisms to attacks by both herbivores and pathogens (see Section 2.19).

Plants re-emit a substantial portion of their assimilated CO₂ back to the atmosphere as volatile organic compounds (VOCs). These substances affect both the chemical and physical properties of the air, where they generate large quantities of organic aerosols that can impact the planet's climate by forming cloud condensation nuclei that may lead to enhanced cooling during the day by reflecting a greater portion of the incoming solar radiation back to space. In addition, many VOCs protect numerous plants from a host of insect pests.

To see how these phenomena may be affected by the ongoing rise in the atmosphere's CO₂ concentration and by localized areas and time periods of high ozone (O₃) pollution, Himanen *et al.* (2009) exposed groups of both normal (non-transgenic) oilseed rape (*Brassica napus* ssp. *oleifera* L.) plants and transgenic plants, containing an introduced gene that produces *Bacillus thuringiensis* (Bt) crystal endotoxin (Cry) proteins that limit herbivorous insect attacks, to air of 360 and 720 ppm CO₂, as well as O₃-free air and air

of 100 ppb O₃. These experiments were conducted in controlled-environment chambers where the plants were grown from seed for 17–18 days in 0.66-liter pots filled with a 2:1:1 mixture of fertilized compost, *Sphagnum* peat, and sand. The non-transgenic plants grown in CO₂-enriched air produced 27% more shoot biomass than those grown in ambient air, and the transgenic plants produced 25% more. In the O₃-enriched air, the non-transgenic plants produced 29% less shoot biomass than those grown in O₃-free air, and the transgenic plants produced 34% less. In addition, on a per-dry-weight basis, Himanen *et al.* say the “doubled CO₂ significantly increased terpenoid emissions from intact oilseed rape plants compared with those released from the corresponding plants grown in control CO₂,” and they report there were no O₃-induced increases in VOC emissions. Thus, in addition to the fact that “production of *Bacillus thuringiensis* crystal endotoxin proteins in a crop plant limits specific herbivorous insect attack without the need for chemical treatments,” the seven scientists conclude “elevated CO₂ conditions could modify herbivore-induced defenses [VOC emissions] at the vegetative stage, and enhance indirect defense in the future.”

Although many studies have explored the direct effects of atmospheric CO₂ enrichment on plant growth and development, Klaiber *et al.* (2013) note the effects of elevated CO₂ on the behavioral responses of insect pests associated with major food crops have not been thoroughly investigated: “the potential effects of plant acclimation to CO₂ on host plant colonization by specialized herbivorous insects, which is a key step in the process of plant attack leading to potential yield losses, are largely unknown.”

Klaiber *et al.* “used a model system comprised of Brussels sprout (*Brassica oleraceae* var. *gemmifera*) and a specialized herbivorous insect, the cabbage aphid (*Brevicoryne brassicae*) to test for the effects of various periods of exposure to an elevated (2 x ambient) CO₂ concentration on key plant functional traits and on host plant location behavior by the insect, assessed as plant colonization rates.”

Plant height, leaf number, leaf area, fresh weight, and dry weight all increased in the elevated CO₂ treatments with respect to values obtained under ambient conditions, regardless of the length of CO₂ exposure. Leaf stomatal conductance also benefited at the higher CO₂ level, being reduced by nearly 50% by the end of the 10-week experiment. With respect to plant/herbivore interactions, the four Swiss scientists say “doubling the ambient CO₂ concentration had a

marked effect on plant colonization by winged aphids particularly when plants were exposed to CO₂ for longer periods.” After an exposure of only two weeks, for example, there was no difference in colonization rate, whereas after six and 10 weeks “elevated CO₂ led to a respective 15 and 26% reduction of colonization rates” by the cabbage aphid. The authors also note plant volatile emissions, which have been linked to attracting insects, were reduced significantly at the higher CO₂ concentration. Klaiber *et al.* conclude, “in agroecosystems, reduced crop plant colonization by an herbivorous pest insect under elevated CO₂ might be advantageous.”

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 that are normally viewed in a more favorable light.

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Climate Change Reconsidered II: Biological Impacts

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5.5.3.2 Woody Plants

Insect pests have vexed Earth's trees in the past and likely will continue to do so in the future. The ongoing rise in the atmosphere's CO₂ content may affect this phenomenon, for better or for worse. The sections that follow review the results of several studies that have addressed this subject as it applies to woody plant species. These studies suggest Earth's woody plants will fare much better in a CO₂-enriched future with respect to the periodic assaults of leaf-damaging herbivores.

5.5.3.2.1 Cotton

Bt toxins produced by *Bacillus thuringiensis* supplied to plants via foliar application have been used as a means of combating crop pests for more than 50 years. The effectiveness of this pest management technique depends primarily on the amount of Bt-produced toxins ingested by susceptible insects. Consequently, Coviella and Trumble (2000) wondered whether atmospheric CO₂ enrichment might enhance the effectiveness of the technique by inducing susceptible insects to eat more treated foliage and thus be more effectively eradicated. If soil nitrogen levels are low, foliar nitrogen concentrations in CO₂-enriched air are often reduced from what they are at the current atmospheric CO₂ concentration, and, it is supposed, insects thus must eat more foliage to get the amount of nitrogen they require for proper growth and development. In eating more foliage, the insects would ingest more Bt-produced toxins, and they would be more severely affected by them.

To test this hypothesis, Coviella and Trumble grew cotton plants in 20 three-liter pots in each of six Teflon-film chambers in a temperature-controlled

greenhouse; 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 received high levels of nitrogen (N) fertilization, while half received low levels (30 as opposed to 130 mg N/kg soil/week). After 45 days, leaves were removed from the plants and dipped in a solution containing *Bacillus thuringiensis*, after which known amounts of treated leaf material were fed to *Spodoptera exigua* larvae and their responses measured and analyzed.

These protocols revealed plants grown in the elevated CO₂ chambers did indeed have significantly lower foliar nitrogen concentrations than plants grown in the ambient CO₂ chambers under the low N fertilization regime, but this was not the case under the high N regime. Also, older larvae fed with foliage grown in elevated CO₂ with low N fertilization consumed significantly more plant material than those fed with foliage grown in ambient CO₂, but again no differences were observed in the high N treatment. In addition, and “consistent with the effect of higher Bt toxin intake due to enhanced consumption,” the researchers found “insects fed on low N plants had significantly higher mortality in elevated CO₂,” but again, no such effect was evident in the high N treatment. Coviella and Trumble conclude, “increasing atmospheric CO₂ is making the foliar applications more efficacious,” especially in the case of soils low in nitrogen.

In addition to applying Bt toxins to plants by spraying, the ability of plants to produce them internally has been achieved by means of genetic engineering. However, there is concern foreign genes from agricultural plants may be transferred into wild relatives of transgenic crop lines and thereby upset the “balance of nature.” In one of the first studies to address this concern, Coviella *et al.* (2000) grew cotton plants in the same manner as Coviella and Trumble—in 12 Teflon-film chambers in a temperature-controlled greenhouse, where six of the chambers were maintained at an atmospheric CO₂ concentration of 370 ppm and six were maintained at 900 ppm. Half the plants in each chamber were of a transgenic line containing the Bt gene for the production of the Cry1Ac toxin that is mildly toxic to *Spodoptera exigua*, and the other half were of a near isogenic line without the Bt gene. In addition, half the plants in each chamber received high levels of nitrogen (N) fertilization, while half received low levels (30 as opposed to 130 mg N/kg soil/week). Between 40 and 45 days after emergence, leaves were removed from the plants and fed to the *S. exigua*

larvae, after which a number of larval responses were measured and analyzed, along with various leaf properties.

The researchers 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; the transgenic plants from the low-N, high CO₂ treatment produced lower levels of Bt toxin than did the transgenic plants from the low-N, ambient CO₂ treatment. The high level of N fertilization only partially compensated for this latter high-CO₂ effect. In the ambient CO₂ treatment there was also a significant increase in days to pupation for insects fed transgenic plants, but this difference was not evident in elevated CO₂. In addition, pupal weight in ambient CO₂ was significantly higher in nontransgenic plants, and, again this difference was not observed in elevated CO₂.

Coviella *et al.* say their 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 nontransgenic plants for some key insect developmental/fitness variables including length of the larval stage and pupal weight.” These results, in turn, suggest that 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 on the natural world.

Coviella *et al.*’s results suggest transgenic plants designed to produce Bt-type toxins may become less effective in carrying out the objective of their design as the air’s CO₂ content continues to rise. Coupling this observation with the fact that the foliar application of *Bacillus thuringiensis* to crops should become even more effective in a higher-CO₂ world of the future, as per the findings of Coviella and Trumble, it could be argued the implantation of toxin-producing genes in plants is not the way to proceed in the face of the ongoing rise in the air’s CO₂ content, which reduces the effectiveness of the genetic implantation technique at the same time it increases the effectiveness of foliar application. It is important to see what other researchers have learned about the subject.

Chen *et al.* (2005b) grew well-watered and fertilized cotton plants of two varieties (GK-12, expressing Cry1A (c) genes from *Bacillus thuringiensis*, and Simian-3, a non-transgenic cultivar

from the same recurrent parent) in pots in open-top chambers maintained at either 376 or 754 ppm CO₂ in Sanhe County, Hebei Province, China, from planting in mid-May to harvest in October. Throughout this period, several immature bolls were collected and analyzed for chemical characteristics. Others were stored under refrigerated conditions for later feeding to larvae of the cotton bollworm, when various parameters related to bollworm growth and development were monitored. The scientists 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, Chen *et al.* report elevated CO₂ slightly decreased the body biomass of the cotton bollworm and reduced moth fecundity. The Bt treatment was even more effective in this regard, and in the combined Bt-high-CO₂ treatment the negative cotton bollworm responses were expressed most strongly.

In a parallel study, Chen *et al.* (2005a) grew transgenic *Bacillus thuringiensis* cotton (GK-12) plants from seed for a period of 30 days in well-watered and fertilized sand/vermiculite mixtures in pots located in controlled-environment chambers maintained at atmospheric CO₂ concentrations of 370, 700, and 1,050 ppm. Three generations of cotton aphids (*Aphis gossypii*) were subsequently allowed to feed on some of the plants, and a subset of the aphid-infected plants was supplied with predatory ladybugs. Chen *et al.* report “plant height, biomass, leaf area, and carbon:nitrogen ratios were significantly higher in plants exposed to elevated CO₂ levels,” and “more dry matter and fat content and less soluble protein were found in *A. gossypii* in elevated CO₂.” They report “cotton aphid fecundity significantly increased ... through successive generations reared on plants grown under elevated CO₂.” They also report “significantly higher mean relative growth rates were observed in lady beetle larvae under elevated CO₂,” and “the larval and pupal durations of the lady beetle were significantly shorter and [their] consumption rates increased when fed *A. gossypii* from elevated CO₂ treatments.” Hence, they conclude, their study “provides the first empirical evidence that changes in prey quality mediated by elevated CO₂ can alter the prey preference of their natural enemies.” They found this phenomenon could “enhance the biological control of aphids by lady beetle” while enhancing control by means of negative Bt-induced effects on the aphids.

Wu *et al.* (2011) state, “secondary metabolites present in plants provide protection against invaders

Climate Change Reconsidered II: Biological Impacts

because of their antimicrobial activity (Kamra *et al.*, 2006),” and “elevated CO₂ leads to plants allocating more carbohydrate resources to their secondary metabolism (Agrell *et al.*, 2004; Casteel *et al.*, 2008),” which may thus induce them to “generate higher concentrations of defensive compounds that are toxic [to] herbivorous insects (Coviella and Trumble, 1999).” Preeminent in this group of compounds are condensed tannins, naturally occurring secondary carbon compounds produced in the leaves of virtually all families of plants that comprise up to 50% of the dry weight of their leaves. Another such compound of note is gossypol, a natural toxin present in the cotton plant that helps to protect it from insect pests such as the cotton bollworm.

Wu *et al.* studied the allocation of the carbohydrate resources of two cotton (*Gossypium hirsutum* L.) cultivars—transgenic Bt cotton (cv. GK-12) and non-transgenic Bt cotton (cv. Simian-3)—to condensed tannins and gossypol both before and after injury inflicted on the plants by the cotton bollworm (*Helicoverpa armigera* Hubner) over periods of one, three, and 12 hours in controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 370 or 750 ppm.

Before any bollworm injury to the plants, the extra CO₂ led to increases of 12 and 14% in the condensed tannin concentrations in the foliage of the Bt-transgenic and non-transgenic cotton plants, respectively; increases of 10 and 10% in the gossypol concentrations of the transgenic and non-transgenic plants, respectively; and a 4% decrease in Bt toxin in the transgenic plants. After bollworm injury for periods of one, three, and 12 hours, the non-transgenic plants experienced condensed tannin increases of 14, 9, and 9%, respectively, and transgenic plants experienced increases of 16, 9, and 9%, respectively. Corresponding results for gossypol were increases of 7, 10, and 6% for the non-transgenic cultivar and 7, 7, and 6% for the transgenic cultivar. The transgenic plants also exhibited Bt toxin decreases of 3, 3, and 5%, respectively.

In discussing the implications of their findings, the four Chinese scientists state prior studies have demonstrated increases in condensed tannins and gossypol typically occur “in response to an increasing CO₂ atmosphere, especially in combination with injury caused by herbivorous insects (Drury *et al.*, 1998; Roth and Lindroth, 1994),” and they suggest these increases “may compensate for the Bt toxin loss in the transgenic Bt cotton,” which appears to be an outcome of their study as well. Thus we may expect cotton to become ever less susceptible to damage by

the cotton bollworm as the air’s CO₂ content continues to rise.

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5.5.3.2.2 Maple

Williams *et al.* (2003) studied *Acer rubrum* saplings beginning their fourth year of growth in open-top chambers maintained at four atmospheric CO₂/temperature conditions: (1) ambient temperature, ambient CO₂, (2) ambient temperature, elevated CO₂ (ambient + 300 ppm), (3) elevated temperature (ambient + 3.5°C), ambient CO₂, and (4) elevated temperature, elevated CO₂. They bagged first instar gypsy moth larvae on various branches of the trees and observed their behavior.

They found “larvae feeding on CO₂-enriched foliage ate a comparably poorer food source than those feeding on ambient CO₂-grown plants, irrespective of temperature,” and there was a minor reduction in leaf water content due to CO₂ enrichment. They report 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 found “irrespective of CO₂ concentration, on average, male larvae pupated 7.5 days earlier and female larvae 8 days earlier at elevated temperature.” Noting anything that prolongs the various development stages of insects potentially exposes them to greater predation and parasitism risk, they conclude the observed temperature-induced hastening of the insects’ development likely would expose them to less predation and parasitism risk, which would confer an advantage on this particular herbivore in this particular situation.

Hamilton *et al.* (2004) note many single-species investigations have suggested 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 against putting too much faith in these predictions until relevant real-world ecosystem-level experiments have been completed.

In one such study they conducted at the Duke Forest FACE facility near Chapel Hill, North Carolina (USA), 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 is dominated

by loblolly pine trees that account for fully 92% of the ecosystem’s total woody biomass. In addition, it contains 48 species of other woody plants (trees, shrubs, and vines) that have naturally established themselves in the forest’s understory. Hamilton *et al.* quantify the loss of foliage due to herbivory experienced by three deciduous tree species, one of which was *Acer rubrum*.

The results indicate “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, “elevated CO₂ reduced overall herbivory by more than 40%,” and in 2000 they observed “the same pattern and magnitude of reduction.”

With respect to changes in foliage properties that might have been expected to lead to increases in herbivory, Hamilton *et al.* report 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,” noting 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.* thus conclude their landmark paper by emphasizing that “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 (Stilling *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 world of the future, just the opposite appears 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 by chewing insects on saplings of seven species (including *Acer rubrum*) in 2001, 2002, and 2003; five additional species (including *Acer barbatum*) were included in 2001 and 2003. They found “across the seven species that were 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 were observed 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,” “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 some universal feature of chemistry or structure that affected leaf suitability was altered by the treatment.” Another possibility they discuss is “forest herbivory may decrease under elevated CO₂ because of a decline in the abundance of chewing insects,” citing Stilling *et al.* (2002) to this effect 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 Stilling *et al.* (2002) and Hamilton *et al.* (2004) in open experimental systems suggest that damage to trees may decrease.”

But what if herbivore-induced damage increases, for whatever reason in some situations, in a future CO₂-enriched world?

The likely answer is provided by Kruger *et al.* (1998), who grew well-watered and 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, 50% of the saplings’ leaf area was removed 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.

Kruger *et al.* thus conclude, in a high-CO₂ world of the future “sugar maple might be more capable of tolerating severe defoliation events which in the past have been implicated in widespread maple declines.”

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5.5.3.2.3 Oak

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. They found the elevated air temperature treatment significantly reduced leaf palatability, and leaf toughness increased as a consequence of temperature-induced increases in condensed tannin concentrations. In addition, the higher temperatures significantly reduced leaf nitrogen content, and elevated CO₂ caused a temporary increase in leaf phenolic concentrations and a decrease in leaf nitrogen content.

In one of the first attempts to move outside the laboratory and 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) within 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 found total leaf miner densities were 38% less on the foliage of trees growing in CO₂-enriched air than on the foliage of trees growing in ambient air. In addition, atmospheric CO₂ enrichment consistently reduced the absolute numbers of the study's six leaf miner species. However, 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. In spite of this increase in feeding, the leaf miners in the CO₂-enriched chambers experienced significantly greater mortality than those in the ambient-air chambers. 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.

If extended to agricultural ecosystems, these findings suggest crops may experience less damage from such herbivores in a high-CO₂ world of the future, thus increasing potential harvest and economic gains. In addition, with reduced numbers of leaf miners in CO₂-enriched air, farmers could reduce their dependency on chemical pesticides to control them, thus reducing the negative impacts of these agricultural chemicals on the environment.

In another study conducted on five scrub-oak forest species at the same experimental facility, Stiling *et al.* (2002b) 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 found 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 they found "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." These effects were so powerful that 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 lower for all plant species. In a high-CO₂ world of the future, many plants may be able to better withstand the onslaughts of various insect pests that have plagued them in the past. Another intriguing implication of this finding, as Stiling *et al.* note, is "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 is dominated by two species of scrub oak (*Quercus geminata* and *Q. myrtifolia*) that account for more than 90% of the ecosystem's biomass, focusing on the abundance of a guild of lepidopteran leaf-miners that attack the leaves of *Q. myrtifolia*, as well as various leaf chewers. They followed 100 marked leaves in each of 16 open-top chambers (half of them exposed to ambient air and half exposed to air containing an extra 350 ppm of CO₂) for nine months. "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 report, "both the abundance of the guild of leafmining lepidopterans and damage

caused by leaf chewing insects attacking myrtle oak were depressed in elevated CO₂.” They found 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.

Concentrating on 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 elliotii*. At three-month intervals from May 2001 to May 2003, undamaged leaves were removed from each of these 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 researchers 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 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. In addition, there were 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 they observed in leaf chemical constituents and herbivore damage “suggest that damage to plants may decline as atmospheric CO₂ levels continue to rise.”

Hall *et al.* (2005a) studied 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 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[, 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 we can

determine 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, 2002a, 2003; Hall *et al.*, 2005).”

Focusing their attention on two species of oak tree—*Quercus alba* L. (white oak) and *Quercus velutina* Lam. (black oak)—Knepp *et al.* (2007) examined host plant preference and larval performance of *A. polyphemus* when fed foliage of the two tree species that had been grown in either ambient or CO₂-enriched air (to 200 ppm above ambient) in a long-running FACE experiment at the Forest Atmosphere Carbon Transfer and Storage (FACTS-1) research site in the Piedmont region of North Carolina (USA). They found “growth under elevated CO₂ reduced the food quality of oak leaves for caterpillars,” and “consuming leaves of either oak species grown under elevated CO₂ slowed the rate of development of *A. polyphemus* larvae.” In addition, they report feeding on foliage of *Q. velutina* grown under elevated CO₂ led to reduced consumption by the larvae and greater mortality. The researchers opine, “reduced consumption, slower growth rates, and increased mortality of insect larvae may explain [the] lower total leaf damage observed previously in plots of this forest exposed to elevated CO₂,” as documented by Hamilton *et al.* (2004) and Knepp *et al.* (2005).

Stiling *et al.* (2010) note in a CO₂-enriched atmosphere, “plant quality for herbivores is reduced because of decreases in plant nitrogen concentrations and increases in secondary metabolites (Poorter *et al.*, 1997; Curtis and Wang, 1998; Peñuelas and Estiarte, 1998),” but “Stiling *et al.* (2009) recently showed that, over long time periods under continuously elevated CO₂, the increases in plant biomass under elevated CO₂ over compensate for reductions in foliage quality by providing a greater quantity of biomass for herbivores.” Seeking to determine whether this might also be true for insectivores and detritivores, Stiling *et al.* employed pitfall trapping over the last three of 11 years of continuous CO₂ enrichment (to 350 ppm above ambient) in eight of 16 open-top chambers that enclosed portions of a scrub-oak ecosystem in Florida (USA) composed of a mix of three oak tree species (*Quercus myrtifolia*, *Q. geminata*, and *Q. chapmanii*) that accounted for

approximately 90% of the total aboveground ecosystem biomass, and they employed sticky traps over another six months of the study.

The three researchers report 110,618 insects and other arthropods from 25 orders were recovered from the pitfall traps, and 39,305 insects and other arthropods from 14 orders were found on the sticky traps. These data, they write, “revealed increases of insect herbivore species such as Thysanoptera (thrips), Hemiptera, and Lepidoptera, but no effects on insectivores such as spiders, parasitic wasps, and ants, or on detritivores such as Diptera (flies), Psocoptera (book lice), Blattodea (cockroaches), Collembola (spring tails), Orthoptera (crickets) and Coleoptera (beetles).”

Stiling *et al.* conclude the “increase in the number of herbivores, including rasps, suckers, and chewers, under elevated CO₂” was “likely caused by an increase in plant biomass under elevated CO₂,” which for the scrub-oak ecosystem they studied amounted to 67% (Seiler *et al.*, 2009). But they additionally conclude, “increases in plant biomass and herbivore abundance brought about by elevated CO₂ do not influence insect abundance at other trophic levels such as insectivores, parasitoids and predators, or decomposers.” They note their results are similar to those of two other studies (Sanders *et al.*, 2004; Hillstrom and Lindroth, 2008) that also “failed to detect effects of elevated CO₂ on most guilds.” Thus, the “bottom-up effect brought about by higher plant biomass as a result of many years of elevated CO₂” in this experiment appears to enhance abundance of herbivores only.

The evidence cited above suggests herbivore damage to oak trees by various insect pests will decline as the air’s CO₂ concentration continues to climb.

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Climate Change Reconsidered II: Biological Impacts

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5.5.3.3 Other Plants

Gleadow *et al.* (1998) grew eucalyptus seedlings in glasshouses maintained at 400 and 800 ppm CO₂ for a period of 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, suggestive of a potential for increased prunasin production had the saplings been under attack by herbivores.

In a study involving mechanical defoliation, Lovelock *et al.* (1999) grew seedlings of the tropical tree *Copaifera aromatica* for 50 days in pots placed within 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, attesting to the benefits of atmospheric CO₂ enrichment in helping trees deal with herbivory.

Docherty *et al.* (1997) grew beech and sycamore saplings in glasshouses maintained at atmospheric CO₂ concentrations of 350 and 600 ppm, and groups of three sap-feeding aphid species and two sap-feeding leafhopper species were allowed to feed on them. Overall, elevated CO₂ had few significant effects on the performance of the insects, although there was a non-significant tendency for elevated CO₂ to reduce the individual weights and populations of the aphids.

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 larvae placed on the ambiently grown foliage, regardless of nitrogen treatment. This effect was so pronounced that 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. Since the nun moth is a deadly defoliator that resides in most parts of Europe and East Asia between 40 and 60°N latitude and is commonly regarded as the coniferous counterpart of its close relative the gypsy moth, which feeds primarily on deciduous trees, the results of this study suggest the ongoing rise in the air's CO₂ content likely will lead to significant reductions in damage to spruce and other coniferous trees by this voracious insect pest.

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 during the daylight hours of one full growing season. They found “elevated CO₂ had little effect on both primary and secondary metabolites of aspen.” Thus it was not surprising to learn “elevated CO₂ had few biologically significant effects on forest tent caterpillar performance.” Elevated O₃, on the other hand, altered foliar composition much more than did elevated CO₂, and, as they discovered, it improved tent caterpillar

performance under ambient CO₂ conditions, but not in CO₂-enriched air. In addition, elevated O₃ decreased the larval survivorship of the parasite of the caterpillar. Without an increase in the air's CO₂ content commensurate with that projected for O₃ over the coming half-century, therefore, quaking aspen—the most widely distributed tree in North America—would be in for a world of hurt.

Mattson *et al.* (2004) note “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 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. Feeding trials with caged Eurasian hares (*Lepus timidus*) were then carried out, and a number of chemical analyses were made of the tops of the seedlings and the basal parts of their stems.

In a second experiment, Mattson *et al.* grew paper birch (*Betula papyrifera*) from seed for two 140-day growing seasons in well-watered and fertilized pots placed within 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 and scoring the wood, on the basal third of the seedlings, and these tissues were tested for the presence of various herbivore-deterrent chemical constituents.

“As expected,” they write, the results indicate “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 reduced rabbit feeding on paper birch stems by about

51%, whereas neither temperature nor severe early-season defoliation (another experimental treatment) affected the trees' 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.” As the air's CO₂ content continues to rise, at least these two species of birch trees apparently will have a significantly easier time of getting established and growing to maturity.

Sanders *et al.* (2004) studied effects of atmospheric CO₂ enrichment on the plant and arthropod communities of the understory of a closed-canopy sweetgum plantation (which reduces the light available to the understory between 70 and 95% during the growing season) in a FACE study where the air's CO₂ content was increased by approximately 48%. The authors report under such conditions there were large adjustments in the relative productivities of the five dominant species that account for more than 90% of the biomass and annual production of the understory vegetation. Overall, however, the total understory productivities of the two CO₂ treatments were not significantly different from each other. Also, Sanders *et al.* report, “C:N ratios for four of the five dominant plant taxa did not differ between ambient and elevated CO₂,” and “there were no overall treatment or species x treatment effects” with respect to this parameter.

The three scientists further report they “found no effect of elevated CO₂ on herbivory,” and “even for the one species that showed an effect of CO₂ on C:N ratio, herbivores did not compensate by foraging more.” In addition, total arthropod abundance did not differ between ambient and elevated CO₂ plots, nor did the abundances of detritivores, omnivores, or parasitoids. They conclude, “changes in plant community composition did not translate into differences in arthropod communities.” Sanders *et al.* state “idiosyncratic, species-specific responses to elevated CO₂ may buffer one another: the abundances of some species increase while others decrease,” and, therefore, “to understand the potential effects of global [environmental] change on the complexity of multitrophic interactions that structure most communities, field experiments on entire communities are necessary.”

Noting the “detrimental effects of ozone on plants are well known,” and “carbon dioxide [CO₂]

generally affects trees in opposite ways to ozone [O₃],” 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 and published between 1990 and 2005.”

With respect to ways elevated O₃ may benefit insect herbivores that tend to damage trees, Valkama *et al.* 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, 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,” 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 by 7% below what it was in ambient air. This analysis of the vast majority of pertinent experimental data obtained prior to 2006 suggests the ongoing 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 otherwise capable of being done to Earth’s forests by voracious insect pests.

In a study involving only changes in temperature, Andrew and Hughes (2007) “investigated how the relationship of herbivorous insects and their host plants may change under a warmer climate” by “transplanting a host plant species to locations subject to mean annual temperatures 1.2°C higher than at the species’ current warmest boundary and 5.5°C higher than at its coolest edge.” They “compared the structure and composition of the herbivorous insect community that colonized the transplants (i) to that of the host plant species within its natural range and (ii) to a congeneric plant species that grew naturally at the transplant latitude.” In addition, they “investigated whether the herbivore community and rates of herbivory were affected by the latitudinal origin of the transplants.”

According to the two Australian researchers, their study indicated “rates of herbivory did not significantly differ between the transplants and plants at sites within the natural range,” and “there were no significant differences in herbivore species richness or overall rates of herbivory on the transplants originating from different latitudes.” They state in the abstract of their paper, “if this result holds for other

plant-herbivore systems, we might expect that under a warmer climate, broad patterns in insect community structure and rates of herbivory may remain similar to that at present, even though species composition may change substantially.” Or as stated in their concluding paragraph, “if these results can be generalized to other plant hosts, we might predict that as climate zones shift poleward and mobile organisms like flying insects respond by migrating to stay within their current climatic envelope, plants will be colonized by new herbivore species within similar guilds to those currently supported,” and “changes in the composition, but not necessarily the structure, of these new communities may, therefore, result.”

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)—within climate-controlled closed-top chambers from mid-June to October 2002 at the Mekrijärvi 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, while mimicking 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 then determined total plant shoot and root biomass once the plants went dormant in October.

As best as can be determined from the authors’ 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 in the no N fertility treatment (29 and 30%, respectively, vs. 13%). The same was true of the combined elevated CO₂ and elevated temperature treatment, where the corresponding treatment-induced biomass increases were 34 and 36% vs. 20%. These results indicate 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 elevated CO₂ increased the plant biomass of the undefoliated seedlings by approximately 25%, that of the 25%-defoliated seedlings by

Terrestrial Animals

24%, and that of the 50%-defoliated seedlings by 22%. The elevated CO₂ and elevated temperature treatment increased the plant biomass of the same three categories of seedlings by approximately 31%, 30%, and 29%, respectively. The six Finnish scientists conclude “climatic change”—which they specifically define to mean elevated atmospheric temperature and CO₂—“will have a positive impact on the compensatory ability of defoliated silver birch seedlings.”

One year later in a similar analysis, Huttunen *et al.* (2008) studied the leaf palatability of first-year silver birch (*Betula pendula*) seedlings to adult blue alder leaf beetles (*Agelastica alni*), periodically measuring a host of seedling parameters related to plant chemical and morphological defense properties. The seedlings were grown in climate-controlled closed-top chambers maintained at ambient and twice-ambient atmospheric CO₂ concentrations and at ambient and ambient plus 2°C air temperatures. The authors also examined the additional effects of three levels of added soil nitrogen (none, moderate, and high) plus two levels of manual defoliation (25% and 50%) on leaf palatability.

The researchers’ findings were varied and complex, indicative of complicated interactions with the potential to cascade through several trophic levels and change the dynamics of forest ecosystems. “In the worst scenario,” as they describe what could happen, “the consequences may include widespread damage to trees.” However, they report, their study indicated 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.”

Hamilton *et al.* (2012) write, “the response of complex plant and animal communities to global change is highly variable (Tylianakis *et al.*, 2008),” but they note “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 approximately 200 ppm, and where three other such plots were maintained at the normal ambient CO₂ concentration—Hamilton *et al.* counted arthropods found in each of the six plots every two weeks throughout June and July 2005, in order to assign them to different feeding guilds. In addition, “stable isotope data for spiders collected in ambient and elevated CO₂ plots were analyzed to determine the extent to which herbivorous prey species moved into and out of the elevated CO₂ plots.”

The seven U.S. scientists say their isotopic data “gave no indication that the treatment plots represented a ‘boundary’ to the movement of insects.” In addition, there was no detectable effect of elevated CO₂ on the total number of individual arthropods in the two sets of treatment plots. However, “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.”

Novick *et al.* (2012) write “warmer climates induced by elevated atmospheric CO₂ are expected to increase damaging bark beetle activity in pine forests,” yet they say, “the effect of elevated CO₂ on resin production—the tree’s primary defense against beetle attack—remains largely unknown.” They note “resin physically ejects or entombs attacking beetles and, when volatile components of resin have evaporated, seals wounds in the bark,” as revealed by the studies of Ruel *et al.* (1998) and Wilkens *et al.* (1998). Novick *et al.* assessed the effect of elevated CO₂ on resin production of dominant-and-unfertilized 27-year-old loblolly pine (*Pinus taeda* L.) trees growing under both ambient and elevated (ambient + 200 ppm) atmospheric CO₂ concentrations in the Duke Forest of North Carolina (USA) over the period March to October 2009.

The four researchers report the elevated CO₂ treatment increased resin flow by 140% in dominant trees growing in unfertilized subplots. This CO₂-induced resin flow enhancement “persisted throughout the growing season.” Novick *et al.* conclude, “forests with low- to mid-range fertility”—which, in their words, “currently represent the majority of southern pine forests (Fox *et al.*, 2007)” —“may become increasingly protected from bark beetle

attacks in an elevated CO₂ climate.” They note, “previous studies have shown that even more modest increases in resin flow (i.e., enhancements less than or equal to 100%) significantly increase the survival probability of pine trees experiencing bark beetle attack,” as demonstrated by Reeve *et al.* (1995) and Strom *et al.* (2002).

Working at the aspen free-air CO₂ enrichment (Aspen FACE) site in north-central Wisconsin (USA), Nabity *et al.* (2012) investigated how herbivore damage types (leaf-chewing, gall-forming, and leaf-folding) alter 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 leaf-chewing insects impact photosynthesis in birch (*Betula papyrifera*) trees. They 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.” Nabity *et al.* conclude their findings suggest “at least for these species,” elevated CO₂ “may reduce the impact of herbivory on photosynthesis,” a very positive development.

The balance of evidence suggests Earth’s non-woody plants are adequately prepared to deal with the challenges of herbivorous insects as the air’s CO₂ content continues to rise.

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5.5.4 Butterflies

- Global warming is creating opportunities for butterflies to expand their populations and ranges, just the opposite of alarmist projections of range contractions and butterfly species demise in response to a CO₂-induced warming of Earth.

IPCC claims butterflies are at risk of extinction due to global warming. This section reviews research studying how butterflies respond to rising air temperatures and CO₂ concentrations and comes to a very different conclusion.

5.5.4.1 Response to Temperature

Research on the impact on butterflies of temperature changes has found impacts on populations and ranges and also has revealed how butterflies adapt, evolve, and in other ways respond to changes in temperature. The following sections summarize that research.

5.5.4.1.1 Population Dynamics

In response to model-based projections in which global warming enhances the prospect for animal species demise, several researchers have conducted studies on butterflies to test the viability of this hypothesis. Fleishman *et al.* (2001), for example, used comprehensive data on butterfly distributions from six mountain ranges in the U.S. Great Basin to study how butterfly populations of that region may respond to IPCC-projected climate change. Their work revealed “few if any species of montane butterflies are likely to be extirpated from the entire Great Basin (i.e., lost from the region as a whole).” The three researchers note “during the Middle Holocene, approximately 8000–5000 years ago, temperatures in the Great Basin were several degrees warmer than today.” They conclude, “we might expect that most of the montane species—including butterflies—that currently inhabit the Great Basin would be able to tolerate the magnitude of climatic warming forecast over the next several centuries.”

Other scientists have focused on the response of butterflies to warming during the twentieth century, warming IPCC claims is unprecedented in the past one to two thousand years.

Davies *et al.* (2006) studied the silver-spotted skipper butterfly (*Hesperia comma*), noting during the twentieth century it “became increasingly rare in

Britain [as] a result of the widespread reduction of sparse, short-turfed calcareous grassland containing the species' sole larval host plant, sheep's fescue grass," while describing the "refuge" colonies of 1982 as but a "remnant" of what once had been. To examine whether global warming might drive the already-decimated species to extinction, the four researchers analyzed population density data and estimates of the percent of bare ground and the percent of sheep's fescue available to the butterflies, based on surveys conducted in Surrey in the chalk hills of the North Downs, south of London, in 1982 (Thomas *et al.*, 1986), 1991 (Thomas and Jones, 1993), 2000 (Thomas *et al.*, 2001; Davies *et al.*, 2005), and 2001 (R.J. Wilson, unpublished data). They also assessed egg-laying rates in different microhabitats, the effects of ambient and oviposition site temperatures on egg-laying, and the effects of sward composition on egg location. This multifaceted work revealed, "in 1982, 45 habitat patches were occupied by *H. comma*," but "in the subsequent 18-year period, the species expanded and, by 2000, a further 29 patches were colonized within the habitat network." In addition, they found "the mean egg-laying rate of *H. comma* females increased with rising ambient temperatures" and "a wider range of conditions have become available for egg-laying."

Davies *et al.* write, "climate warming has been an important driving force in the recovery of *H. comma* in Britain [as] the rise in ambient temperature experienced by the butterfly will have aided the metapopulation re-expansion in a number of ways." First, they note, "greater temperatures should increase the potential fecundity of *H. comma* females," and "if this results in larger populations, for which there is some evidence (e.g. 32 of the 45 habitat patches occupied in the Surrey network experienced site-level increases in population density between 1982 and 2000), they will be less prone to extinction," with "larger numbers of dispersing migrant individuals being available to colonize unoccupied habitat patches and establish new populations." Second, "the wider range of thermal and physical microhabitats used for egg-laying increased the potential resource density within each grassland habitat fragment," and "this may increase local population sizes." Third, "colonization rates are likely to be greater as a result of the broadening of the species realized niche, [because] as a larger proportion of the calcareous grassland within the species' distribution becomes thermally suitable, the relative size and connectivity of habitat patches within the landscape increases." Fourth, "higher temperatures may directly increase

flight (dispersal) capacity, and the greater fecundity of immigrants may improve the likelihood of successful population establishment." Davies *et al.* conclude, "the warmer summers predicted as a consequence of climate warming are likely to be beneficial to *H. comma* within Britain," and "warmer winter temperatures could also allow survival in a wider range of microhabitats."

Dennis and Sparks (2007) analyzed data on the general abundance of Lepidoptera in Britain over the period 1864–1952, based on information assembled by Beirne (1955) via his examination of "several thousand papers in entomological journals describing annual abundances of moths and butterflies." The two researchers report "abundances of British Lepidoptera were significantly positively correlated with Central England temperatures in the current year for each month from May to September and November," and "increased overall abundance in Lepidoptera coincided significantly with increased numbers of migrants," having derived the latter data from Williams (1965). In addition, they report Pollard (1988) subsequently found much the same thing for 31 butterfly species over the period 1976–1986, and Roy *et al.* (2001) extended the latter investigation to 1997 and found "strong associations between weather and population fluctuations and trends in 28 of 31 species which confirmed Pollard's (1988) findings." These observations indicate the warming-driven increase in Lepidopteran species and numbers in Britain has been an ongoing phenomenon since the end of the Little Ice Age.

Checa *et al.* (2009) studied the composition and structure of butterfly communities of the "rotting-carrion guild" of the Nymphalidae family over a period of 13 months (April 2002–April 2003) in areas surrounding the Yasuni Scientific Research Station in the Ecuadorian Amazon inside the Yasuni National Park. They obtained their data using traps baited with rotten shrimp that had been fermenting for 11–20 days. Checa *et al.* captured 9,236 individual Nymphalidae butterflies representing 208 species, including two species that had not previously been found in Ecuador, and two "new" species that had not previously been found anywhere. They discovered "a constant replacement of species throughout the year," and "these communities had the highest species richness and abundance during the months with high temperatures." They note the mean temperature of their study area "only varies over one degree during the whole year."

The four researchers comment on "temperature's central role in the biology and life history of

butterflies,” noting “several key processes for butterfly survival depend on regulation of internal temperature,” including mimetism and fast flight (Chai and Srygley, 1990), and fecundity and longevity, which they say have been found to be “higher at higher temperatures (Karlsson and Wiklund, 2005).” Hence, they conclude, “the tight relationship between temperature and butterfly population levels,” or abundance, as well as butterfly species richness, likely will be “of major importance” for tropical butterflies in surviving potential future global warming.

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5.5.4.1 2 Range Expansion

IPCC claims the increase in temperature predicted to result from the ongoing rise in the air's CO₂ content will be of such magnitude and speed that many species of plants and animals will not be able to migrate poleward in latitude or upward in elevation rapidly enough to avoid extinction, as they are forced to seek cooler living conditions. However, there are many reasons for rejecting this contention, one of the most powerful being increases in the air's CO₂ content generally enable plants to endure warmer weather, so there is little or no need for them to shift the heat-limiting warm-temperature boundaries of their ranges as temperatures rise (See Sections 3.13, 4.2.3, and 4.4, this volume). At the cold-limiting cool-temperature boundaries of their ranges, on the other hand, warming provides opportunities for plants to push poleward and upward, which results in expansions of their ranges and reductions in their risk of extinction.

This section reviews several studies examining butterfly range habitat, revealing butterflies may be mimicking the respective shifts and stability of the cold- and heat-limited boundaries of the ranges of the plants on which they depend for food.

Parmesan *et al.* (1999) examined the distributional changes of non-migratory butterfly species whose northern boundaries were in northern Europe and whose southern boundaries were in southern Europe or northern Africa, over the prior century of global warming. They found the northern range boundaries shifted northward for 65% of the 52 species examined, remained stable for 34%, and

Climate Change Reconsidered II: Biological Impacts

shifted southward for 2%. As to the southern boundaries, of the 40 species examined there, 22% shifted their southern range boundary northward, for 72% it remained stable, and for 5% it shifted southward. Because “nearly all northward shifts involved extensions at the northern boundary with the southern boundary remaining stable,” as the 13 researchers explain, “most species effectively expanded the size of their range when shifting northwards.”

Thomas *et al.* (2001) documented an unusually rapid expansion of the ranges of two butterfly species (the silver-spotted skipper and the brown argus) along with two cricket species (the long-winged cone-head and Roesel’s bush cricket). They observed the warming-induced “increased habitat breadth and dispersal tendencies have resulted in about 3- to 15-fold increases in expansion rates.” In commenting on these findings, Pimm (2001) remark the geographical ranges of these insects were “expanding faster than expected” and the synergies involved in the many intricacies of the range expansion processes were “unexpected.”

Crozier (2004) notes “*Atalopedes campestris*, the sacheem skipper butterfly, expanded its range from northern California into western Oregon in 1967, and into southwestern Washington in 1990,” where she reports temperatures rose by 2–4°C over the prior half-century. In an attempt to assess the importance of this regional warming for the persistence of *A. campestris* in the recently colonized areas, Crozier “compared population dynamics at two locations (the butterfly’s current range edge and just inside the range) that differ by 2–3°C.” Then, to determine the role of over-winter larval survivorship, she “transplanted larvae over winter to both sites.”

According to Crozier, “combined results from population and larval transplant analyses indicate that winter temperatures directly affect the persistence of *A. campestris* at its northern range edge, and that winter warming was a prerequisite for this butterfly’s range expansion.” Noting “populations are more likely to go extinct in colder climates,” Crozier writes, “the good news about rapid climate change [of the warming type] is that new areas may be available for the introduction of endangered species.” The species she studied responded to regional warming by extending its northern range boundary, thereby expanding its range.

Menendez *et al.* (2006) provided what they call “the first assessment, at a geographical scale, of how species richness has changed in response to climate change,” concentrating on British butterflies. They tested “whether average species richness of resident

British butterfly species has increased in recent decades, whether these changes are as great as would be expected given the amount of warming that has taken place, and whether the composition of butterfly communities is changing towards a dominance by generalist species.” They determined “average species richness of the British butterfly fauna at 20 x 20 km grid resolution has increased since 1970–82, during a period when climate warming would lead us to expect increases.” They also found, as expected, “southerly habitat generalists increased more than specialists,” which require a specific type of habitat that is sometimes difficult for them to find, especially in the modern world where habitat destruction is commonplace. In addition, they determined observed species richness increases lagged behind those expected on the basis of climate change.

These results “confirm,” according to the nine U.K. researchers, “that the average species richness of British butterflies has increased since 1970–82.” Some of the range shifts responsible for the increase in species richness take more time to occur than those of other species, and the researchers state their results imply “it may be decades or centuries before the species richness and composition of biological communities adjusts to the current climate.”

In another analysis from Britain, Gonzalez-Megias *et al.* (2008) investigated species turnover in 51 butterfly assemblages by examining regional extinction and colonization events that occurred between the two periods 1976–1982 and 1995–2002. The five researchers found regional colonizations exceeded extinctions: “over twice as many sites gained species as lost species,” so “the average species richness of communities has increased.” They also found species abundances following colonization likewise increased, because of “climate-related increases in the [land’s] carrying capacity.”

Comparing their results with a broader range of animal studies, Gonzalez-Megias *et al.* found “analyses of distribution changes for a wide range of other groups of animals in Britain suggest that southern representatives of most taxa are moving northwards at a rate similar to—and in some cases faster than—butterflies (Hickling *et al.*, 2006),” and they report, “as with butterflies, most of these taxonomic groups have fewer northern than southern representatives, so climate-driven colonisations are likely to exceed extinctions.” They suggest “most of these taxa will also be experiencing slight community-level increases in species richness.”

White and Kerr (2006) “report butterfly species’ range shifts across Canada between 1900 and 1990

and develop spatially explicit tests of the degree to which observed shifts result from climate or human population density,” describing the latter factor as “a reasonable proxy for land use change.” In this category they included such elements as “habitat loss, pesticide use, and habitat fragmentation,” all of which anthropogenic-driven factors have been tied to declines of various butterfly species. In addition, they state to their knowledge, “this is the broadest scale, longest term dataset yet assembled to quantify global change impacts on patterns of species richness.” They found butterfly species richness “generally increased over the study period, a result of range expansion among the study species.” They further found this increase “from the early to late part of the 20th century was positively correlated with temperature change,” which had to have been the cause of the increase, for they also found species richness was “negatively correlated with human population density change.”

Westwood and Blair (2010) measured the responses of 19 common butterfly species of the boreal forests of Manitoba (Canada) to temperature changes experienced there during 1971–2004, focusing on each species’ date of first appearance, week of peak abundance, and length of flight period. Autumn temperatures were found to have warmed significantly, and the two Canadian researchers observed “13 of 19 species showed a significant increase in flight period extending longer into the autumn,” when “flight period extensions increased by 31.5 ± 13.9 days over the study period.” They also note “two species, *Junonia coenia* and *Euphydryas phaeton*, increased their northerly ranges by ~150 and 70 km, respectively.”

Westwood and Blair state “warmer autumns and winters may be providing opportunities for range extensions of more southerly butterfly species held at bay by past climatic conditions.” They cite other investigators who have obtained similar results, stating “northward expansions in butterfly species range correlating with northward shifts in isotherms have been documented in both Europe and North America (Karl *et al.*, 1996; Parmesan, 1996; Parmesan *et al.*, 1999; Hill *et al.*, 1999; Hickling *et al.*, 2006),” and “in Canada, the Gorgone checkerspot (*Chlosyne gorgone*, Hubner) and the Delaware skipper (*Anatrytone logan*, W.H. Edwards) have recently expanded their northern ranges significantly (Kerr, 2001).”

Forister *et al.* (2010) analyzed 35 years of butterfly presence-absence data collected by a single observer at 10 sites approximately every two weeks

along an elevation gradient stretching from sea level to an altitude of 2,775 meters in the Sierra Nevada Mountains of Northern California (USA). During the data-collection period both maximum and minimum temperatures rose, low-altitude habitat was negatively affected by encroaching land development, and there was no systematic variation in precipitation. The eight researchers found species richness over this period “declined at half of the sites, with the most severe reductions at the lowest elevations,” where “habitat destruction [was] greatest.” At intermediate elevations, they report, there were “clear upward shifts in the elevational ranges of species, consistent with the influence of global warming.” And at the highest site, they found species richness increased, and “in addition to an increase in richness, abundance has also generally increased at the highest-elevation site.”

Noting the Arctic is predicted to be especially susceptible to potential threats from climate change, citing Overpeck *et al.* (1996), Franzen and Ockinger (2012) studied temporal changes in the insect species richness and community composition of wild bees, butterflies, and moths over a period of 64 years at five sites in northern Sweden’s Padjelanta National Park (one of the largest National Parks in Europe, located just north of the Arctic Circle, between 66°45’ and 67°35’N, and 15°06’ and 18°36’E). The insect data were collected during surveys conducted over the period 2006–2008 and were compared with similar data collected in 1998 and 1944, while corresponding climate data were obtained from a weather station located at 66.89°N, 18.02°E.

The two researchers determined there had been a significant increase in the daily mean temperature during the vegetation season (May–September) between 1944 and 2008, when the temperature rose at a rate of 0.015°C per year, yielding an increase of almost 1°C over the 64-year study period. With respect to insect responses, they found the total number of bumble bee, butterfly, and moth species increased from 52 in 1944 to 64 in 2008; for wild bees, which increased only from 15 to 16 species, the increase was not statistically significant. For butterflies and moths, the combined species number increase (from 37 to 48) was statistically significant. Franzen and Ockinger state, “high alpine insect species are apparently still performing relatively well,” noting “both southern species, such as *Erebia ligea* and *Polyommatus icarus*, and high alpine species, such as *Boloria chariclea* and *Lasionycta staudingeri*, seem to have colonized the area,” and “ranges and species richness are even increasing in

our study region, due to retreating glaciers and plant colonizations.” In light of these real-world observations, they say “it is possible that warming will simply improve the performance and abundance of species in cold areas, as their mobility increases and new habitats become available,” citing Ashton *et al.* (2009), Bale and Hayward (2010), and Kullman (2010).

According to Oliver *et al.* (2012), “climate warming threatens the survival of species at their warm, trailing-edge range boundaries but also provides opportunities for the ecological release of populations at the cool, leading edges of their distributions,” so “as the climate warms,” they continue, “leading-edge populations are expected to utilize an increased range of habitat types, leading to larger population sizes and range expansion.” Oliver *et al.* tested “the hypothesis that the habitat associations of British butterflies have expanded over three decades of climate warming.” They characterized “the habitat breadth of 27 southerly distributed species from 77 monitoring transects between 1977 and 2007 by considering changes in densities of butterflies across 11 habitat types.”

In response to the overall climate warming that occurred between 1977 and 2007, but “contrary to expectation,” as the five UK researchers report, 20 of the 27 species of butterflies they studied “showed long-term contractions in their habitat associations, despite some short-term expansions in habitat breadth in warmer-than-usual years,” when the butterflies they studied spread out from their primary habitat to occupy other sites. They say these findings suggest some non-climatic driver must be responsible for most of the habitat contractions of British butterflies over the past three decades, for they note, “butterfly population declines in the past century have been primarily driven by habitat destruction and degradation, particularly in relation to agricultural intensification and abandonment,” citing Asher *et al.* (2001) and Warren *et al.* (2001). They lament the likelihood these other anthropogenic-induced constraints “appear to be out-weighing the positive effects of a warming climate on habitat breadth.” In the final sentence of their paper, they suggest, “only if other non-climatic drivers can be reduced or reversed will species be able to fully exploit any emerging opportunities provided by climate warming.”

It appears the real world of nature is behaving just the opposite of alarmist projections of range contractions and butterfly species demise in response to a CO₂-induced warming of Earth.

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5.5.4.1.3 Adaptation, Evolution, and Phenotypic Responses

Few studies have investigated adaptive or evolutionary responses of butterflies to increased temperature. But those that have done so suggest butterflies are well-equipped to manage any of the temperature changes projected by IPCC for the future.

Hughes *et al.* (2007) examined evolutionary

changes in adult flight morphology in six populations of the speckled wood butterfly—*Pararge aegeria*—along a transect from its distribution core to its warming-induced northward-expanding range margin. The results were compared with the output of an individual-based spatially explicit model developed “to investigate impacts of habitat availability on the evolution of dispersal in expanding populations.” The empirical data the researchers gathered in Britain “were in agreement with model output” and “showed increased dispersal ability with increasing distance from the distribution core.” This included favorable changes in thorax shape, abdomen mass, and wing aspect ratio for both males and females, as well as thorax mass and wing loading for females. The researchers state, “increased dispersal ability was evident in populations from areas colonized >30 years previously.”

Hughes *et al.* suggest “evolutionary increases in dispersal ability in expanding populations may help species track future climate changes and counteract impacts of habitat fragmentation by promoting colonization.” However, they report, in the specific situation they investigated, “at the highest levels of habitat loss, increased dispersal was less evident during expansion and reduced dispersal was observed at equilibrium, indicating that for many species, continued habitat fragmentation is likely to outweigh any benefits from dispersal.”

Another means by which butterflies can cope with higher temperatures is through the production of heat-shock proteins (HSPs). According to Karl *et al.* (2008), HSPs “are thought to play an important ecological and evolutionary role in thermal adaptation,” where “the up-regulation of stress-inducible HSPs may help organisms to cope with stress thus enhancing survival (Sorensen *et al.*, 2003; Dahlhoff, 2004; Dahlhoff and Rank, 2007).” Working with *Lycaena tityrus*, a widespread temperate-zone butterfly that ranges from western Europe to central Asia, Karl *et al.* tested this hypothesis by comparing expression patterns of stress-inducible HSPs across replicated populations originating from different altitudes and across different ambient temperatures. Their observations revealed “a significant interaction between altitude and rearing temperature [that] indicates that low-altitude animals showed a strongly increased HSP70 expression at the higher compared with at the lower rearing temperature.” This is exactly where one would expect to see such a response in light of its obvious utility in warmer conditions.

Karl *et al.* observe “HSP70 expression increased substantially at the higher rearing temperature in low-

altitude butterflies ... [which] might represent an adaptation to occasionally occurring heat spells,” suggesting this response should serve these organisms well if the dramatic warming predicted by IPCC should come to pass.

Pateman *et al.* (2012) note there are many situations in nature where one species has a close-to-exclusive relationship with another species, such as a predator-prey relationship in the animal kingdom, an animal-plant symbiotic relationship such as that between corals and the zooxanthellae they host, or the relationship between a butterfly and the plant species that acts as a host for the larval stage of the butterfly. Such interactions, according to Pateman *et al.*, are most commonly regarded as additional constraints, “because they may limit species to a narrower set of physical conditions (and, hence, narrower geographic ranges) than their fundamental climatic niches might otherwise allow.” Thus if the world warms to a substantial degree, there may be a mismatch between the climatic needs of the two species, resulting in one or both of them suffering from the change in climate.

Pateman *et al.* studied the brown argus butterfly (*Aricia agestis*), which “has spread northward in Great Britain by ~79 km in 20 years, which is 2.3 times faster than the average expansion rate documented for species globally (Chen *et al.*, 2011),” endeavoring to discover what accelerated the butterfly’s dramatic rate of range expansion. They analyzed the effect of climate on brown argus butterfly populations associated with different larval host plants, based on count data developed by volunteers who monitored more than 200 fixed transects in Britain, as described by Pollard and Yates (1993). Results revealed warmer summers typically result in higher brown argus larval population densities on both rockrose and Geraniaceae plants, but under cooler conditions the rockrose host plant was more favorable than Geraniaceae plants. Over the past two decades, as the frequency of warm summers increased, the five UK researchers found the brown argus butterfly adapted by expanding its larval presence onto Geraniaceae plants they had largely avoided under cooler conditions. That led to a significant expansion in the size of their range, as they had an additional plant species on which to lay their eggs and have their larvae develop successfully.

The five researchers state in the concluding sentence of the abstract of their paper, “interactions among species are often seen as constraints on species’ responses to climate change, but we show that temperature-dependent changes to interspecific interactions can also facilitate change.” Or as they

state in the concluding sentence of the body of their paper, “we suggest that altered interactions among species do not necessarily constrain distribution changes but can facilitate expansions,” thereby providing another real-world example of a previously unappreciated means by which an animal species can benefit from global warming and expand its range of territorial occupancy. And contrary to the view that generalist species will more rapidly exploit new regions made available by climate change, field assays of butterflies in recently colonized areas are composed of more specialized species, such as the UK brown argus butterfly, because of their aggressive colonization of their widely dispersed host plant (Bridle *et al.*, 2014).

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5.5.4.2 Response to Elevated CO₂

Few studies have been conducted on the response of butterflies to increased levels of atmospheric CO₂, but those that have been done suggest rising CO₂ will confer a net benefit on their growth and survival.

Early work on the subject was provided by Groverde *et al.* (1999). Birdfoot Deer Vetch (*Lotus corniculatus*) is a cyanogenic plant that produces foliar cyanoglycosides to deter against herbivory by insects. The Common Blue Butterfly (*Polyommatus icarus*), however, regularly feeds on this plant—it possesses an enzyme that detoxifies these cyanide-containing defensive compounds. To study the effects of elevated CO₂ and genotype on the leaf quality of Birdfoot Deer Vetch and the larval development of the Common Blue Butterfly, Groverde *et al.* grew four genotypes of *Lotus corniculatus*, differing in cyanoglycoside and tannin concentrations, in controlled environmental chambers receiving atmospheric CO₂ concentrations of either 350 or 700 ppm.

Elevated CO₂ significantly increased leaf tannin and starch contents in a genotypically dependent and independent manner, respectively, while decreasing leaf cyanoglycoside contents, regardless of genotype. Atmospheric CO₂ enrichment did not significantly affect leaf water, sugar, protein, or nitrogen content. Thus, these CO₂-induced changes in leaf chemistry (higher starch and tannin and lower cyanoglycoside concentrations) increased its palatability, as indicated by greater leaf dry weight consumption of CO₂-enriched leaves by butterfly larvae. In addition, increased leaf consumption of CO₂-enriched leaves led to greater larval biomass and shorter larval developmental times, indicating atmospheric CO₂ enrichment affected leaf quality to positively influence larvae of the Common Blue Butterfly. Moreover, larval mortality was lower when feeding on CO₂-enriched, rather than ambiently grown, leaves. Thus, as the CO₂ content of the air rises, it is likely Birdfoot Deer Vetch plants will increase their photosynthetic rates and differentially invest their additional carbon gains in storage, structural, and defensive compounds. Atmospheric CO₂ enrichment likely will increase leaf starch and tannin contents and decrease cyanoglycoside contents, without affecting sugar, protein, water, and nitrogen contents. Col-

lectively, these chemical changes would improve the palatability of Birdfoot Deer Vetch leaves to the Common Blue Butterfly larvae.

In a follow-up study four years later, Groverde *et al.* (2004), abandoned the controlled environment chamber design of Groverde *et al.* (1999) and grew Birdfoot Deer Vetch plants from seed for three months in tubes recessed into the ground under natural conditions in a nutrient-poor calcareous grassland where an extra 232 ppm of CO₂ was supplied to them via a screen-aided CO₂ control (SACC) system (Leadley *et al.*, 1997; 1999) and insect larvae were allowed to feed on the plants (half of which received extra phosphorus fertilizer) for the final month of the experiment.

The 63% increase in atmospheric CO₂ concentration enhanced the total dry weight of plants growing on the unfertilized soil by 21.5% and that of the plants growing on the phosphorus-enriched soil by 36.3%. The elevated CO₂ treatment had no effect on pupal and adult insect mass. Groverde *et al.* report there were “genotype-specific responses in the development time of *P. icarus* to elevated CO₂ conditions,” with larvae originating from different mothers developing better under either elevated CO₂ or ambient CO₂, and for still others the CO₂ concentration had no effect on development. Condensed tannins in the foliage of plants growing on the nutrient-poor calcareous soil were increased by 23.7% in the CO₂-enriched air.

The results of this study and its predecessor suggest the ongoing rise in the air’s CO₂ content likely will be positive for *L. corniculatus* plants, while ranging from positive to nil for the insect herbivore *P. icarus* that feeds on them. In addition, the authors suggest rising levels of CO₂ might be “a selective factor, affecting both plant and herbivore populations and their interaction,” and, therefore, “genotype-specific responses must be considered because this will affect the outcome of elevated CO₂ for plant-herbivore interactions.” It is currently unclear what the range of those potential outcomes might be. Finally, since the presence of condensed tannins in foliage eaten by ruminants tends to decrease their emissions of methane, it might be expected the CO₂-induced increases in the concentrations of these substances in the leaves of *L. corniculatus* may help reduce the atmospheric concentration of this powerful greenhouse gas in a CO₂-enriched world of the future.

Groverde *et al.* (2002) raised larvae of the satyrid butterfly (*Coenonympha pamphilus*) in seminatural, undisturbed calcareous grassland plots exposed to

atmospheric CO₂ concentrations of 370 and 600 ppm for five growing seasons. Elevated atmospheric CO₂ concentration was shown to increase foliar concentrations of total nonstructural carbohydrates and condensed tannins in the grassland plants. In what is often considered a negative impact, however, it decreased foliar nitrogen concentrations. Nevertheless, this phenomenon had no discernible negative impact on butterfly growth and performance characteristics. Larval developmental time, for example, was not affected by elevated CO₂, nor was adult dry mass. The elevated CO₂ increased lipid concentrations in adult male butterflies by nearly 14%, and marginally increased the number of eggs in female butterflies.

As atmospheric CO₂ concentrations increase, larvae of the satyrid butterfly likely will not be negatively affected by feeding on grassland plants that may exhibit reduced foliar nitrogen concentrations. Increases in the air's CO₂ concentration may increase the fitness of this butterfly species. Adult males exposed to elevated CO₂, for example, exhibited greater body concentrations of lipids, compounds used as energy resources in these and other butterflies. In addition, elevated CO₂ increased egg numbers in females, which also suggests an increase in fitness. Thus, this species—and perhaps others—likely will respond positively to future increases in the air's CO₂ concentration.

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5.5.5 Other Insects

5.5.5.1 Response to Temperature

It is important to determine what effect global warming might have on the delicate balance between various plants and the insects that feed on them. Several researchers have done just that for several insect species. This section examines what has been reported for other types of insects not previously discussed in this chapter.

In some cases, researchers have found higher temperatures do indeed inhibit insect growth and survival. For some insect species, humankind might consider this a good thing.

Zhang *et al.* (2009), for example, note “the Oriental migratory locust (*Locusta migratoria manilensis*) has been one of the most damaging agricultural pests throughout Chinese history.” Based on the decadal locust abundance data of Ma (1958) for the AD 950s–1950s, the decadal Yangtze Delta flood and drought frequency data of Jiang *et al.* (2005) for the AD 1000s–1950s, and the decadal mean temperature records of Yang *et al.* (2002) for the AD 950s–1950s, Zhang *et al.* employed wavelet analysis “to shed new light on the causal relationships between locust abundance, floods, droughts and temperature in ancient China.”

The international team of Chinese, French, German, and Norwegian researchers say coolings of 160- to 170-year intervals dominated climatic variability in China over the past millennium, and these cooling periods promoted locust plagues by enhancing temperature-associated drought/flood events. The six scientists say their results suggest “global warming might not only imply reduced locust plague[s], but also reduced risk of droughts and floods for entire China.” They note these findings “challenge the popular view that global warming necessarily accelerates natural and biological disasters such as drought/flood events and outbreaks of pest insects,” the view long championed by the assessment reports of the Intergovernmental Panel on Climate Change. In direct contrast to that view, Zhang *et al.* say their results are an example of “benign effects of global warming on the regional risk of natural disasters.”

Reineke and Hauck (2012) note “the grape leafhopper *Empoasca vitis* is regarded as a major insect pest in many European grapevine growing areas, with an increasing importance realized in recent years, maybe as a result of climatic change.”

Reineke and Hauck studied in the laboratory the

development of larval instars of two leafhopper species, *E. vitis* and *E. rosae*, on grapevine leaves under different temperature regimes. The two German researchers report the shortest larval developmental time they observed occurred at night temperatures of 13–15°C and day temperatures of 23–25°C, which they say “was in agreement with predicted optimal temperatures for both species.” In addition, “at the temperature regime of 20°C night and 30°C day temperature, either no egg hatch was observed or early development of first-instar larvae was not successful for both species.” Reineke and Hauck conclude, “these results suggest that warm (18°C) nights and moderately warm (28°C) days are representing the upper thermal threshold for development of both *E. vitis* and *E. rosae* embryonic stages on grapevine leaves, questioning current assumptions of an increasing importance of *E. vitis* as a grapevine pest under future climate change.”

Bertelsmeier *et al.* (2013) write, “climate change and invasive species are two of the most serious threats of biodiversity,” noting “a general concern is that these threats interact, and that a globally warming climate could favor invasive species,” with the result that “many native species are displaced, leading to local extinctions of fauna and flora.” They note “several studies suggest that climate change could exacerbate the threat posed by invasive species, especially poikilotherms [animals having a body temperature that varies with the temperature of their surroundings], by removing thermal barriers and allowing them to establish at higher latitudes.”

The three French researchers focused their attention on ants, because “ants are among the worst invasive species (Rabitsch 2011; Holway *et al.* 2002; Lach and Hooper-Bui 2010),” and “they are small, numerous and colonial” and can therefore “rapidly colonize a new habitat.” They studied the big-headed ant, *Pheidole megacephala*, considered one of the world’s 100 worst invasive species. They used ecological niche models to estimate the species’ potential suitable habitat in 2020, 2050, and 2080 with an ensemble forecast obtained from five modeling techniques, including three global circulation models and two CO₂ emission scenarios, by means of which they generated world maps with suitable climatic conditions and assessed changes, both qualitatively and quantitatively.

“Surprisingly,” Bertelsmeier *et al.* write, their results suggest “the invasion of big-headed ants is not only unlikely to benefit from climate change, but may even suffer from it,” as their projections showed “a global decrease in the invasive potential of big-

headed ants as early as 2020 and becoming even stronger by 2080, reaching a global loss of 19.4% of area with favorable climate.” They note this finding is just the opposite of classical views of global climate change, wherein the ranges of many invading species are believed to increase in response to warming, especially those that are currently limited by climate. *P. megacephala* “will experience very little shifts in potential habitat,” the French scientists conclude, as their niche envelope, presenting favorable climatic conditions, “will mostly shrink.”

The analysis of Bertelsmeier *et al.* suggests, as they clearly state, “the worst invasive species of today may not be the worst invasive species of tomorrow,” if Earth begins to warm again. After the planet’s nearly two-decade climate-change hiatus, it’s anyone’s guess as to when that might happen.

Other insect species have benefited from a little global warming, as illustrated by recent temperature-induced expansions of their ranges.

Hickling *et al.* (2005), for example, analyzed changes in the northern and southern range boundaries of 37 non-migratory British Odonata (dragonfly and damselfly) species—four of which have northern ranges, 24 of which have southern ranges, and nine of which are ubiquitous—between the two ten-year periods 1960–1970 and 1985–1995. Their work revealed all but two of the 37 species increased their ranges between the two ten-year periods. They report their “findings that species are shifting northwards faster at their northern range margin than at their southern range margin, are consistent with the results of Parmesan *et al.* (1999),” adding, “this could suggest that species at their southern range margins are less constrained by climate than by other factors.”

Poniatowski and Fartmann (2011) state the majority of central European orthopterans (an order of insects that includes grasshoppers, crickets, and locusts) “are flightless and have low dispersal ability,” citing Reinhardt *et al.* (2005). However, they note, “since the 1980s—the beginning of the strong global temperature increase—some short-winged (brachypterous) species have been able to expand their ranges rapidly,” as reported by Thomas *et al.* (2001), Simmons and Thomas (2004), Gardiner (2009), and Wissmann *et al.* (2009). In those cases, the scientists write, “long-winged (macropterous) individuals of the predominantly short-winged (flightless) species are assumed to have been responsible for the range shifts,” citing the findings and conclusions of Simmons and Thomas (2004), Gardiner (2009), and Hochkirch and Damerau (2009).

Poniatowski and Fartmann studied the migration behavior of *Metrioptera roeselii*, a medium-sized bush-cricket, 13–26 mm in total length, which is currently expanding its range northwards in large parts of Europe (Kleukers *et al.*, 2004; Gardiner, 2009; Wissmann *et al.*, 2009).” This species is wing-dimorphic, but they note “the short-winged (brachypterous) morph dominates.”

Based on their analyses of the relationships between bush-cricket densities and several meso-climate/weather parameters, the two German researchers found cricket abundances were positively correlated with warm and dry weather conditions during the hatching times of the nymphs, leading them to conclude, “the development of long-winged individuals is determined by density stress (crowding), as has been shown for locusts (Uvarov, 1966).” They further note, “similar results have also been reported for other bush-crickets,” citing Ando and Hartley (1982), Sanger (1984), and Higaki and Ando (2003). Poniatowski and Fartmann conclude, “the rapid northward range expansion of *M. roeselii* is indirectly driven by climate change,” explaining, “favorable (warm/dry) weather conditions lead to high densities at high latitudes (cf. Bale *et al.*, 2002) and in turn result in many macropters,” the “potential dispersers” that get the species where it needs to go in order to survive in a world of evolving warmth.

Instead of experiencing range expansions in response to rising temperatures, other insect species have invoked adapted mechanisms allowing them to maintain their populations and habitat area.

Sparks *et al.* (2010) note “honeybees are an essential component of modern agriculture,” and “large acreages of pollinator-dependent crops, such as apples, almonds, blueberries and cranberries, require managed pollinators, mainly the honeybee, to ensure maximized production.” They report several modern studies suggest synchronization of pollinator activity and flowering may be changed by rapid global warming, leading to deficient pollination when it is most needed and resulting in reduced crop productivity. Noting little work has focused on this imagined problem, the six Polish scientists decided to investigate the dates of honeybees’ first cleansing flights, which occur in the early spring of each year after overwintering and “are undertaken by worker bees excreting faeces accumulated in their recta while restricted in the hive for the winter during cold weather.”

Sparks *et al.* analyzed annual records of the first observed cleansing flights of honeybees from 80–130 hives for each of the 25 years of the 1985–2009

period in the vicinity of Poznan, Poland. They found a significant relationship between the date of the first cleansing flight and the January to March mean temperature, as well as the previous June to September mean temperature. In the two-variable model of this phenomenon they developed, “the regression coefficients suggested a 1°C increase in previous June to September mean temperature was associated with a 9.11 ± 2.36 day advance, and a 1°C increase in January to March temperature was associated with a 3.41 ± 1.00 day advance, in first cleansing flight date.”

Thus they discovered “first cleansing flight dates in [their] study advanced by over 1 month during the 25 years that observations were kept,” and this advancement was “similar to changes reported in first appearance dates of other insects (e.g. Roy and Sparks, 2000; Sparks *et al.*, 2005; Harrington *et al.*, 2007), including other hymenopterans like wasps (Tryjanowski *et al.*, 2010).” This demonstrates, as has been observed by still others, “cleansing behavior is related to late winter/spring temperature (e.g. Kronenberg and Heller, 1982; Seeley, 1985),” and provides more evidence of honeybees “continued synchrony with the plant species that rely heavily on this major pollinator,” as the plants’ flowering dates fluctuate with the ups and downs of spring temperatures and their longer-term trends.

Bartomeus *et al.* (2011) preface their analysis by noting “the phenology of many ecological processes is modulated by temperature, making them potentially sensitive to climate change,” and because of this fact, “mutualistic interactions may be especially vulnerable because of the potential for phenological mismatching if the species involved do not respond similarly to changes in temperature.” Bartomeus *et al.* explored this situation with real-world data by presenting “an analysis of climate-associated shifts in the phenology of wild bees, the most important pollinators worldwide, and [comparing] these shifts to published studies of bee-pollinated plants over the same time period.” They “used long-term data to compare phenological shifts for 10 bee species to shifts in 106 native plant species that are visited by these same bee species,” which typically “have annual cycles that include an obligatory larval or adult diapause before spring emergence.” The plant data for this comparison were provided by Primack *et al.* (2004) and Miller-Rushing *et al.* (2006) for Massachusetts (AD 1885–2003), by Bradley *et al.* (1999) for Wisconsin (1936–1999), by Cook *et al.* (2008) for New York (1931–2008), and by Abu-Asab *et al.* (2001) for Washington, DC (1970–1999, a time interval

bracketing the period of greatest temperature increase), and the bee data were developed by Bartomeus *et al.*

The results indicate “over the past 130 years, the phenology of 10 bee species from northeastern North America has advanced by a mean of 10.4 ± 1.3 days,” and “most of this advance has taken place since 1970, paralleling global temperature increases.” The scientists note “when the best available data are used to estimate analogous rates of advance for plants, these rates are not distinguishable from those of the bees.” Bartomeus *et al.* conclude, among the generalist bee species they studied, “bee emergence is keeping pace with shifts in host-plant flowering.” This finding suggests historical global warming—which IPCC contends has been unprecedented over the past millennium or two—has not detrimentally interfered with the longstanding mutually beneficial relationship between the emergence of adult wild bees and the flowering of the plants they visit.

Balanya *et al.* (2006) determined the magnitude and direction of shifts over time [13 to 46 years, mean = 24.1 years] in chromosome inversion frequencies and in ambient temperature for 26 populations of the cosmopolitan fly species *Drosophila subobscura* on three continents, to determine whether “ambient temperatures have warmed at these sites and also whether genotypes characteristic of low latitudes have increased in frequency.” The authors report warming occurred at 22 of the 26 sites they investigated, and “chromosome frequencies shifted toward a more low-latitude pattern in 21 of the 22 sites that warmed over the sample interval,” indicating “inversion frequencies have changed in step with climate on three continents.” As a result, “genotype frequencies and climate at a given site have become more equatorial over the sample intervals,” with the observed shifts being “equivalent to moving the historical sample site $\sim 1^\circ$ of latitude closer to the equator.”

The authors describe the genetic shift they uncovered as “exceptionally rapid,” being “detectable even for samples separated by fewer than two decades.” In addition, they say, “the ability of *D. subobscura* (Rodriguez-Trelles *et al.*, 1998; Orenge and Prevosti, 1996; Sole *et al.*, 2002)—and probably other species with short generation times (Bradshaw and Holzapfel, 2001; Umina *et al.*, 2005; Levitan and Etges, 2005; Kinnison and Hendry, 2001)—to respond genetically and rapidly to imposed environmental shifts may partially buffer their persistence in a globally warming world (Bradshaw and Holzapfel, 2006).”

Zivanovic and Mestres (2011) collected *Drosophila subobscura* flies from a swampy area on the bank of the Danube river near the town of Apatin, approximately 200 km northwest of Belgrade, Serbia, and analyzed inversion polymorphisms in them, comparing their results (from 2008 and 2009) with results obtained from flies collected at the same site in June 1994, because, as they put it, “genes located within inversions are associated with a variety of traits including those involved in climate adaptation,” citing Hoffmann and Rieseberg (2008). The scientists found a significant increase in the frequency of certain chromosomal arrangements characteristic of southern latitudes, which they describe as “warm adapted,” and a significant decrease in the frequency of such arrangements characteristic of northern latitudes, which they describe as “cold adapted.”

The two researchers say their observations suggest they have detected “the effect of selection on chromosomal polymorphism composition,” and, therefore, “some form of natural selection appears to be acting as a reaction to the increase in temperature associated with [the] many heat waves that have markedly affected the Balkan Peninsula,” especially over the past decade and a half. They also note their results “agree with those from southwestern and central European populations (Rodriguez-Trelles and Rodriguez, 1998; Sole *et al.*, 2002; Balanya *et al.*, 2004, 2006, 2009).” In addition, they note similar things have been observed in *D. melanogaster* in Australia, citing Anderson *et al.* (2005) and Umina *et al.* (2005), and in *D. robusta* in North America, citing Levitan and Etges (2005). They report, “the climate change of recent decades has led to heritable genetic changes in animal species as diverse as birds, squirrels and mosquitoes (Bradshaw and Holzapfel, 2006),” revealing many forms of animal life may be well equipped to evolve with sufficient rapidity to survive the challenges of rapid global warming.

Nyamukondiwa and Terblanche (2010) write, “acclimation, acclimatization or hardening responses all describe different forms of phenotypic plasticity (i.e. the ability of an organism to respond to environmental stimuli with a change in phenotype),” as described by West-Eberhard (2003) and Whitman (2009). In addition, they state, “phenotypic plasticity may alter the performance of an organism through compensatory modifications of physiological function and tolerance as a result of changes in environmental conditions,” suggesting this multifaceted phenomenon likely will play a major role in determining future geographic distributions of insects in a warming world.

The two South African scientists explored the phenomenon as it operates in two species of fruit fly (*Ceratitis rosa* and *C. capitata*). Using a full-factorial design, as they describe it, they investigated one-week-long acclimation responses of each species' critical minimum and maximum temperature (CT_{min} and CT_{max}) to exposure to temperatures of 20, 25, and 30°C, as well as their interactions with short-term sub-lethal temperature exposures to the same conditions as arrived at via different rates of warming. They report, "generally, increasing the acclimation temperature significantly increased CT_{max} , whereas decreasing the acclimation temperature significantly lowered CT_{min} ." In addition, "slower ramping rates significantly increase CT_{max} in both *C. rosa* and *C. capitata*." This suggests "more time during heating (i.e. a slower heating rate) provides the flies with an opportunity to develop some heat protection, and therefore suggests that *C. capitata*, and possibly also *C. rosa*, might have short-term phenotypic plasticity of high temperature tolerance." They describe this as being "similar to the rapid heat hardening or the heat shock responses in *Drosophila* (Loeschcke and Hoffmann, 2006; Johnson *et al.*, 2009) and other insect species (Huang *et al.*, 2007)."

Nyamukondiwa and Terblanche conclude fruit flies "are capable of adjusting their thermal tolerance within a single generation at both weekly and hourly time scales," noting "high temperature acclimation improves high temperature tolerance, in keeping with much of the literature on thermal acclimation (Whitman, 2009)." They also state "both *C. rosa* and *C. capitata* have the capacity to adjust their thermal tolerance over short timescales in the wild," further stating this phenomenon will "probably allow both species to track changes in ambient temperature and survive sudden extremes of temperature that might otherwise be potentially lethal," citing Chown and Nicolson (2004).

This phenomenon is not restricted to flies. The two researchers indicate, for example, in several insect species "survival of lethal temperatures or critical thermal limits to activity can be significantly improved by prior exposure to sub-lethal temperatures," citing Lee *et al.* (1987), Kelty and Lee (2001), Shreve *et al.* (2004), and Powell and Bale (2006). This phenomenon is a major mechanism used by insects to cope with temperature variation at both daily (Kelty and Lee, 2001; Kelty, 2007; Overgaard and Sorensen, 2008) and seasonal (Powell and Bale, 2006; Hoffmann *et al.*, 2005; Terblanche *et al.*, 2006) time scales.

Harada *et al.* (2011) write "in temperate areas,

insects are adapted physiologically or behaviourally to either [1] tolerate seasonally fluctuating changes in temperature through diapause or to [2] avoid adverse conditions through migration," with the most predictable time cue for seasonal adaptation by insects being photoperiod (Tauber *et al.*, 1986). Thus, "it is assumed that the critical photoperiod of insects is becoming gradually shortened as a result of global warming," and if populations are adapting to the consequent longer growing seasons and later onsets of winter, it would be expected that the number of yearly broods produced "should increase, that photoperiodic responses of diapause induction and wing-form determination will continue to diminish ... and that overwintering adults will cease to migrate between water courses and overwintering land sites far from water, and will begin overwintering nearer summer habitats."

In an effort to determine whether such adjustments have been occurring in the life cycle of nymphs of the water strider *Aquarius paludum* in the Kochi prefecture of Japan over the past two decades, Harada *et al.* measured a number of pertinent parameters that had been assessed by Harada and Numata (1993) two decades earlier, over the period 1989–1991. They found *A. paludum* nymphs were trivoltine (i.e., produced three broods yearly) in 1991, but more recently the generation number appears to have increased to four or more. They also found overwintering adults of both sexes had no mature flight muscles in October and November 2008, which "contrasts with previous observations," and "the 2008 population also shows a low flight propensity in response to shorter day lengths."

The Japanese scientists from Kochi University thus opine, "the absence of mature flight muscles in the autumn, and the lower flight propensity under shorter days, may comprise evidence of a cessation of dispersal between the freshwater summer habitats and overwintering sites on land far from the bodies of water." And they observe, "the increase in daily-minimum temperature during the winter in the Kochi-Nankoku area over the last 15 years may allow adults of *A. paludum* to overwinter without dispersal nearer to their summer habitat," which could lead to the proportion of adults overwintering close to the water bodies increasing from the current estimate of 60 to 70% to between 90 and 100% within ten years. Thus, they conclude, *A. paludum* populations in the Kochi-Nankoku region "are continuing to show adaptive change, apparently in relation to global warming."

Brakefield and de Jong (2011) note "a variety of processes can enable organisms, including insects, to

respond successfully to climate change (Stenseth *et al.*, 2002; Bradshaw and Holzapfel, 2006; Parmesan, 2006),” including “habitat tracking, phenotypic plasticity and genetic adaptation.” Evidence for the first of these mechanisms, in their words, “is becoming commonplace,” as is the case with many species of butterflies that are “clearly responding with northern extensions in their range limits (Parmesan and Yohe, 2003; Hickling *et al.*, 2006),” as well as with moths and other insects that “are moving up altitudinal gradients (Chen *et al.*, 2009).” On the other hand, they write, “the extent to which changes in phenotypic plasticity are (or will be) involved in the numerous reports of changes in phenology (Brakefield, 1987; Roy and Sparks, 2000; Amano *et al.*, 2010) is not clear.” And they remark, “there are as yet few reports of genetic changes within populations linked to climate change,” although “the pitcher plant mosquito, *Wyeomyia smithii*, showed a genetic response to climate change, which involved changes in sensitivity to photoperiod (Bradshaw *et al.*, 2006),” which “could be detected over a period as short as five years.”

Hoping to contribute to the search for genetic responses to climate change, Brakefield and de Jong report on the most recent data describing changes in a cline in the frequency of melanism morphs of the two-spot ladybird beetle, *Adalia bipunctata* L., along a transect that extends inland from the seacoast in the Netherlands.

At the time of the beetle’s first survey in 1980, the two researchers report, “the frequency of melanics increased over some 40 km from 10% near the coast to nearly 60% inland.” Additional surveys in 1991 and 1995 “demonstrated some progressive change in cline shape,” and new samples from 1998 and 2004 confirmed these dynamics, so “over a period of about fifty generations of the beetle, the cline had decayed rapidly to yield rather uniform frequencies of melanic morphs at around 20% along the whole transect by 2004.” They remark, “climate data and evidence for thermal melanism in this species support our contention that these dynamics reflect a dramatic example of a rapid genetic response within populations to climate change and local selection.” Brakefield and de Jong conclude by stating their study “adds to potential examples of how some organisms are likely to be responding to climate change through direct genetic responses within populations.”

It appears rising temperatures will be beneficial for some insect species, but perhaps not for others. Nevertheless, it does not appear there will be a

widespread extinction of insect species, as most will adapt as they likely have done as temperatures have waxed and waned in the past.

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Climate Change Reconsidered II: Biological Impacts

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5.5.5.2 Response to Elevated CO₂

As the air's CO₂ content continues to rise, it is important to determine what effect this might have on the delicate balance between various plants and the insects that feed on them. This section reviews the results of studies that have reported on insects not previously discussed at any length, where it is seen the ongoing rise in the air's CO₂ content likely plays an important role in negating the damage being done to Earth's vegetation by voracious insect pests.

Docherty *et al.* (1997), in addition to studying aphids, studied two sap-feeding leafhopper species that were allowed to feed on saplings of beech and sycamore grown in glasshouses maintained at atmospheric CO₂ concentrations of 350 and 600 ppm. As far as they could determine, there were no significant effects of the extra CO₂ on either the feeding or performance characteristics of either leafhopper species.

In a literature review of more than 30 studies published two years later, Whittaker (1999) found chewing insects (leaf chewers and leaf miners) showed either no change or reductions in abundance in response to atmospheric CO₂ enrichment. They note, however, population reductions in this feeding guild often were accompanied by increased herbivory in response to CO₂-induced reductions in leaf nitrogen content.

Contemporaneously, Brooks and Whittaker (1999) removed grassland monoliths from the Great Dun Fell of Cumbria, UK—which contained eggs of a destructive xylem-feeding spittlebug (*Neophilaenus lineatus*)—and grew them in glasshouses maintained for two years at atmospheric CO₂ concentrations of 350 and 600 ppm. During the course of their

experiment, two generations of the xylem-feeding insect were produced; in each case, elevated CO₂ reduced the survival of nymphal stages by an average of 24%. Brooks and Whittaker suggest this reduction in survival rate may have been caused by CO₂-induced reductions in stomatal conductance and transpirational water loss, which may have reduced xylem nutrient-water availability.

Stiling *et al.* (1999) report the results of what may have been the first attempt to study the effects of elevated CO₂ on trophic webs in a natural ecosystem; specifically, a nutrient-poor scrub-oak community in Florida (USA), where 16 open-top chambers of 3.6-m diameter were fumigated with air of either 350 or 700 ppm CO₂ for approximately one year. At the end of this period, total leaf miner densities were 38% less on the CO₂-enriched foliage than on the foliage of the ambiently grown plants. Moreover, atmospheric CO₂ enrichment consistently reduced the numbers of all six species of leaf miners studied. In a compensatory development, exposure to elevated CO₂ increased the amount of leaf area consumed by the less-abundant leaf miners by approximately 40%. Nevertheless, leaf miners in the CO₂-enriched chambers experienced significantly greater mortality than those in the control chambers. Although CO₂-induced reductions in leaf nitrogen content were determined to have played a minor role in the mortality increase, the greatest factor contributing to this phenomenon was a fourfold increase in parasitization by various wasps that could more readily detect the more-exposed leaf miners on the CO₂-enriched foliage.

Three years later, Stiling *et al.* (2002) reported even more dramatic effects of elevated CO₂ on leaf chewers. The relative levels of damage by these insects (primarily larval lepidopterans and grasshoppers) were significantly lower in the elevated CO₂ chambers than in the ambient CO₂ chambers for all five of the plant species that accounted for more than 98% of the total plant biomass of the ecosystem. In addition, the response to elevated CO₂ was the same across all plant species. Also, they report more host-plant-induced mortality was found for all miners on all plants in elevated CO₂ than in ambient CO₂. These effects were so powerful that in addition to the relative densities of insect herbivores being reduced in the CO₂-enriched chambers, and even though there were more leaves on 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. Stiling *et al.* 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,” a beneficial effect.

In a natural ecosystem in Wisconsin (USA) comprised predominantly of trembling aspen (*Populus tremuloides* Michx.), Percy *et al.* (2002) studied the effects of increases in CO₂ alone (to 560 ppm during daylight hours), O₃ alone (to 46.4–55.5 ppb during daylight hours), and CO₂ and O₃ together on the forest tent caterpillar (*Malacosoma disstria*), a common leaf-chewing lepidopteran found in North American hardwood forests. By itself, elevated CO₂ reduced caterpillar performance by reducing female pupal mass, and elevated O₃ alone improved caterpillar performance by increasing female pupal mass. When both gases were applied together, the elevated CO₂ completely counteracted the enhancement of female pupal mass caused by elevated O₃. Hence, either alone or in combination with undesirable increases in the air’s O₃ concentration, elevated CO₂ tended to reduce the performance of the forest tent caterpillar. This finding is particularly satisfying because, in the words of Percy *et al.*, “historically, the forest tent caterpillar has defoliated more deciduous forest than any other insect in North America” and because “outbreaks can reduce timber yield up to 90% in one year, and increase tree vulnerability to disease and environmental stress.”

Also working at the Aspen FACE site in northern Wisconsin, USA, Kopper and Lindroth (2003) studied the effects of elevated CO₂ (560 ppm) and elevated O₃ (1.5 x ambient) on trembling aspen (*Populus tremuloides* Michaux) trees, while the aspen blotch leafminer (*Phyllonorycter tremuloidiella* Braun) was allowed to naturally colonize the trees. Although there were some minor alterations in foliar chemistry in the CO₂- and O₃-enriched treatments, they produced “little to no change in larval performance,” although both elevated CO₂ and O₃ “reduced colonization rates by nearly half.”

Holton *et al.* (2003) reared both 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, also at the Aspen FACE site in northern Wisconsin, where trees were 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 during the daylight hours of one full growing season. They found “elevated CO₂ had little effect on both primary and secondary metabolites of aspen.” Thus, “elevated CO₂ had few biologically significant effects on forest tent caterpillar performance.” Elevated O₃, on the other hand, altered foliar composition much

more than did elevated CO₂; and, as they discovered, it improved tent caterpillar performance under ambient CO₂ conditions, but not in CO₂-enriched air. In addition, elevated O₃ decreased the larval survivorship of the parasite of the caterpillar.

These findings suggest the ongoing rise in the air's CO₂ content likely will be very important to the future well-being of quaking aspen trees, especially when atmospheric O₃ concentrations are increasing concurrently. Elevated levels of atmospheric CO₂ are known to significantly increase the productivity of aspen trees, making them more robust (Percy *et al.* (2002). Moreover, the extra CO₂ of this study totally thwarted the positive impact of the extra O₃ on caterpillar performance, thus eliminating a major negative consequence for the trees. As the authors note, "aspen growth is significantly increased under high CO₂, but decreased under high O₃," and "that difference is likely to be exacerbated by the impacts of CO₂ and O₃ on herbivorous insects and parasitoids as documented in this study." Without an increase in the air's CO₂ content commensurate with that projected for O₃ over the coming half-century, therefore, quaking aspen—the most widely distributed tree in North America—would suffer.

Johns *et al.* (2003) performed, in their words, "a factorial experiment to examine the effects of elevated CO₂ and increased temperature on both the leaf-chewing adults and leaf-mining larvae of two closely related beetle species, *Octotoma championi* Baly and *Octotoma scabripennis* Guerin-Meneville (Coleoptera: Chrysomelidae), feeding on the host plant *Lantana camara* L. (Verbenaceae)." The study was conducted in environment-controlled growth chambers maintained at atmospheric CO₂ concentrations of 360 or 700 ppm and at low (22°C/18°C) or high (25°C/21°C) day/night temperatures, where well-watered and fertilized plants were grown from cuttings for just over 13 months. Under the high temperature treatment, plants grown at ambient CO₂ suffered wilting and premature leaf loss, despite daily watering, but this effect was ameliorated at elevated CO₂. They also report "the wilting of plants in the ambient CO₂/high temperature treatment reduced the emergence success of the beetles," and "consumption rates of free-living beetles were not affected by either CO₂ or temperature," whereas "in short-term trials using excised foliage, beetles given no choice between ambient and elevated CO₂-grown foliage consumed more from ambient plants."

The authors state "this study indicates that under future conditions of higher temperatures, amelioration of water stress in host plants growing in elevated CO₂

may benefit some endophagous insects by reducing premature leaf loss," and they note "under some circumstances, this benefit may outweigh the deleterious effects of lower leaf nitrogen," which is typically described as posing a major problem for insects in a high-CO₂ world of the future. In addition, Johns *et al.* say their results indicate "foliage consumption under elevated CO₂ by mobile, adult insects on whole plants may not be significantly increased, as was previously indicated by short-term experiments using excised foliage."

According to Heagle (2003), the Western flower thrip (*Frankliniella occidentalis*) "is one of the most important and difficult to control plant pests," as "it feeds on numerous plant species and spreads the tomato spotted wilt virus, which also affects numerous plant species." In an effort to learn how this pest might respond to increasing concentrations of atmospheric CO₂, Heagle grew well-watered and fertilized white clover (*Trifolium repens*) plants from virus-free stolons in 1-liter pots filled with Metro Mix 220 and placed between two rows of thrip-invested plants growing in 15-liter pots, after which they were grown for either 27 or 35 additional days in continuous-stirred tank reactor chambers (CSTRs) maintained at either ambient or elevated atmospheric CO₂ concentrations (396 or 745 ppm) and located within a non-filtered-air greenhouse. The USDA researcher reports, "at elevated CO₂, clover shoot weight and laminae weight were ~50% greater, and laminar area was ~20% greater than at ambient CO₂." In addition, he notes the "thrips population size was not significantly affected by CO₂, but laminar area scarred by thrips feeding was ~90% greater at elevated than at ambient CO₂." Nevertheless, because of the CO₂-induced increase in clover growth, "undamaged leaf area was approximately 15% greater at elevated than at ambient CO₂."

Barbehenn *et al.* (2004a) note "it has been hypothesized that herbivores will disproportionately increase their feeding damage on C₃ plants to compensate for the larger changes in C₃ plants in elevated CO₂ (Lincoln *et al.*, 1984, 1986; Lambers, 1993)." This is assumed because 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 (Wand *et al.*, 1999). In a test of this hypothesis, Barbehenn *et al.* 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 grasshopper (*Melanoplus sanguinipes*) nymphs that had been reared to the fourth instar stage were allowed to feed on the grasses' foliage.

As expected, foliage protein concentration decreased much more in the C₃ grass than in the C₄ grass (22% vs. 7%) when the grasses were grown in CO₂-enriched air. However, and "contrary to the hypothesis that insect herbivores will increase their feeding rates disproportionately in C₃ plants under elevated atmospheric CO₂," Barbehenn *et al.* report "*M. sanguinipes* did not significantly increase its consumption rate when feeding on the C₃ grass grown under elevated CO₂," suggesting this observation implies "post-ingestive mechanisms enable these grasshoppers to compensate for variable nutritional quality in their host plants" and noting 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)." Their data indicate, if anything, *M. sanguinipes* growth rates were increased, perhaps by as much as 12%, when they fed on the C₃ foliage that had been produced in the CO₂-enriched, as compared to the ambient-treatment, air.

As was also found by Barbehenn *et al.* (2004b), the CO₂-induced decrease in leaf protein concentration observed in this study did not induce an increase in foliage consumption in the C₃ plant studied, nor did it reduce the growth rate of the herbivore studied. The authors 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)."

Noting the "detrimental effects of ozone on plants are well known," and "carbon dioxide [CO₂] generally affects trees in opposite ways to ozone [O₃]," 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 and published between 1990 and 2005." With respect to ways by which elevated O₃ may benefit insect herbivores that tend to damage trees, Valkama *et al.* 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 found the "relative growth rate of chewers was significantly increased by 3.5% under elevated O₃." However, they discovered "these effects were counteracted by elevated CO₂," such that "elevated O₃ in combination with CO₂ had no effect on herbivore performance." When elevated CO₂ was added to the O₃-enriched air, it not only counteracted the O₃-induced increase in pupal biomass, but reduced it by 7% below what it was in ambient air.

Stiling and Cornelissen (2007) "report the results of the longest-known field study (9 years) to examine the effects of elevated carbon dioxide on leaf miner densities in a scrub-oak community at Kennedy Space Center, Florida [USA]." They then describe the results of various meta-analyses they employed to determine "the effects of elevated CO₂ on both plants (n = 59 studies) and herbivores (n = 75 studies)," where ambient CO₂ concentrations ranged between 350 and 420 ppm and elevated concentrations ranged between 550 and 1,000 ppm. With respect to the first subject of their review, Stiling and Cornelissen report "the densities of all leaf miner species (6) on all host species (3) were lower in every year in elevated CO₂ than they were in ambient CO₂." With respect to the second subject, they write, "elevated CO₂ significantly decreased herbivore abundance (-21.6%), increased relative consumption rates (+16.5%), development time (+3.87%) and total consumption (+9.2%), and significantly decreased relative growth rate (-8.3%), conversion efficiency (-19.9%) and pupal weight (-5.03%)." They also note "host plants growing under enriched CO₂ environments exhibited significantly larger biomass (+38.4%), increased C/N ratio (+26.57%), and decreased nitrogen concentration (-16.4%), as well as increased concentrations of tannins (+29.9%)." Thus with plant biomass increasing and herbivorous pest abundance decreasing (by +38.4% and -21.6%, respectively, in response to an approximate doubling of the atmosphere's CO₂ concentration), it appears plants will fare increasingly well as the air's CO₂ content continues to climb.

Kampichler *et al.* (2008) write, "since CO₂ enrichment alters the composition of live plant tissues, the ongoing global increase of atmospheric CO₂ concentration is expected to affect plant-animal interactions," but "systems studied so far have not included mature trees." They set out to determine "the abundance of dominant leaf-galls (spangle-galls induced by the cynipid wasps *Neuroterus*

quercusbaccarum and *N. numismalis*) and leaf-mines (caused by the larvae of the moth *Tischeria ekebladella*) on freely colonized large oaks in a mixed forest in Switzerland, which received CO₂ enrichment [540 ppm vs. 375 ppm during daylight hours] from 2001 to 2004” by means of “the Swiss Canopy Crane (SCC) and a new CO₂ enrichment technique (web-FACE)” in a forest they describe as “80–120 years old with a canopy height of 32–38 m, consisting of seven deciduous and four coniferous species.”

The German, Mexican and Swiss researchers report elevated CO₂ reduced various leaf parameters (water content, proteins, non-structural carbohydrates, tannins, etc.) at the SCC site, but “on the long term, their load with cynipid spangle-galls and leaf-mines of *T. ekebladella* was not distinguishable from that in oaks exposed to ambient CO₂ after 4 years of treatment.” Kampichler *et al.* conclude, “CO₂ enrichment had no lasting effect in all three [animal] taxa, despite the substantial and consistent change in leaf chemistry of oak due to growth in elevated CO₂.”

Rao *et al.* (2009) determined what foliage-mediated effects atmospheric CO₂ enrichment might have on another pernicious insect pest. They explain castor “is an important non-edible oilseed crop grown in many parts of the arid and semi-arid regions of India,” and the castor semilooper (*Achaea janata*) and tobacco caterpillar (*Spodoptera litura*) “occur during early and late stages of growth of castor, respectively,” when castor oil yields can be reduced “by 30–50% by the semilooper alone” and the tobacco caterpillar “can cause yield losses of 25–40%.”

Rao *et al.* allowed larvae of both species to feed on castor foliage grown in present-day air (presumed to contain 350 ppm CO₂) and in air enriched with CO₂ to concentrations of 550 and 700 ppm. Their results indicate, “compared to the larvae fed on ambient CO₂ foliage, the larvae fed on 700 and 550 ppm CO₂ foliage exhibited greater consumption.” However, the efficiency of conversion of both ingested and digested food into larval biomass “decreased in the case of larvae grown on 700 and 550 ppm CO₂ foliage,” so they “grew slower and took longer time (two days more than ambient) to pupation,” which would allow significantly more time (~13 percent) for them to be preyed upon by higher orders of creatures, many of which are considered to be much less of a threat to crop production than are insect larvae.

In the case of castor beans, then, it would appear in addition to the productivity enhancement likely to be provided by the stimulation of photosynthesis driven by atmospheric CO₂ enrichment—an approximate 34 percent increase in response to a

300 ppm increase in the air’s CO₂ content (Grimmer and Komor, 1999; Grimmer *et al.*, 1999)—a substantial increase in atmospheric CO₂ likely also would curtail yield losses currently caused by the castor semilooper and tobacco caterpillar.

Hillstrom *et al.* (2010) write, “natural forest systems constitute a major portion of the world’s land area, and are subject to the potentially negative effects of both global climate change and invasion by exotic insects.” They report, “a suite of invasive weevils has become established in the northern hardwood forests of North America,” noting it is “unknown” how these insects will respond to continued increases in the air’s CO₂ content.

Hillstrom *et al.* collected 200 mating pairs of *Polydrusus sericeus* weevils—which they describe as “the second most abundant invasive weevil species in northern hardwood forests”—from birch trees growing on the perimeter of the Aspen Face facility in Oneida County, Wisconsin (USA). They fed them leaves taken from the birch, aspen, and maple trees growing within either the facility’s ambient-air rings or its CO₂-enriched rings (maintained at a target concentration of 560 ppm) under controlled laboratory conditions throughout the summer of 2007, while closely monitoring parameters affecting weevil longevity and fecundity.

According to the five researchers, all from the University of Wisconsin’s Department of Entomology, the results indicate feeding the weevils with foliage produced on trees in the CO₂-enriched plots had no effect on male longevity, but it reduced female longevity by 19 percent. They also note, “*Polydrusus sericeus* egg production rate declined by 23% and total egg production declined by 29% for females fed foliage produced under elevated CO₂ compared with ambient CO₂.”

Hillstrom *et al.* conclude, “concentrations of elevated CO₂ above 500 ppm have the potential to decrease *P. sericeus* populations by reducing female longevity and fecundity,” which should be particularly beneficial for the northern hardwood forests of North America that are currently growing under atmospheric CO₂ concentrations of 390 ppm and rising.

The vast majority of pertinent experimental data suggest in the neverending battle between insect herbivores and the plants on whose foliage they feast, the ongoing 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 otherwise capable of being done to Earth’s vegetation by voracious insect pests.

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Climate Change Reconsidered II: Biological Impacts

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5.6 Mammals

- The warming-induced extinctions of mammals that have been predicted to occur are highly unlikely to be realized in nature, and warming in fact opens new territories for mammal range expansions. In addition, rising atmospheric CO₂ concentrations may produce changes in the palatability of the trunk and branch tissues of certain trees that may protect them from being killed by hares and rabbits.

It has been projected global warming will lead to a mass demise, if not extinction, of species across Earth because they will not be able to migrate rapidly enough to keep up with the shifting climatic zones to which they are currently accustomed, or they will literally “run out of places to run,” as in the case of mountain-top dwellers. As logical as that hypothesis might sound, more complex studies, such as the ones reviewed here, indicate it is wrong. Earth’s plants and

animals are not the simpletons the models often characterize them to be; they possess a wide array of strategies for coping with environmental change and re-colonizing former territories after having once been forced out of them.

Norment *et al.* (1999) summarized and compared the results of many surveys of mammal populations observed along the Thelon River and its tributaries in the Canadian Northwest Territories from the 1920s through much of the 1990s. Red squirrel, moose, porcupine, river otter, and beaver were found to have established themselves in the studied area in recent years, significantly increasing its biodiversity. Norment *et al.* suggest the primarily northward range expansions that produced these results may be explained by “a recent warming trend at the northern treeline during the 1970s and 1980s.” Alternatively, they note the influx of new species also may be due to “increasing populations in more southerly areas.” In either case, these several mammal species appear to be faring quite well, and perhaps thriving, in the face of increasing temperatures in this forest-tundra landscape.

Pockely (2001) report the results of a survey of the plants and animals on Australia’s Heard Island, located some 4,000 kilometers southwest of Perth. Over the past 50 years this sub-Antarctic island has experienced a local warming of approximately 1°C that has resulted in a modest retreat of its glaciers; for the first time in a decade, scientists are documenting what this warming and melting has done to the ecology of the island. Pockley reports on the “rapid increases in flora and fauna” that have accompanied the warming, quoting Dana Bergstrom, an ecologist at the University of Queensland in Brisbane, as saying areas that previously were poorly vegetated are now “lush with large expanses of plants.” He also notes populations of fur seals have expanded rapidly. He cites Eric Woehler of Australia’s environment department as informing him fur seals have emerged from “near extinction” to a population of 28,000 adults and 1,000 pups.

Between these far-flung chilly regions (where warming would be expected to enhance the abilities of land mammals to survive and reproduce), Lawler (1998) examined biogeographic relationships of mammals typically found on mountaintops in the Great Basin of western North America, with the objective of determining their future well-being in the face of predicted climate-driven changes in their environment. Contrary to the conclusions of earlier, more simplistic studies that predicted dramatic global warming-induced reductions in the numbers of

mammals in this region, Lawlor concludes “virtually no extinctions can be expected from a projected 3°C rise in temperature.” The results of this study, as well as those of Grayson (2000) and Grayson and Madson (2000), stand in stark contrast to model-based extinction predictions.

Working with the entire population of about 325 red squirrels (*Tamiasciurus hudsonicus*) near Kluane Lake, Yukon (Canada), Reale *et al.* (2003) ear-tagged and monitored the reproductive activity of all females each year from 1989 to 2001, while identifying and similarly dealing with most of their young from birth to adulthood, and weather data were collected at a monitoring station located 50 km from their study site. In addition, noting “spruce cones stored in the autumn of a given year are an important source of food for reproductive females in the spring of the following year,” they counted the number of cones on the top three meters of about 300 trees every August.

The four Canadian researchers report spring temperature rose by nearly 2°C over the course of their study, but there was “no particular trend for precipitation.” They found the mean number of spruce cones available over a female’s lifetime rose more than 35% over the 10 years of their observations, “a large increase in the abundance of food experienced by female squirrels.” They also report the squirrels responded to these environmental changes by advancing breeding by 18 days over the 10-year study period, representing an advancement of six days per squirrel generation. Quoting Reale *et al.*, “this dramatic advancement in breeding comprised a plastic response to increased food abundance as well as a microevolutionary response to selection.” Or as they write in the concluding sentence of their paper, “the combination of phenotypic changes within generations and microevolutionary changes among generations resulted in large phenotypic responses to rapid changes in environmental conditions experienced by this population of squirrels over the past ten years.”

Mattson *et al.* (2004) grew one-year-old seedlings of silver birch trees in closed-top chambers for one summer and autumn in pots containing an unfertilized commercial peat maintained at three soil nitrogen levels and two temperature regimes in air of either 362 or 700 ppm CO₂. Feeding trials with caged Eurasian hares were carried out and a number of chemical analyses made of the tops of the seedlings and the basal parts of their stems. In a second experiment, they grew paper birch trees from seed for two 140-day growing seasons in well-watered and fertilized pots placed within 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 fed *ad libitum*, consuming bark tissue down to and scoring the wood, on the basal third of the seedlings, and these tissues were tested for the presence of various herbivore-deterrent chemical constituents.

“As expected,” the authors state, “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 tend to 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%, while neither temperature nor severe early-season defoliation (another experimental 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.”

Millar and Westfall (2010) studied American pikas, small generalist herbivores that are relatives of rabbits and hares, inhabit patchily distributed rocky slopes of western North American mountains, and are good at tolerating cold. Pikas are widely believed to have a physiological sensitivity to warming, which when “coupled with the geometry of decreasing area at increasing elevation on mountain peaks,” in the words of the two scientists, “has raised concern for the future persistence of pikas in the face of climate change.” They note the species “has been petitioned under California [USA] state and federal laws for endangered species listing.”

In a study designed to investigate the validity of the basis for that classification, Millar and Westfall developed a rapid assessment method for determining pika occurrence and used it “to assess geomorphic affinities of pika habitat, analyze climatic relationships of sites, and evaluate refugium environments for pikas under warming climates.” The researchers gathered data over two field seasons in the Sierra Nevada Mountains of California, the southwestern Great Basin of California and Nevada,

Climate Change Reconsidered II: Biological Impacts

and the central Great Basin of Nevada, as well as a small area in the central Oregon Cascades.

The two U.S. Forest Service researchers report, “whereas concern exists for diminishing range of pikas relative to early surveys, the distribution and extent in our study, pertinent to four subspecies and the Pacific southwest lineage of pikas, resemble the diversity range conditions described in early 20th-century pika records (e.g., Grinnell and Storer, 1924).” The lowest site at which they detected the current presence of pikas, at an elevation of 1,827 meters, “is below the historic lowest elevation of 2350 m recorded for the subspecies by Grinnell and Storer (1924) in Yosemite National Park; below the low elevation range limit for the White Mountains populations given by Howell (1924) at 2440 m; and below the lowest elevation described for the southern Sierra Nevada populations of 2134 m (Sumner and Dixon, 1953).” In addition, they write, “a similar situation occurred for another lagomorph of concern, pygmy rabbit (*Brachylagus idahoensis*), where a rapid assessment method revealed much wider distribution than had been implied from historic population databases or resurvey efforts (Himes and Drohan, 2007).”

Millar and Westfall thus conclude “pika populations in the Sierra Nevada and southwestern Great Basin are thriving, persist in a wide range of thermal environments, and show little evidence of extirpation or decline.” Moreover, the documentation of a similar phenomenon operating among pygmy rabbits suggests still other animals also may be better able to cope with various aspects of climate change than we have been led to believe.

In a study of moose, Lowe *et al.* (2010) write, “intuitively, we would expect that a large northern ungulate with low tolerance for high temperatures would gradually be pushed out of the southern reaches of its range as the climate continues to warm and temperature conditions become increasingly unfavorable,” because “persistent temperatures above the upper critical limit will suppress foraging time and consequently cause mass loss during the summer, and that this reduced condition could affect overwinter survival and productivity,” citing Schwartz and Renecker (1998).

The authors “tested the hypothesis that climate limits the southern distribution of moose (*Alces alces*) by documenting space use and behavior of 36 females at the margin of the species’ range in Ontario, Canada.” They did this in 2006, 2007, and 2008 through the use of “global positioning system (GPS) telemetry to study their habitat use and movement,” in

an attempt “to document behavioral mechanisms indicative of adaptive responses to warm temperatures.” This work was conducted during periods of the year when ambient temperatures frequently exceeded known critical thresholds (-5°C in winter and 14°C in summer) that had been demonstrated by Dussault *et al.* (2004) to induce heat stress in moose.

Lowe *et al.* “detected no differences in habitat use relative to thermoregulation thresholds,” which they deemed to be particularly important during the summer, when they report the temperatures of all habitat classes greatly exceeded—by an average of 6°C , and by as much as 19°C in the first week of August 2006—the 14°C threshold for a large extent of the day and partially during the night. As a result, the three Canadian researchers conclude “moose in their southern range either ameliorate heat stress at a finer resolution than we measured or are more resilient to temperature than previously thought.”

In a contemporaneous study, Garroway *et al.* (2010) write, “many species have responded to contemporary climate change through shifts in their geographic ranges,” and “this could lead to increased sympatry [i.e., partially overlapping ranges] between recently diverged species, likely increasing the potential for hybridization.” They further note this phenomenon “can be positive if it increases genetic variability and creates new gene combinations that increase the potential to adapt.”

To test this hypothesis, between 2002 and 2004 Garroway *et al.* conducted more than 1,600 successful live-trappings of southern (*Glaucomys volans*) and northern (*Glaucomys sabrinus*) flying squirrels throughout portions of Ontario (Canada) and Pennsylvania (USA). From the hairs of these squirrels they extracted nuclear and mitochondrial DNA.

It already had been determined by Bowman *et al.* (2005) that *G. volans* had expanded its range from the south beginning in the mid-1990s in concert with a series of warm winters; the nine Canadian and U.S. researchers’ new findings indicate “the expansion of *G. volans* north into the *G. sabrinus* range in Ontario has resulted in the formation of a new hybrid zone.” In addition, their analyses suggest “the hybridization was recent, coinciding with the recent increase in sympatry.” They state, to their knowledge “this is the first report of hybrid zone formation following a range expansion induced by contemporary climate change.” These findings indicate yet another way in which living organisms can both physically (by shifting their ranges) and genetically (by hybridization) successfully confront the challenges global

warming may present.

Coulson *et al.* (2011) write “environmental change has been observed to generate simultaneous responses in population dynamics, life history, gene frequencies, and morphology in a number of species.” But they wonder, “how common are such eco-evolutionary responses to environmental change likely to be?” asking, “are they inevitable [and] do they require a specific type of change?”

The team of six researchers used theory and data obtained from a study of wolves in Yellowstone Park, which is located mostly in the U.S. state of Wyoming but also reaches into smaller parts of Montana and Idaho. They “used survival and reproductive success data, body weights, and genotype at the K locus (*CBD103*, a β -defensin gene that has two alleles and determines coat color), which were collected from 280 radio-collared wolves living in the park between 1998 and 2009.” They note “body weight and genotype at the K locus vary across U.S. wolf populations” and both traits influence fitness, citing the studies of Schmitz and Kolenosky (1985), Anderson *et al.* (2009), and MacNulty *et al.* (2009).

The four researchers say their results “do reveal that, for Yellowstone wolves, (i) environmental change will inevitably generate eco-evolutionary responses; (ii) change in the mean environment will have more profound population consequences than changes in the environmental variance; and (iii) environmental change affecting different functions can generate contrasting eco-evolutionary dynamics,” which suggests “accurate prediction of the consequences of environmental change will probably prove elusive.”

The general principles Coulson *et al.* found to apply to Yellowstone wolves should clearly apply to all other animals as well, suggesting the “climate envelope” approach used to predict shifts in the ranges of Earth’s many animal species—and sometimes their extinction—in response to IPCC-predicted global warming fails to accurately describe the way real animals respond to climate change in the real world.

Hof *et al.* (2012) note “it is supposed that the large expected climate change at high northern latitudes ... makes species in (sub)arctic regions particularly susceptible (Virkkala *et al.*, 2008; Sala *et al.*, 2000; Jetz *et al.*, 2007), especially the European part of the (sub)arctic, since this region is the most geographically complex with the most infrastructure and great cultural, social, and political heterogeneity (Nilsson *et al.*, 2010).” Hof *et al.* “assessed potential changes in the geographic distribution of all terrestrial

mammal species currently present in (sub)arctic Europe,” along with additional species that might possibly colonize the region from the south. They used “species distribution modeling, incorporating projections of future climate and vegetation, in order to provide a better insight into the magnitude of the risk mammal species are facing, and the potential community level changes they have to endure due to climate change.”

“Contrary to expectation,” the three Swedish researchers report their modeling of species distributions suggests “predicted climate change up to 2080 will favor most mammals presently inhabiting (sub)arctic Europe,” and “no species is predicted to go extinct.” Hof *et al.* conclude, “for most (sub)arctic mammals it is not climate change per se that will threaten them, but possible constraints on their dispersal ability and changes in community composition.”

Canale *et al.* (2012) say, “understanding whether, and to what extent, females can flexibly adjust their energetic investment to reproduction according to unpredicted food shortages is essential to predict whether organisms could compensate climate changes by plastic phenotype adjustments,” citing Bronson (2009), Moreno and Moller (2011), and Wingfield *et al.* (2011). The three researchers “experimentally tested the consequences of chronic-moderate and short-acute food shortages on the reproductive output of a small seasonally breeding primate, the grey mouse lemur (*Microcebus murinus*) under thermo-neutral conditions,” where “two food treatments were respectively designed to simulate the energetic constraints imposed by a lean year (40% caloric restriction over eight months) or by a sudden, severe climatic event occurring shortly before reproduction (80% caloric restriction over a month).” During this time they “assessed the resilience of the early stages of reproduction (mating success, fertility, and gestation to these contrasted food treatments, and on the later stages (lactation and offspring growth) in response to the chronic food shortage only.”

They found “food deprived mouse lemurs managed to maintain constant ... reproductive parameters, including oestrus timing, estrogenization level at oestrus, mating success, litter size, and litter mass as well as their overall number of surviving offspring at weaning,” although “offspring growth was delayed in food restricted mothers.” The three researchers say their results suggest “heterothermic, fattening-prone mammals display important reproductive resilience to energetic bottlenecks,” and “more generally, species living in variable and

Climate Change Reconsidered II: Biological Impacts

unpredictable habitats may have evolved a flexible reproductive physiology that helps buffer environmental fluctuations.”

Tveraa *et al.* (2013) write, “for caribou in Greenland earlier springs have been suggested to result in a lower reproductive success,” based on the assumption “*Rangifer* (caribou/reindeer) might be unable to adjust their timing of reproduction to the earlier surge of high quality food,” and this potential failure could “cause a mismatch between optimal forage conditions and the timing of reproduction.” Therefore, they state, “concerns have been raised regarding the future viability of *Rangifer* in Arctic and sub-Arctic tundra ecosystems.”

Tveraa *et al.* “analyzed a 10-year dataset of satellite derived measures of vegetation green-up, population densities, calf body masses and female reproductive success in 19 reindeer (*Rangifer tarandus*) populations in Northern Norway.” The four Norwegian researchers report “an early onset of spring and high peak plant productivity had positive effects on calf autumn body masses and female reproductive success,” and “the quantity of food available, as determined by the onset of vegetation green-up and plant productivity over the summer, were the main drivers of body mass growth and reproductive success.” Hence, they found no evidence for a negative effect of the speed of spring green-up, nor did they detect “a negative mismatch between early springs and subsequent recruitment.” Tveraa *et al.* conclude the “effects of global warming on plant productivity and onset of spring are likely to positively affect sub-Arctic reindeer.”

The studies presented above show the warming-induced extinctions of mammals that have been predicted to occur are highly unlikely to be realized in nature, and warming in fact opens new territories for mammal range expansions. In addition, rising atmospheric CO₂ concentrations may produce changes in the palatability of the trunk and branch tissues of certain trees that may protect them from being killed by hares and rabbits.

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5.7 Parasites and Other Diseases

One of the perceived great tragedies of CO₂-induced global warming is that rising temperatures will increase the development, transmission, and survival rates of parasites and other diseases in general, leading to biological interactions that will raise the prevalence of disease among animals in the future. This section examines that claim.

In a provocative paper analyzing the intricacies of this complex issue, Hall *et al.* (2006) begin by asking, “Will an increasingly warmer world necessarily become a sicker world?” They pose this question because “increased temperatures can accelerate the fitness of parasites, reduce recruitment bottlenecks for parasites during winter, and weaken hosts,” and “warmer temperatures may allow vectors of parasites to expand their range,” which would enable them to “introduce diseases to novel habitats,” which is frequently claimed about mosquitoes and malaria (see Section 7.2, this volume). They continue, “these doom-and-gloom scenarios do not necessarily apply to all taxa or all situations,” and “warming does not necessarily increase the fitness of all parasites.”

The four biologists and their statistician coauthor note the “virulence of parasites may not change, may decrease, or may respond unimodally to increasing temperatures (Stacey *et al.*, 2003; Thomas and Blanford, 2003).” They also observe, “vital rates increase with temperature until some optimum is reached,” and “once temperature exceeds this optimum, vital rates decline gradually with increasing temperature for some taxa, but rapidly for others,” such that “in some host-parasite systems, a parasite’s optimum occurs at cooler temperatures than the optimum of its host,” citing Carruthers *et al.* (1992), Blanford and Thomas (1999), and Blanford *et al.* (2003) on fungus-grasshopper associations. In such cases, “a host can use warmer temperatures to help

defeat its parasites through behavioral modification of its thermal environment.”

The situation sometimes can be even more complex than this: “warmer temperatures can also lead to shifts in temperature optima (Huey and Hertz, 1984; Huey and Kingsolver, 1989, 1993),” and “the exact evolutionary trajectory of host-parasite systems in a warmer world may depend sensitively upon underlying genetic correlation structures and interactions between host genotypes, parasite genotypes, and the environment (Blanford *et al.*, 2003; Thomas and Blanford, 2003; Stacey *et al.*, 2003; Mitchell *et al.*, 2004).” Consequently, they conclude, “longer-term response of the physiology of host-parasite systems to global warming becomes difficult to predict.”

The researchers also note “other species can profoundly shape the outcome of parasitism in host populations,” and “predators provide an important example” because predators “can actually inhibit epidemics by selectively culling sick hosts and/or by maintaining host densities below levels required for parasites to persist (Hudson *et al.*, 1992; Packer *et al.*, 2003, Lafferty, 2004; Ostfeld and Holt, 2004; Duffey *et al.*, 2005; Hall *et al.*, 2005).” Therefore, Hall *et al.* conclude, “global warming does not necessarily mean that disease prevalence will increase in all systems.”

Morgan and Wall (2009) echo many of the salient points raised in the Hall *et al.* paper and further elucidate the complex nature of this topic. With respect to the relationship between temperature and parasitic development, the two authors note, “just as development rates of many parasites of veterinary importance increase with temperature, so [too] do their mortality rates [increase].” They reiterate, “temperature will also affect mortality indirectly through the action of predators, parasitoids, pathogens and competitors, whose development and abundance are also potentially temperature sensitive,” so “the net effect of climate change could be complex and far from easily predicted.”

The two UK researchers suggest “several biological mechanisms (including increased parasite mortality and more rapid acquisition of immunity), in tandem with changes in husbandry practices (including reproduction, housing, nutrition, breed selection, grazing patterns and other management interventions), might act to mitigate increased parasite development rates, preventing dramatic rises in overall levels of diseases.” Because “optimum mitigation strategies will be highly system specific and depend on detailed understanding of interactions between climate, parasite abundance, host availability

and the cues for and economics of farmer intervention,” they conclude “there is a need for research that considers likely effects of climate change and mitigation strategies in terms of the whole host-parasite system, including anthropogenic responses, and not just in terms of parasite population dynamics.” One year later, two such papers were published, both attempting to account for the response of human behavior on parasite abundance and disease incidence.

Focusing on cutaneous myiasis (blowfly strike) in sheep, Wall and Ellse (2011) employed a stochastic simulation model “to examine the changes in the seasonal incidence of ovine cutaneous myiasis on farms in the United Kingdom and the likely effects of changes in husbandry and control strategies” in the face of projected changes in climate. The authors note “the ability of this model to successfully account for observed patterns of strike has been confirmed previously by comparison of predicted with observed strike incidence patterns observed on 370 farms in England and Wales,” citing Wall *et al.* (2002).

The two UK researchers report, “the simulations show that the range of elevated temperatures predicted by current climate change scenarios result in an elongated blowfly season with earlier spring emergence and a higher cumulative incidence of strike,” and “overall, higher temperatures increased strike incidence disproportionately in ewes in early summer, but had relatively less direct effect on the pattern of lamb strike incidence,” noting “a 3°C increase in average temperature approximately doubles the cumulative incidence of strike in lambs but results in four times more strikes in ewes.” However, as the researchers conclude in the abstract of their paper, “the simulations suggest that integrated changes in husbandry practices are likely to be able to manage expected increases in strike, given the range of climate changes currently predicted.” They explain in the body of the paper, “modest changes in husbandry practices should be able to manage expected increases in strike, under the range of climate changes currently predicted,” demonstrating “consideration of the likely impact of climate change must take into account animal management practices as well as parasite biology (Morgan and Wall, 2009).”

Working with two additional co-authors on the same host and parasite, Wall *et al.* (2011) came to a similar conclusion, reporting, “the models suggest that simple changes in some husbandry practices, such as shearing or trap use, could have an important effect in reducing early season ewe strike incidences,” and “practical measures exist which, with modest

Terrestrial Animals

changes in husbandry practices, should be able to manage expected increases in strike.” The key message of this latter work is the authors’ conclusion that “simple extrapolations of the known effects of temperature on ectoparasite development,” in an attempt to “predict changes in disease incidence in a warmer climate,” is simply “too simplistic.” They emphasize “attempts to predict the likely impact of climate change on disease incidence must take into account changes in farmer behavior and animal management practices as well as parasite biology.”

Baffoe *et al.* (2012) write, “with the prospect of warmer temperatures as a consequence of ongoing climate change, it is important to investigate how such increases will affect parasitoids and their top-down suppression of herbivory in agroecosystems.” They studied a parasitoid that afflicts a common beetle that feeds on several short-rotation species of commercially coppiced willow trees in northern and central Europe, a trophic cascade described in more detail by Peacock *et al.* (1999), Bjorkman *et al.* (2003), and Dalin (2011). Baffoe *et al.* conducted laboratory experiments in which they “studied how the performance and biocontrol efficiency of the willow ‘bodyguard’ *Perilitus brevicollis* Haliday (Hymenoptera: Braconidae) were affected at different constant temperatures (10, 15, 20, 25°C) when parasitizing a pest insect, the blue willow beetle (*Phratora vulgatissima* L., Coleoptera: Chrysomelidae).” They did this by focusing on “the parasitoid’s thermal threshold for development, development rate, adult body size, survival rate and the herbivore’s consumption rate.”

The four Swedish scientists report parasitism had no impact on herbivory at 10°C, but “parasitoid performance (survival and development rate) generally increased with increasing temperature up to 20°C.” In addition, “the feeding capacity of the studied parasitized herbivores is reduced more at high than low temperatures.” Thus, “these data suggest that *P. brevicollis* should become a better biocontrol agent if temperatures increase,” a transformation that should have substantial positive consequences for willow trees in northern and central Europe, as well as for the enterprise of their commercial harvesting.

Bentley and Burgner (2011) examined the host/parasite relationship between juvenile sockeye salmon (*Oncorhynchus nerka*) and the tapeworm *Triaenophorus crassus* in an Alaskan watershed that had experienced a 1.9°C increase in summer water temperature over the prior 46 years. At the beginning of their experiment, Bentley and Burgner hypothesized the warming of the region “would have

resulted in a corresponding increase in fish metabolism, and thus potential consumption rates, that would increase infestation rates of the tapeworm *Triaenophorus crassus*.” To test their hypothesis, they compared infestation rate data for *T. crassus* collected between 1948 and 1960 with similar data obtained in 2008 and 2009 from the Wood River system of Bristol Bay, Alaska.

The two U.S. researchers from the University of Washington’s School of Aquatic and Fishery Sciences report, “comparing the average summer air temperature to the parasite prevalence of juvenile sockeye salmon, we found no significant relationship over the fifteen years of collected data.” Moreover, “evaluating the influence of average summer air temperature on the parasite infestation rates of juvenile sockeye salmon, we again found no significant relationship for either parasite abundance or parasite intensity.” They note, “when we compared the 13 years of historic parasite prevalence to equivalent data collected in 2008 and 2009, we did not find a statistically significant positive long-term trend in the data,” and “the parasite abundance of examined sockeye salmon smolts also did not exhibit a statistically significant long-term trend using the eight years of historic data and the two years of contemporary data.” Finally, “evaluating the relationship between time and parasite intensity produced similar results as the other five comparisons, with there not being a statistically significant positive relationship.”

Bentley and Burgner conclude their data demonstrate “the complex effects of warming have not summed to generate a measurable change in the infestation rates of juvenile sockeye salmon in the Wood River system.” Given the many factors involved in host/parasite interrelationships, together with their great complexities, it is quite possible global warming will never significantly impact parasite infestation rates in the animals they attack.

Shifting from parasites to infectious diseases, Kampen and Werner (2010) write, “with few exceptions, vector-borne diseases have long been considered of minor importance in central and northern Europe.” However, they note, “since the advent of bluetongue disease (BTD) in 2006, and the 2007 chikungunya fever outbreak in Italy, this attitude has changed.” Focusing on BTD, a non-contagious insect-borne viral disease of ruminants (mainly sheep, but also affecting antelope, buffalo, cattle, deer, dromedaries, and goats) caused by the bluetongue virus (BTV), Kampen and Werner describe what is known about the outbreak of this

serious animal disease in central Europe.

The two German researchers report “BTD was the first ‘exotic’ disease to arrive,” but “it did not slowly spread northwards but jumped in through a still unknown entry point.” It all started, as they describe it, “with about 2000 affected ruminant farming facilities in 2006 in the central western part of Europe,” where the BTV–8 virus—which they say “had never been observed in Europe before,” and for which DNA sequencing data suggested sub-Saharan Africa as its most likely point of origin—“managed to overwinter and spread in all directions in 2007, producing almost 60,000 outbreaks (farms affected) in ten European countries up to early 2008.” And now, they say, the BTV–1 virus strain “appears to be approaching from the south, with some 4900 outbreaks in France in 2008,” reiterating, “nobody had expected a novel and independent virus introduction into central Europe together with indigenous biting midges able to transmit BTV.”

As for possible routes of introduction of the virus, they mention BTV-positive ruminants imported either legally or illegally, virus-carrying midges transported by wind over hundreds of kilometers, accidental importation by ship or aircraft, contaminated vaccines, and trade with the products of infected animals.

Kampen and Werner conclude, “it is due to continuing globalization rather than to climate change that even central and northern Europe are at risk of new pathogens as well as vectors of disease entering and establishing.”

Conte *et al.* (2009) note, “the midge *Culicoides imicola* is the principal vector of bluetongue virus (BTV) that causes an infectious disease of domestic and wild ruminants,” and “over the last ten years, BTV has invaded Mediterranean countries and much of Northern Europe,” inducing several scientists to contend the BTV vector had expanded its range northward “because of rising temperatures,” as suggested by Mellor (2004), Purse *et al.* (2005), and Mellor *et al.* (2008). However, Goffredo *et al.* (2003) made a careful examination of *Culicoides* population data in Italy prior to 2000 and determined “trapping conditions of previous collections would have had very little chance of catching *C. imicola*” or detecting its presence, suggesting there was insufficient evidence for a warming-induced northward expansion of the BTV vector because it already may already been present there but undetected.

In response to even earlier fears of a potential BTV invasion, a national surveillance program for *C. imicola* had been established in Italy in 2000, where

70,000 light-trap collections were made at about 3,800 sites. Using the first year of data obtained from this program, Conte *et al.* defined the spatial distributions of three *C. imicola* infection zones: zone I (endemicity), zone II (transition), and zone III (absence). Using data from 2002–2007, they quantified how *C. imicola* populations evolved through time in these three zones, working under the logical assumption that “a species that is undergoing geographical range expansion should have a population that remains stable over time in zone I and increases in zones II and III.”

The three researchers say their results indicate there was “no detectable range expansion of *C. imicola* population in Italy over the past six years.” They report “a weak, but significant reduction was observed in the transition zone.” Conte *et al.* therefore conclude their data “support the hypothesis that the spread of BTV in Italy is not because of the geographical expansion of its main vector, but to a modification of the interaction between the virus, the vector and the environment, as may also have been the case in northern Europe.” They say their results show “precautions should be taken when inferring range progression for species requiring highly targeted forms of sampling and for which a constant probability of detection over time should be established.” This research demonstrates it is easy to blame global warming for the poleward expansion of a vector-spread disease, but quite another thing to prove that claim.

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5.8 Polar Bears

- 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 commercial hunting by humans, which has historically taken a huge toll on polar bear populations.

In its contribution to IPCC's *Fourth Assessment Report*, Working Group II claimed global warming is "inducing declining survival rates, smaller size, and cannibalism among polar bears" (IPCC, 2007-II). It predicted a bleak future for the species if atmospheric CO₂ concentrations continue to rise. However, 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 commercial hunting by humans, which has historically taken a huge toll on polar bear populations.

Polar bears evolved from brown bears (*Ursus arctos*). While it was formerly thought this speciation event occurred sometime in the past 400,000 years and probably no more than 200,000 years ago (Arnason *et al.*, 1995; Davis *et al.*, 2008; Harington, 2008), that picture has now changed. The oldest polar bear fossil ever found (dated to 110,000–130,000 years old) was reported in 2008 (Ingolfsson *et al.*, 2008) and a complete mitochondrial DNA (mtDNA) sequence of it was generated two years later (Lindqvist *et al.*, 2010). This discovery spawned a suite of papers on polar bear genetics that fail to agree when polar bears arose as a distinct species: Edwards *et al.* (2011) suggest a possible range of 400,000 to two million years ago; Hailer *et al.* (2012), suggest a date of about 600,000 years ago; and Miller *et al.* (2012), suggest this event occurred four to five million years ago.

Although there is some disagreement about the onset of this species, it is clear that because the oldest polar bear fossil is at least 110,000–130,000 years old, polar bears have survived at least one glacial-interglacial cycle and perhaps as many as 10 or more.. Focusing on the last major interglacial (MIS 5e, the Eemian, which lasted from ca. 130,000–115,000

years ago), there not only appears to have been less winter Arctic ice than today (including no ice in the Bering Sea), but late summer ice was reduced to a remnant off northern Greenland and Ellesmere Island (Polyak *et al.*, 2010). During the current interglacial, or Holocene, there were at least two warm periods (the Early Holocene Climatic Optimum and the Medieval Warm Period) when sea ice was less extensive than it is now (Atkinson, 2009; Dyke and England, 2003; Dyke *et al.*, 1996; Kaufman *et al.*, 2004; Polyak *et al.*, 2010; Steffensen *et al.*, 2008).

Polar bears obviously survived large-scale and often sudden climate changes in the historic past, such as those described above. This does not mean their populations remained constant throughout this period; their numbers likely rose in some periods and declined in others. But past changes in climate have not led to their extinction, which leads to the question: Why would temperature changes predicted to be of the same scale or less than those that occurred in the past be projected to cause a near-future extinction of polar bears?

In order to ascertain whether there are indeed risks to polar bears from model-predicted increases in global temperature and associated sea ice decline, researchers have examined various aspects of polar bear population dynamics and life history traits as they relate to temperature changes that have taken place over the past 30 years. Several of their findings are presented in the subsections below, where it is seen that polar bears are well-equipped to adapt with the challenges they may face as a result of any CO₂-induced global warming.

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5.8.1 Population

The world’s polar bear populations live in the wild only in the Northern Hemisphere on land and sea ice in the area surrounding the North Pole. Polar bears tend to stay in, or return to, local areas (Taylor and Lee, 1995; Bethke *et al.*, 1996; Taylor *et al.*, 2001), although some migration is known to occur (Messier *et al.*, 2001; Amstrup *et al.*, 2004). Their range expands and contracts with the accretion and contraction of sea ice with the seasons, with bears moving south during the winter as sea ice advances (Amstrup *et al.*, 2000). In some areas (e.g., Hudson Bay, Foxe Basin, Baffin Bay, and James Bay) polar bears move from sea ice to land for several months during the summer open-water season (Ferguson *et al.*, 1997; Lunn *et al.*, 1997; Taylor *et al.*, 2001, 2005).

The total polar bear population is unknown, since its numbers in the Arctic Basin, East Greenland, Chukchi Sea, and the Kara Sea have never been counted (Aars *et al.*, 2006; Obbard *et al.*, 2010). The official estimate has been given as 20,000–25,000 since 2005 (Aars *et al.*, 2006; Obbard *et al.*, 2010), despite claims of declining numbers. The total has remained stable despite the fact that the former estimate for the Chukchi Sea was reduced from 2,000 to zero between 2005 and 2009.

There is even less certainty regarding the number of polar bears in the 1950s and 1960s, with most estimates around 5,000 to 10,000. Virtually all scientists agree polar bear populations have grown since the 1970s. For example, Derocher (2009) has stated, “after the signing of the International Agreement on Polar Bears in the 1970s, harvests were controlled and the numbers increased. There is no argument from anyone on this point.” Ramsay and

Stirling (1988) wrote, “if a population was reduced in the past and the causal agent was no longer in effect, then the population would be expected to recover to its approximate pre-decline level.”

Even though polar bear populations grew during the second half of the twentieth century, a time when IPCC claims there was a rapid increase in global temperatures and loss of sea ice, Derocher and others say this population growth is evidence of the effects of hunting bans and quotas and does not contradict their claim that warming temperatures and melting sea ice have hurt polar bear populations. They point, with apparent merit, to negative demographic impacts on polar bear populations identified in the Southern Beaufort Sea and in Western Hudson Bay, and possible adverse nutritional impacts in the Northern Beaufort Sea and Southern Hudson Bay, due to changes in local sea ice conditions.

But this observation falls short of providing evidence global warming threatens polar bears with extinction. If anthropogenic global warming were a real threat to polar bears, its effects should be observable throughout the Current Warm Period, not just the last few years, and the warming would have to affect more than only a small number of subpopulations, as appears to have been the case (see discussion below). The modified argument—that global warming only in recent years is negatively affecting only some subpopulations of polar bears but not others—is not what is being reported in daily newspapers or even what IPCC claims. The real-world long-term trends in polar bear populations contradict what would be expected if the theory of anthropogenic global warming were true.

The polar bear population is divided into 19 subpopulations for management purposes (see Figure 5.8.1.1). In 2005, according to the IUCN Polar Bear Specialist Group, five subpopulations were declining, five were stable, two were increasing, and on seven there was insufficient data on which to base a decision (Aars *et al.*, 2006). Significantly, four of the five subpopulations listed as declining were at risk due to hunting, not reduced sea ice (Aars *et al.*, 2006). This is hardly a picture of a species in steep decline, or even in decline at all. It certainly does not provide an empirical basis for predictions of imminent extinction.

More recently, this view has changed somewhat (Obbard *et al.*, 2010). Seven subpopulations are now considered data-deficient (no trend given, including one that was rated as increasing in 2005), seven are listed as declining (including one subpopulation considered to have ‘data deficient’ status and

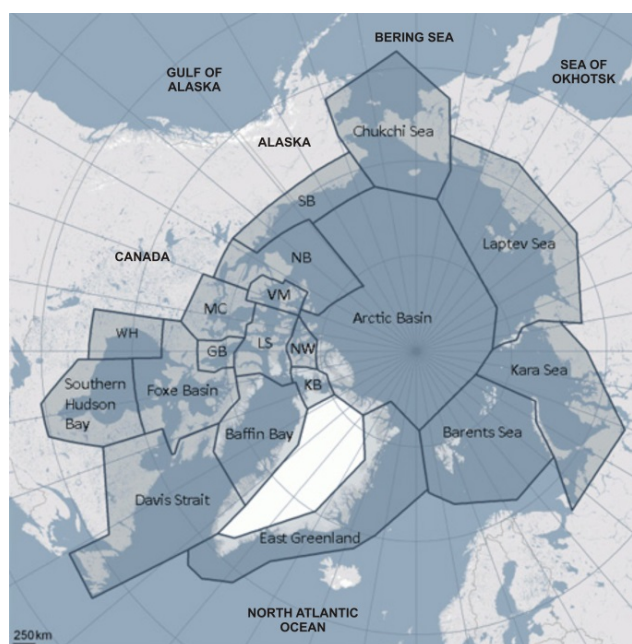


Figure 5.8.1.1. Polar bear subpopulations, as defined by the IUCN Polar Bear Specialist Group. Modified from map provided by the PBSG (2009). GB, Gulf of Boothia; KB, Kane Basin; LS, Lancaster Sound; MC, M'Clintock Channel; NB, Norwegian Bay; VM, Viscount Melville; NB, Northern Beaufort; SB, Southern Beaufort; WHB, Western Hudson Bay.

another—the Chukchi—that has never been surveyed but is determined to have a “reduced” status and declining trend based on sea ice reductions and suspected poaching), three are considered stable, and one is considered to be increasing. Suspected overhunting and/or poaching are considered the primary reason five of the seven declining populations are at risk, based on modeled projections over the next 10 years. For another, declines in body condition, modeled over the next 10 years, are the basis for it being given a “declining” trend (Southern Beaufort).

Only one of the seven declining populations (Western Hudson Bay) has documented a statistically significant decline in population numbers. Obbard *et al.* state, “our status report currently indicates that two subpopulations (WH [Western Hudson Bay] and SB [Southern Beaufort]) have likely declined due to climate change. It is thought that there may also be some impacts of climate change in other populations (CS [Chukchi Sea], SH [Southern Hudson Bay]), however data are not conclusive or available.” New research in the Chukchi by Rode *et al.* (2014) suggests bears there are in good condition and reproducing very well, indicating projected negative

Terrestrial Animals

effects due to declining summer sea ice have not materialized.

In addition, whereas the decline in Western Hudson Bay polar bear numbers (about 22%) is stated to have occurred between 1987 and 2004 (Regehr *et al.*, 2007a), Obbard *et al.* (2010) acknowledge this population had been stable prior to 1998 (Stirling *et al.*, 1999). This means the statistically significant decline really occurred between 1998 and 2004 (seven years), during which there was no apparent trend in sea ice breakup dates (Regehr *et al.*, 2007a), although both 1998 and 2003 were relatively early breakup years (occurring about June 14 both years, according to the new method used by Cherry *et al.*, 2013). If the population was still on a declining trend after 2004, there should be fewer polar bears in Western Hudson Bay now than in 2004.

No data have yet been made available from mark-recapture studies undertaken between 2005 and 2011, but an aerial survey, similar to those conducted in the Barents Sea and Baffin Bay, was conducted by the Nunavut Government in 2011 (Stapleton *et al.*, 2012a). Stapleton and colleagues' estimate of the current population number is about 1,000 (95% confidence interval, range of 715–1398). Although the two methods (mark-recapture and aerial survey) cannot be directly compared, the authors say the aerial survey was “consistent with the 2004 capture-based estimate but inconsistent with projections suggesting continued decreases in abundance.” So while Obbard *et al.* (2010) say “data from this subpopulation [WHB] provide the best indications of how polar bears respond to the negative effects of climate warming,” it appears the population has not continued to decline as predicted.

Similar aerial surveys have been done to the north, in Foxe Basin by Stapleton *et al.* (2012b). In that study, the authors undertook a helicopter survey throughout the territory of Foxe Basin polar bears in the summers of 2009 and 2010, concluding “our abundance estimates were highly consistent between years and survey methods, (~2,580 bears (95% CI: about 2,100–3,200), and were comparable to an estimate from the early 1990s. Our results suggest that Nunavut's management regime has enabled polar bear abundance in FB to remain relatively stable.”

Hunting historically has been the greatest threat to polar bear populations. The arrival of snowmobiles, helicopters, and high-powered rifles led to “harvest” levels that were not sustainable (Taylor *et al.*, 2002; Taylor *et al.*, 2006; Taylor *et al.*, 2008). Hunting was largely unregulated until passage of the 1974 International Agreement for the Conservation of Polar

Bears and Their Habitat. Greenland didn't institute a quota for polar bear hunting until 2006 (Polar Bear Technical Committee, 2006). Annual kills for most populations now have been substantially reduced, but it will take at least 20 years for populations to recover.

The range of polar bears is affected by changes in climate but not in a linear fashion with temperature or the extent or thickness of sea ice. Sea ice extent and thickness are only indirectly related to polar bear populations. Only two subpopulations—the Western Hudson Bay (WH) and Southern Beaufort Sea (SB) populations—may have declined (Ferguson *et al.*, 2005; Regehr *et al.*, 2006, 2007a,b; Rode *et al.*, 2007; Hunter *et al.*, 2007); one of these (WH) is disputed (Dyck *et al.*, 2007), and the other (SB) is not a statistically significant decline.

Taylor and Dowsley (2008) summarized recent population surveys as follows: Of six polar bear populations recently evaluated during the climate warming period, two populations appear to have been reduced (WH, SB), two populations appear to have remained constant (SH, NB), one population appears to have increased (DS), and one was abundant but the information was not sufficient to estimate a trend (BS). Seven other populations (VM, LS, NW, BB, KB, MC, GB) surveyed during the period of climate warming had vital rates sufficient to sustain substantial rates of harvest (*i.e.*, hunting) at the time they were studied. Information from a Foxe Basin (FB) population survey was sufficient to document the population had remained abundant although it had been harvested at a relatively high rate and the survival and recruitment estimates necessary to determine trend were not available. The biological information on the remaining four populations (CS, LS, KS, EG) and the few bears that may inhabit the Arctic Basin is insufficient to suggest anything about current numbers or trend.

Taylor and Dowsley say “the increase to current high numbers of polar bears in the Davis Strait has occurred during the current warming period, and has occurred with declining sea ice conditions that are sometimes less than 40% coverage at winter maximum (Stirling and Parkinson, 2006). Clearly the DS bears do manage to hunt successfully in unconsolidated pack ice.” They comment, as do Dyck *et al.* (2007), that polar bears have been observed to successfully hunt seals in tidal flats along shores during ice-free periods. “Considered together,” Taylor and Dowsley conclude, “these demographic data do not suggest that polar bears as a species are headed for extinction in the next three generations (45 years)

or the foreseeable future. The demographic data do support increased monitoring, and augmenting periodic population surveys with ecological and behavioral studies.” They also observe, “to date, no population has been expatriated due to climate change effects, so the effect of decreased densities, alternative food sources, or behavioral adaptation to less ice on population persistence is not known.”

Stirling and Derocher (2012) contend “polar bears will largely disappear from the southern portions of their range by mid-century.” Western Hudson Bay is clearly included in this subset of all polar bear territory, as it lies below the Arctic Circle. But what other portions of the range lie below this point? Southern Hudson Bay, the Bering Sea, most of the Chukchi Sea, and most of Davis Strait also lie below the Arctic Circle; their population status already has been discussed. However, Southern Hudson Bay (SH), which extends to about 52°N, should presumably show more pronounced effects from global warming than even Western Hudson Bay to the north.

Obbard *et al.* (2010) say in their summary, “recent analysis of coastal survey data (Stirling *et al.* 2004) suggests polar bear numbers in SH have remained unchanged in recent years” and they consider this population to be one of three “stable” polar bear subpopulations. In a more comprehensive study of Southern Hudson Bay bears, Obbard *et al.* (2007) state, “reductions in survival of juvenile, subadult and senescent polar bears were demonstrated for the WH population (Regehr *et al.*, 2007), but were only weakly supported by our data.” Obbard *et al.* (2007) also note, “abundance in the Southern Hudson Bay population was unchanged between two intensive capture-recapture periods, which were separated by almost 20 years (1984–86 vs. 2003–05. This was so despite the evidence for a decline of 22% in abundance for the neighboring Western Hudson Bay population over roughly the same period (*i.e.*, 1987–2004; Regehr *et al.*, 2007).” They conclude, “it appears that changes in environmental factors such as sea ice distribution and duration ... have not yet resulted in unambiguous changes in survival or to a consequent reduction in population size in the SH population to this date.” This is in spite of the fact that Obbard *et al.* (2006), in a dedicated study of Southern Hudson Bay polar bears, found body condition (fatness) was “significantly poorer for bears captured from 2000 to 2005 than for bears captured from 1984 to 1986,” and concluded, “the significance of a trend toward poorer body condition over time is unknown.” Nonetheless, in 2009 the province of

Ontario listed Southern Hudson Bay polar bears as a “threatened” species (Obbard *et al.*, 2010).

The deep water over the Arctic Basin is often assumed to be of such low productivity (*e.g.*, Amstrup *et al.*, 2007; Fischbach *et al.*, 2007; Obbard *et al.*, 2010) that it is largely unsuitable for polar bears except as a transit corridor. This assumption is contradicted by measurements of significant amounts of phytoplankton and ice algae (*e.g.*, Gosselin *et al.*, 1997; Stirling, 1997) as well as reports at the North Pole of “small fish” (estimated as 5–8cm, presumably young polar cod, *Boreogadus saida*) thrown up by icebreakers, and algal growth visible on the underside of broken ice chunks (Todd *et al.*, 1992). Polar cod and their prey are the food of ringed seals and are known to live under ice of all types, including multiyear and first-year drifting sea ice regardless of the ocean depth (Lønne and Gulliksen, 1989). The cracks (“leads”) that continuously develop in moving multiyear ice allow thinner first-year ice to form, creating habitat for seals and thus potential food for polar bears (Stirling, 1997). Although the Arctic Basin is undoubtedly less productive than continental shelf areas, it may be more productive than has been assumed.

Ovsyanikov (2010) summarizes preliminary results of two distinct pieces of polar bear research conducted by Russian biologists from 2005–2008: on Wrangel Island in the Chukchi Sea and in the central Arctic Basin. Although the Wrangel Island work was a continuation of population monitoring that has been ongoing since 1990, the Arctic Basin surveys conducted in 2005 and 2007 were the first of this kind.

The late-summer Arctic Basin surveys were split between two years, each taking a different route: the 2005 expedition surveyed northward from Wrangel Island (in the far eastern Russian Arctic), on both sides of the 180° meridian up to 79°15' N, and the 2007 trip surveyed north from Franz Joseph Land (in the far western Russian Arctic, at about 81°N, 60°E), to the North Pole and back. Observations were taken 24 hours/day from the ship bridge for the duration of the trips, and sightings of both bears and ringed seals were recorded.

In 2005, 18 bears were seen north of Wrangel, 12 of these above 75°N, which marks the edge of the continental shelf at this location. Ten of the bears seen were in four family groups, and three of these families were observed north of the continental shelf. All were in good physical condition. A female and her single cub-of-the-year were observed feeding on a ringed seal at 78°50.20' N, 177°27.40' W, where

Terrestrial Animals

water depth under the ice was 1,500 m. In addition, seven tracks of lone bears were recorded north of the continental shelf. A total of 48 ringed seals were observed from Wrangel Island to 79°15' N, more than half of these between 78°–79° N.

In 2007, the survey ship worked the other side of the Arctic Basin, north of Franz Joseph Land, where the continental shelf ends at around 82°–83° N (Weber, 1983). Seven polar bears were sighted beyond 81° N, all of them in good condition and all recorded on fields of substantial ice. One female was observed and photographed at the North Pole on 1–2 August 2007. A total of 61 tracks of single bears were also recorded, with a concentration around 82° N. Eleven ringed seals also were observed, five between 82° and 83° N, three between 83° and 87° N, and three between 89° and 90° N (including one at the North Pole). A lower proportion of the observations of seals and bears were noted beyond the continental shelf north of Franz Joseph Land than were sighted north of Wrangel Island but a few seals and at least one bear were recorded close to, or at, the North Pole.

Ovsyanikov suggests ringed seals living at the periphery of the Arctic Ocean move into the central Arctic Basin as the pack ice recedes in late summer and polar bears that choose to stay on the pack ice (rather than moving onto land) move along with the seals and the ice into the central Arctic beyond the continental shelves. Previous reports also have documented the presence of both ringed seals (Todd *et al.*, 1992) and polar bears in the central Arctic Basin (Van Meurs and Splettstoesser, 2003), and in 1992–1993, a female tracked via satellite by Durner and Amstrup (1995) migrated from Prudhoe Bay in the southern Beaufort to northern Greenland via the central Arctic Basin (going as far north as 88°).

Ovsyanikov's Arctic Basin survey confirms ringed seals and polar bears do not require ice that is positioned over shallow, continental shelf waters, although higher densities of both species undoubtedly exist in such areas (e.g., Derocher *et al.*, 2004). Ovsyanikov's study, although limited, is the first systematic look at polar bears and ringed seal abundance within the Arctic Basin. Further surveys may reveal the Arctic Basin is a more important habitat for polar bears than has been assumed, especially given the new finds of significant blooms of phytoplankton under thick annual ice (Arrigo *et al.*, 2011), discussed previously.

Years prior to the discovery reported by Arrigo and colleagues in 2011, Amstrup (2003) said, "Despite apparent preferences for the more productive waters near shorelines and polynyas (areas

of persistent open water), polar bears occur throughout the polar basin including latitudes >88°N (Stefansson 1921; Papanin 1939; Durner and Amstrup 1995)." Amstrup also notes "the frequency of recent observations deep in the polar basin, however, mandates recognition that a separate stock could occur there." Although polar bear research in the remote and formidable Arctic Basin has so far been marginal, evidence to date suggests a significant population of polar bears live their entire lives in the Arctic Basin, although their official contribution to the global population estimate is still zero (Obbard *et al.*, 2010).

Polar bears are adapted to extremes of both warming and cooling that can and do occur. Under hostile climate conditions, polar bears will move out of affected areas and return when conditions improve and when the sea ice is neither too thick nor too ephemeral. If local sea ice changes continue for whatever reason, some subpopulations may be expatriated or decline to low numbers. However, polar bears as a species are not in danger of extinction and have not reached worrying levels of population decline.

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5.8.2 Life History

5.8.2.1 Choice of Den Location by Females

In the fall, pregnant polar bear females make maternity dens in drifted snow, either on land or drifting pack ice, where they hibernate over the winter (Mauritzen *et al.*, 2001). The tiny cubs are born during hibernation (from mid-November to January) and are nursed within the den for at least two months. Mothers and cubs emerge around March-April. Individual females appear to have preferences for den location: females that den on land and those that den on ice are known in most subpopulations studied, except western Hudson Bay and around Svalbard in the Barents Sea, where all females appear to den on land (Mauritzen *et al.*, 2001; Ferguson *et al.*, 2000; Fischbach *et al.*, 2007; Lentfer, 1975; Zeyl *et al.*, 2010). According to Amstrup (2003), although it was once believed there were several high-density “core” areas for denning, “over much of their range, we now

know, polar bears den in a more diffuse pattern where individual dens are scattered over broad reaches of habitat at low density.” And as Zeyl *et al.* (2010) have stated, “long-term fidelity of denning areas and faithfulness to denning substrate (*i.e.*, land vs. ice) has been observed.”

Do females switch their den locations from one year to the next? If so, what is the level of loyalty (“fidelity”) to either the area (the particular place on land) or the substrate (land vs. ice)? As all Svalbard-area females appear to den on land, the issue addressed in the paper by Zeyl *et al.* was whether mothers switched from one denning area to another within the Svalbard region, and whether related individuals (especially mothers and daughters) tended to den in the same area.

The authors used data collected from a technique called “mark-recapture,” along with results from analysis of mitochondrial DNA (mtDNA, the kind inherited from mothers) to investigate the amount of loyalty individual female polar bears had to five denning areas around Svalbard. They also used these data to address whether any loyalty to a specific area was transmitted from mothers to daughters to such an extent that it would result in genetic clustering of mtDNA haplotypes in different den areas.

The results of the study indicate female polar bears have a moderate degree of loyalty to their chosen den areas (3/13 females switched areas from one year to the next) and daughters had a tendency to den in the same areas as their mothers (only 2/8 did not). There was not, however, the kind of genetic clustering expected if such loyalty had been ongoing over a long period of time. Although the distances between successive mark-recapture locations for Svalbard females were similar to distances reported for land-denning females in western Hudson Bay (23.7 km vs. 34 km, respectively), these were much lower than documented for females in the Beaufort Seas (308 km), where a significant proportion of bears den on sea ice (Amstrup and Gardner, 1994), the authors note. Zeyl and colleagues also note the level of denning site loyalty demonstrated by female polar bears on Svalbard is markedly lower than recorded for brown bears, their closest living relatives (who of course always den on land).

Zeyl and colleagues suggest female polar bears may switch the precise location of their dens from one year to the next depending on prevailing snow or sea ice conditions. In a similar study, Fischbach *et al.* (2007) documented some females who switched between pack ice dens and land dens (*i.e.*, a switch of substrate type). Zeyl *et al.* suggest there is more

flexibility than previously assumed in den site choice among polar bear females.

The demonstrated willingness of polar bear females to switch den locations from one year to the next, despite a general tendency towards den site loyalty, almost certainly gives them the flexibility they need as a species to persist in the face of sea ice conditions that vary from year to year. The ability of polar bear females to shift from one den site location to another or one substrate to another is just one aspect of the kind of plasticity needed to survive in this habitat.

Amstrup and Gardner (1994) stated, “contrary to previous hypotheses (Stirling and Andriashek, 1992), substantial polar bear denning occurs in the Beaufort Sea region of northern Alaska and adjacent Canada. Bears that den on pack ice are subject to risks not encountered by bears that den on land. Unstable, moving ice caused early abandonment of dens and, apparently, loss of cubs. However, the persistence of pack-ice denning indicated that those risks are not overwhelming.”

As one Russian polar bear researcher commented years ago regarding bears in the eastern Russian Arctic (Kochnev, 2006), “our investigations on Wrangel Island have shown the polar bear is a very plastic animal: it can rapidly change its way of life, spatial distribution and behavior according to new ecological conditions.” Zeyl and colleagues (2010) seem to agree, stating, “females are likely able to change denning locations if unsuitable ice conditions prevent them from reaching their preferred denning areas. We consider this plasticity an important attribute of polar bears when facing climate change.”

Working in the same Southern Beaufort region as Fischbach *et al.* (2007), Schliebe *et al.* (2008) found in 2000–2005 an average of 3.7% of polar bears spent time on land between mid-September and the end of October; the rest were on the pack ice. They state, “across all years and survey dates between mid-September and the end of October, an average of 4 ± 2 bears/100 km (57 ± 28 bears total) were observed. Thus, a maximum of 8.0% and an average of 3.7% of the estimated 1,526 bears in the SBS population (Regehr *et al.*, 2006) were observed on land.” This means there were, on average, only 56 bears on land in the fall each year (out of 1,526 bears), suggesting most pregnant females in the Southern Beaufort made their dens in the pack ice and never came to land in fall. Schliebe *et al.* conclude, “overall, we did not detect an increasing trend in polar bear densities along the Beaufort Sea coast of Alaska during the six years of this study,” indicating bears were not being

forced on land due to declining summer ice coverage.

These studies make it apparent an unknown number of polar bear females den in the offshore pack ice and many Southern Beaufort bears never set foot on land. Amstrup (2003), in his discussion of pack-ice denning in the Beaufort Sea, says this about offshore denning: “despite the absence of conclusive reports, sea-ice denning probably occurs at some level in other areas.” Amstrup suggests these areas include the Arctic Basin, given “the recent recognition of a possible polar basin stock of polar bears.” In addition, he suggests the “linear coastline of central Arctic Russia may be more similar to the Beaufort Sea than other areas, and hence may be another area where sea-ice denning is common.”

Given the known and predicted use of offshore ice for denning, it is rather astonishing that the report supplied in support of the listing of the polar bear as a threatened species in the United States (Bergen *et al.*, 2007) modeled only future changes to terrestrial denning habitat. Since those models did not address offshore sea ice denning habitat at all, it means those studies ignored a huge amount of polar bear habitat that is likely critical to their resilience to changing sea ice conditions.

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5.8.2.2 Mortality Due to Den Collapse

In a list of suggested risks to polar bears in a warmer world, Derocher *et al.* (2004) state, “An additional concern specific to female polar bears in dens with altricial cubs is the possibility that rain might become more frequent in late winter and cause the snow cover over dens to collapse and suffocate the occupants.” Stirling and Derocher (2012) provide more up-to-date and detailed information on this concern. Their paper summarizes all of the known anecdotal reports of rain on snow events that led to the collapse of polar bear maternity dens and/or ringed seal birthing lairs. They state “such rain on snow events are predicted to increase as the climate warms in the Arctic.”

Stirling and Derocher describe four incidents: one case of a maternity den collapse (involving a six-year-old, probably first-time mother and two cubs three to four weeks old) in the southern Beaufort in 1989, apparently caused by warm weather followed by heavy snow in late January, reported originally by Clarkson and Irish (1991); a rain event in early March 1990 in western Hudson Bay that was not associated with den collapses and which led to “no evidence of dead bears the following summer”; rain and warm

weather in early April 1979 in southeastern Baffin Island that resulted in “increased predation mortality of ringed seal pups” by polar bears and Arctic foxes; a warm period, also in southeastern Baffin Island, in late April 1990, that was reported to have generated a tripling of polar bear predation success on newborn ringed seal pups because ringed seal birthing lairs were easier to break or had melted and collapsed.

These details indicate each of the den collapse incidents occurred in 1990 or before, not in more recent years as might be expected if such events were associated with warmer temperatures. It appears there has not been a single documented event of this kind since 1990, despite increasing temperatures and “progressive unidirectional changes to sea ice distribution” (Stirling and Derocher, 2012). Instead, it appears warm spells in winter and rain in the spring occur rarely in the Arctic, even in a warming world, and do not pose a significant risk to polar bears or their ringed seal prey. Anecdotal reports such as these are not evidence and do not contribute to our understanding of how polar bears respond to unidirectional climate change.

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5.8.3 Nutrition and Reproductive Success

Researchers have expressed concern over the relationships between temperature and sea ice breakup and the nutrition and physical condition of polar bears and reproductive success. Closer scrutiny of these claims suggests they lack empirical bases.

5.8.3.1 Nutritional Stress and Declines in Body Condition

According to Stirling and Derocher (2012), “the most comprehensive long-term research on polar bear demography, body condition, subpopulation size, abundance, and reproductive success has been

conducted on the Western Hudson Bay sub-population.” For bears in this subpopulation, they found “statistically significant relationships have been documented between progressively earlier dates of sea ice breakup (which shortens the feeding time for polar bears at the most important time of the year just before coming ashore, and lengthens the fasting period),” and declines in the following parameters: mean body condition during the fall ice-free period; mean weights of suspected pregnant females prior to denning in fall; and survival of juvenile, subadult, and old (senescent) adult bears.

These claimed correlations between these life history parameters and “progressively earlier dates of sea ice breakup” in Western Hudson are based on published sea ice data only up to 1998. As their figure caption notes, data after that time (1999 to 2007) is attributed to “N.J. Lunn and I. Stirling, unpublished data.” In contrast, the figure they include showing global sea ice declines, based on Stroeve *et al.* (2007), is updated to 2011 with publicly available data provided by the U.S. National Snow and Ice Data Center. Moreover, although Stirling and Derocher say “the mean mass of adult females declined (by about 20%) between 1980 and 2007” (mass being a “proxy” for body condition, which they say is tied closely to litter size, age at weaning, and cub survival), the data used to reach this conclusion are for 1980 to 2004 only: the data from 2006 to 2007 are not available in the peer-reviewed literature. This means the data on which these claims are made are strikingly out of date and/or unavailable, and the conclusions may no longer be valid.

Stirling and Derocher’s claim of “progressive unidirectional changes to sea ice distribution” may be accurate for global sea ice coverage but not for ice on Hudson Bay. In a recent paper on breakup in Western Hudson Bay, Cherry *et al.* (2013) show between 1991 and 2009, there was considerable variability in breakup dates. Polar bears left the ice later in 2009 than in 1992, indicating breakup dates have not been progressively earlier since 1992. Only nine of 19 breakup dates in this period fell in June (with none falling in the first half of the month), suggesting there was little or no impact on the critical November–June feeding period. And although some bears apparently chose a favorite location to come ashore even if there was enough ice to spend more time hunting, many bears were flexible enough in their choice of where and when they left the ice to adapt to yearly variability in conditions. Overall, it appears variability may be the most prominent feature of sea ice breakup dates for Western Hudson Bay and most

polar bear females can and do take these variations in stride.

Polar bears in the Southern Beaufort region have also been reasonably well-studied. This subpopulation is shared between the United States and Canada and comprises most of the north coast of Alaska and about an equal length of the western Canadian Arctic coastline. It is characterized by a dynamic mix of annual and multiyear sea ice. Bears in the Southern Beaufort routinely den on the sea ice rather than on land and reach their maximum weights in the fall, rather than in summer, as do bears in Western Hudson Bay—probably because they spend little, if any, time on land during the summer.

Durner and Amstrup (1996) note, “polar bears in western Hudson Bay differ from other populations because the sea ice substrate required for hunting melts completely by late summer (Ramsay and Stirling, 1988), and all members of the population fast or consume only low-energy food (Derocher *et al.*, 1992). On the other hand, polar bears inhabiting certain areas of the Canadian Arctic archipelago (e.g., Viscount Melville Sound) may be food deprived because of stable sea ice conditions during winter and low seal densities (Messier *et al.*, 1994). Because polar bears in Alaska [*i.e.*, the Southern Beaufort] follow seasonal changes in dynamic pack ice (Amstrup and DeMaster, 1988), they may not face the food scarcity that characterizes the Hudson Bay population during summer and the northern Canadian population during the winter.”

In other words, even before there were declines in sea ice coverage purportedly caused by global warming, polar bear biologists saw marked differences among subpopulations in patterns of body condition changes from season to season. In light of that understanding, do reports that blame global warming for declines in polar bear size and body condition (and associated declines in cub production and/or survival) stand up to scrutiny?

Rode *et al.* (2010) studied polar bears in the Southern Beaufort between 1982 and 2006. They used a subjective definition of sea ice conditions, called “optimal ice habitat,” which is not a quality measured by satellites but “resource selection function (RSF) models” that use data from satellite-collared polar bears (1985–1995) to show where the bears that researchers captured on land or near shore moved throughout the year. Using this method, a decline in area (km²-months) of “optimal ice habitat” (ice neither too thin nor too thick) could mean sea ice got thicker, got thinner, or disappeared—it is not possible to tell which. Rode *et al.* (2010) conclude,

“the decline over time in the availability of sea ice corresponded with declining trends in most measures of bear sizes and condition.” But because their “decline over time in availability” is not a straightforward decline in sea ice extent or timing of the ice-free period, but a decline in “optimal ice habitat,” it is unlikely this parameter is really useful in addressing whether reduced levels of summer sea ice in the Southern Beaufort are the proximate cause of negative impacts on polar bears.

In direct contraction of a statement made by Obbard *et al.* (2010), discussed in more detail near the end of this section, Rode *et al.* (2010) say, “declines in the size of bears in this population have occurred during a time period when the number of bears in the region also appears to be lower than previously thought (Regehr *et al.*, 2006), and the trend in numbers appears to be downward (Regehr *et al.*, 2010). Though the mechanism associated with population-level change is not clear, nutritional limitations in the population are apparent as a result of the observed declines in bear skull sizes and body lengths. ... Thus, nutritional factors may also have played a role in the observed population-level changes.” Although nutritional stress has indeed been documented for this area, there has not been a statistically significant decline in the population, a point reiterated by Regehr *et al.* (2007): “changes in the sea ice have not yet been associated with changes in the size of the SB polar bear population (Regehr *et al.*, 2006).” Obbard *et al.* (2010) concur.

Even more surprising is recent research on polar bears in the neighboring Chukchi Sea subpopulation (shared between the United States and Russia), which has shown either no negative effects or marked improvement despite at least twice as much summer sea ice loss as in the Southern Beaufort. Rode *et al.* (2014) captured, measured, and released polar bears on the sea ice between mid-March and early May, 2008–2011; others did similar work in 1986–1994. Rode *et al.* compared data collected on body condition, litter size, and juvenile survival (“reproductive indices”) in the Chukchi Sea between the two periods (1986–1994 and 2008–2011). They also compared body condition and reproduction in the Chukchi and neighboring Southern Beaufort for the period 2008–2011. They evaluated these metrics in relation to sea ice loss and prey availability; for Chukchi bears in 2008–2011 only, they also determined diet composition from analysis of fat samples (“fatty acid signatures”) and fasting behavior from analysis of blood samples (“levels of blood urea nitrogen and creatinine”).

The authors found “in 2008–2011, CS [Chukchi] bears were either larger and in better condition, or similar in size and condition, to CS bears in 1986–1994.” They also found “no difference in the number of yearlings per female, yearling litter size, or the annual percentage of females with yearlings between periods in the CS. ... Overall, CS bears in 2008–2011 were larger and in better condition than SB [Southern Beaufort] bears during the same period.” The number of yearlings per female in spring was also higher in the Chukchi Sea than in the Southern Beaufort.

Most surprisingly, Chukchi bears were larger and heavier than virtually all other subpopulations studied. Rode *et al.* (2014) found “spring COY litter sizes are among the highest reported for 18 of 19 polar bear populations. ... [S]pring litter sizes of CS yearlings from the study were also higher than other populations.” The authors note, “the larger body mass of adult females in the CS corresponded not only with larger litter sizes, but also with heavier yearlings (Fig.5 [in original document]) which have a greater chance of survival.” Rode *et al.* state, “body size, condition, and reproductive indices of CS polar bears did not decline over time between 1986–1994 and 2008–2011 despite a 44-day increase in the number of reduced-ice days. Furthermore, CS bears were larger, in better condition, and appeared to have higher recruitment compared to the adjacent SB population during 2008–2011. These differences were biologically significant.”

In the Chukchi subpopulation, the authors conclude, “body condition was maintained or improved when sea ice declined” and “continued high biological productivity in the Chukchi and northern Bering seas may be allowing polar bears and their prey to prosper despite habitat loss.” Regarding Southern Beaufort bears, they state, “Our evaluation of nutritional ecology for polar bears is consistent with lower prey availability in the SB compared to the CS.”

These results were unexpected because the Southern Beaufort and Chukchi Seas are considered similar ice ecoregions and polar bears were predicted to respond similarly to summer sea ice loss. Both have been classified as “divergent” ice ecoregions by researchers attempting to predict how polar bear habitat might fare over the next 25 to 95 years based on computer-projected sea ice declines (Amstrup, 2011; Amstrup *et al.*, 2008, 2010; Durner *et al.*, 2009). Durner and colleagues, for example, state, “within the Divergent ecoregion, rates of decline are projected to be greatest in the Southern Beaufort, Chukchi, and Barents Sea subpopulations.” Two

conclusions can be drawn from this study: Declines in summer sea ice extent can markedly benefit polar bear survival, and extent of sea ice loss in summer is not the paramount determiner of polar bear health and population status, at least over the short term.

In the eastern Arctic, there also has been recent work done on Davis Strait polar bears, the most southerly polar bear subpopulation. Whereas the southernmost portion of the Southern Hudson Bay region (James Bay) lies at about 52°N and the southernmost portion of Western Hudson Bay lies at about 55°N, bears in the Davis Strait polar bear subpopulation occur regularly to at least 50°N, with some moving as far south in spring as 47°N.

Based on mark-recapture studies undertaken from 1974 to 1979 and from 2005 to 2007, Peacock *et al.* (2013) state, “the overall amount of sea ice declined and breakup has become progressively earlier” since the 1970s. Nonetheless, they “estimated the abundance of the Davis Strait polar bear subpopulation to 2,158, which results in a relatively high population density of polar bears of approximately 5.1 bears/1,000 km² of sea ice habitat (Taylor and Lee, 1995). This density is greater than polar bear densities in other seasonal-ice subpopulations, which are approximately 3.5 bears/1,000 km².” So despite declining sea ice since the 1970s, the density of bears in this region has reached a higher level than any other subpopulation known that loses ice completely in summer. The authors conclude, “survival and reproduction of bears in southern Davis Strait was greater than in the north and tied to a concurrent dramatic increase in breeding harp seals (*Pagophilus groenlandicus*) in Labrador.”

They suggest the Davis Strait polar bear subpopulation is characterized by “low recruitment rates, average adult survival rates, and high population density.” The high density of bears in this region may be affecting recruitment (*i.e.*, reproduction), the authors conclude, “low reproductive rates may reflect negative effects of greater densities or worsening ice conditions.” In other words, polar bear populations with a high density of animals may show changes to life history parameters similar to those expected in populations affected by declines in sea ice. However, effects of high density and less time spent feeding due to reduced sea ice appear to be viable explanations for the observed conditions in Davis Strait, and these factors are not necessarily mutually exclusive. Nevertheless, polar bears in Davis Strait appear to be increasing in number, not declining as reported by the IUCN/SSC Polar Bear Specialist Group (Obbard *et al.*, 2010) and others, despite the declines in sea ice.

In a similar study that compared Davis Strait polar bears to those in Baffin Bay to the North, Rode *et al.* (2012) “examined trends in body condition metrics of captured bears and relationships with summertime ice concentration between 1977 and 2010 for the Baffin Bay (BB) and Davis Strait (DS) polar bear populations.” Both of these regions are dominated by annual (first year) ice. They conclude, “we suggest that declining body condition in BB may be a result of recent declines in sea ice habitat. In DS, high population density and/or sea ice loss may be responsible for the declines in body condition. ... Though a decline in body condition was observed for DS between 1978 and 1994, there was no relationship between body condition and sea ice concentrations at that time.” In other words, the decline in condition of polar bears in Davis Strait may be evidence the population has reached “carrying capacity” despite the declining trend in annual sea ice extent. This result suggests declines in body condition may not necessarily be the harbinger of doom for polar bears some researchers have proposed but instead a signal more bears exist than the local habitat can support.

One of the presumed repercussions of polar bears that end up in poor condition due to nutritional stress, especially if they get to the point of starving, is an increase in propensity for infanticide and cannibalism. These phenomena are well-known in all bears (Taylor *et al.*, 1985), but there have been no long-term, carefully designed scientific studies on infanticide or cannibalism among polar bears, so no baseline data exist with which to compare recent anecdotal reports. This has not stopped some polar bear researchers and conservation advocates from using these anecdotal observations as a kind of “supporting evidence” for contending polar bears are already being negatively impacted by global warming.

Stirling and Derocher (2012) state, “There have been several well-publicized observations that are consistent with predictions of the effects of climate warming on polar bears, but cannot be statistically linked. For example, intraspecific aggression and cannibalism were predicted to increase in polar bears with climate warming (Derocher *et al.*, 2004, Table 1). Observations of infanticide and cannibalism by thin adult males on land during the open water period have been documented (e.g., Lunn and Stenhouse, 1985; Derocher and Wiig, 1999; Amstrup *et al.*, 2006; Stone and Derocher, 2007).”

However, of the references cited, only Lunn and Stenhouse (1985) report a confirmed instance of a thin (*i.e.*, starving) adult male killing and consuming another adult bear during the open water period, and

that event occurred in 1984. Amstrup *et al.* (2006), who report three incidents of cannibalism in the Southern Beaufort, did not know the condition of the bears that killed and partially consumed other bears, as no one witnessed these attacks. In addition, contrary to the notion that cannibalism is associated with starvation, in the most recent case published (one not mentioned by Stirling and Derocher), Stirling and Ross (2011) report three cases of cannibalism on the sea ice around Svalbard, all of which involved males in good or very good condition killing other young bears. They say “the three observations we describe are different from most other reports of infanticide and cannibalism in polar bears because they took place between midsummer and early autumn. ... All three adult males appeared to be in good physical condition (*i.e.*, not obviously thin), and one was both very large and very fat.”

Stirling *et al.* (2008), in a follow-up to the report of Amstrup *et al.* (2006), state, “these observations, along with cannibalized and starved polar bears found on the sea ice in the same general area in the springs of 2004 through 2006, suggest that during those years, polar bears in the southern Beaufort Sea were nutritionally stressed.” They point out several severe winter storms piled up thick ridges of sea ice in the landfast ice zone, which made seal hunting difficult for polar bears. They acknowledge the nutritional stress was caused by heavy ice conditions in 2004 and 2005 (confirmed by Harwood *et al.*, 2012 and Melling *et al.*, 2005) but suggest the heavy ice may have been caused by open water many months prior in the Chukchi Sea far to the west. However, there have been heavy ice years in this region every decade since the 1960s (long before there was increased open water in the fall) and starving bears in spring were documented in most of those heavy ice years (Stirling, 2002; Stirling and Lunn, 1997; Stirling *et al.*, 2008), suggesting the cause of heavy spring ice is something other than increased open water in the summer.

The impact of the most recent heavy ice years on ringed seals is documented by Harwood *et al.* (2012), for the Amundson Gulf, which lies in the south half of the Northern Beaufort polar bear subpopulation (and immediately east of the Southern Beaufort areas discussed above). They examined “the relationship between ringed seal body condition and reproduction and spring sea ice conditions in prime ringed seal habitat” in the western Canadian Arctic between 1992 and 2011. They found “failure to ovulate was obvious in 2005, the most extreme late ice clearance year in our series, when only 30.0% of the mature adult

females sampled ovulated.” The authors conclude, “Seals sampled in years of late ice clearing had, on average, lower body condition than those sampled in years of earlier ice clearing, particularly in the case of subadults” and for mature females, “marked declines were seen in 1974 (Smith, 1987), in 1987 (Kingsley and Byers, 1998), and in 2005 (this study), all times when seals were in significantly poorer body condition. ... Signals were detected in the most extreme ice years (e.g., when fast ice breakup occurred 3–8 weeks later than the average since 1970) and were linked to the degree of severity of winters, as indicated by the annual ice regime.” They note, “In the Beaufort/Amundsen regions, for example, observations over the last 40 years have revealed large fluctuations in ice presence and thickness over intervals of years to decades, with so far only small trends towards earlier ice clearance and longer open water seasons (Melling and Riedel, 2004; Melling *et al.*, 2005).”

Pilfold *et al.* (2012) corroborate the declines in ringed seal pup production documented by Harwood *et al.* (2012) in their study of the age composition of ringed seals killed by polar bears in the eastern Beaufort from 1971 to 2006. They show, in their Figure 3, a higher proportion of pups were killed during the low or average spring ice years of 1971–1973 (when about 45% of seals killed were pups) and 2007–2011 (about 80% pups) than in the heavy spring ice years of 1974 to 1975 (none killed were pups), 1985 to 1987 (about 10% pups), or in 2003 to 2006 (about 40% pups). In other words, since the early 1970s, polar bears killed fewer seal pups in springs with heavy sea ice conditions, suggesting fewer seal pups were available.

Another perspective on these events is provided by Cherry *et al.* (2009), who compared the fasting physiology of eastern Beaufort Sea polar bears during two known heavy spring ice periods: 1985–1986 and 2005–2006. In their analysis of the proportion of urea vs. creatinine (considered an indicator of fasting) from blood samples drawn in the eastern Beaufort Sea (which include the southern portion of the Northern Beaufort subpopulation) in April–May 1985–1986 and 2005–2006, they found “the proportions of polar bears fasting were 9.6% in 1985, 10.5% in 1986, 21.4% in 2005, and 29.3% in 2006. ... The increased number of polar bears in a physiological fasting state from all sex, age, and reproductive classes in 2005 and 2006 corresponded with broad scale changes in Arctic sea ice composition, which may have affected prey availability.” They write, “none of the bears displayed physical or behavioral traits indicative of an

animal in the advanced stages of starvation.” This seems to corroborate the finding by Amstrup *et al.* (2006), who found in the spring of 2004, the year before Cherry *et al.* took their samples, “70 of 148 (47%) of bears captured as independent animals (*i.e.*, not including cubs captured with their mothers) were in the lean condition classes 1 and 2.” This is perhaps not very surprising, as polar bears are generally at their leanest in March, and if they are slow to put on weight for any reason over the spring months, by April or May they would not yet be in optimum condition (although they might be so a few months later).

Cherry *et al.*’s discussion of the “changes in Arctic sea ice” in their introduction attempts to imply the changes over time in the percentage of fasting bears was caused by reduced ice and more open water. They say, for example, “the Arctic ice-ocean system has been warming faster than global averages since the 1960s.” They conclude, “Beaufort Sea bears reach their lightest weights in late March and rely on a 2–3 month spring feeding period, when fat and naïve ringed seal pups are available, to gain the fat reserves necessary for survival and reproduction (Stirling and Øritsland, 1995; Stirling, 2002). ... [T]he recent increase in bears fasting during April and May suggests that there has been a decrease in prey availability at that time of year. ... [T]he precise means through which prey have apparently become less available to polar bears in the Beaufort Sea remains unknown.” But as discussed above, “the precise means” have been documented—evidence from this region suggests heavy sea ice in the spring during 2004–2006, which resulted in precipitous declines in ringed seal pup production, was almost certainly the cause of more bears fasting (Harwood *et al.*, 2012; Melling *et al.*, 2005; Stirling, 2002; Stirling *et al.*, 2008).

Regehr *et al.* (2010) provide another attempt to shift attention from heavy ice conditions in spring to low sea ice conditions in late summer. These researchers “evaluated the effects of sea ice conditions on vital rates (survival and breeding probabilities) for polar bears in the southern Beaufort Sea” with models, based on data collected from 2001 to 2006 on polar bears and the number of ice-free days each year. They conclude, “in the most supported models, polar bear survival declined with an increasing number of days per year that waters over the continental shelf were ice free. In 2001–2003, the ice-free period was relatively short (mean 101 days) and adult female survival was high (0.96–0.99, depending on reproductive state). In 2004 and

Terrestrial Animals

2005, the ice-free period was longer (mean 135 days) and adult female survival was low (0.73–0.79, depending on reproductive state). Breeding rates and cub litter survival also declined with increasing duration of the ice-free period. Confidence intervals on vital rate estimates were wide.”

Regehr *et al.* did not include possible effects of heavy sea ice conditions in spring in their models, which, as shown above, tends to have a direct negative impact on polar bear life history parameters in the eastern Beaufort (Harwood *et al.*, 2012; Melling *et al.*, 2005; Stirling, 2002; Stirling and Lunn, 1997). Regehr *et al.*’s models considered only number of ice-free days in summer as a possible association. As a consequence their results and conclusions add little to our understanding of changes in polar bear survival or body condition in the Southern Beaufort.

It should be noted that despite the repeated bouts of less-than-optimum conditions every decade or so, polar bear numbers in the Southern Beaufort appear to have remained remarkably stable. Obbard *et al.* (2010) note,

through the 1980s and early 1990s, observations suggested that the SB subpopulation was increasing. Amstrup *et al.* (2001) found the SB subpopulation may have reached as many as 2,500 polar bears in the late 1990s. However, that estimate was not considered reliable due to methodological difficulties, and management decisions continued to be based on a population size of 1,800. Results from an intensive mark-recapture study conducted from 2001–2006 in both the USA and Canada indicated that the SB subpopulation included 1,526 (95% CI = 1,211–1,841) polar bears in 2006 (Regehr *et al.*, 2006). This suggests that the size of the SB subpopulation declined between the late 1990s and 2006, although low precision in the previous estimate of 1,800 precluded a statistical determination.”

In other words, although there is evidence of nutritional stress in 2004–2006, it did not result in a statistically significant decline in numbers of polar bears in the Southern Beaufort region.

In addition, polar bears that live in the region around Banks Island and the Amundsen Gulf in the past were often included in studies of the “eastern Beaufort,” but they now are considered part of the Northern Beaufort subpopulation, one of the few subpopulations some researchers consider as having a stable population trend (Obbard *et al.*, 2010; Stirling *et al.*, 2011).

Surprisingly, one question seldom addressed in studies on nutritional stress and associated behaviors such as cannibalism is this: Do polar bears ever starve under conditions that cannot be blamed on sea ice changes? Indeed, they do. Amstrup (2003) notes

starvation of independent young as well as very old animals must account for much of the natural mortality among polar bears. ... Also, age structure data show that subadults aged 2–5 years survive at lower rates than adults (Amstrup, 1995), probably because they are still learning hunting and survival skills. ... I once observed a 3-year-old subadult that weighed only 70 kg in November. This was near the end of the autumn period in which Beaufort Sea bears reach their peak weights (Durner and Amstrup, 1996), and his cohorts at that time weighed in excess of 200 kg. This young animal apparently had not learned the skills needed to survive and was starving to death.

It appears the anecdotal reports of cannibalism, infanticide, and den collapses due to spring rain are being included for their emotional appeal to the public but are not associated with recent declines in local or global sea ice or with recent increases in temperature. Data supporting claims of declines in body condition for Western Hudson Bay polar bears are seriously out of date and/or unpublished, and in the Southern Beaufort, declines in body condition due to heavy ice conditions in spring have been documented every decade since the 1960s. Despite attempts to blame these phenomena on global warming, peer-reviewed research suggest otherwise.

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Climate Change Reconsidered II: Biological Impacts

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5.8.3.2 Changes in Reproductive Success

A warmer Arctic portending dramatic declines in sea ice is predicted to have significant effects on the reproductive success of polar bears, based on changes already documented in some subpopulations. Stirling and Derocher (2012) have this to say about reproductive success in the western Hudson Bay subpopulation: “the proportion of independent yearlings fell from over 81% before 1980 to a mean of 34% in 1980–1992 (Derocher and Stirling, 1995). By the late 1990s, the proportion of independent yearlings dropped to <10% (Stirling *et al.*, 1999) and by the early 2000s was almost nonexistent (I. Stirling, unpublished data).”

In the 1999 paper the authors cite, Stirling *et al.* say this: “The proportion of yearlings that were independent in the annual capture samples fluctuated widely at 3–4 year intervals, but overall the maximum proportions have declined from about 60% in 1982 to 15–20% since 1991 (Fig. 6). There was no statistically significant relationship between the proportion of lone yearlings and the time of [sea ice] breakup in the same year ($r = -0.205$, $n = 14$, $p = 0.46$).” More importantly, Stirling *et al.* (1999) also point out, “for about the last 12 years [ending 1998], estimates of population size have remained relatively constant (Lunn *et al.*, 1997; this study), indicating that the declines in condition and natality have not led to a decline in population.” In other words, the well-documented change from weaning at 2.5 years rather than 1.5 years had no immediate negative impact on the population up to 1992, and any additional data collected on this phenomenon are not available in the peer-reviewed literature.

Derocher and Stirling (1995) state: “the results of our analyses suggest that the unique reproductive characteristics of polar bears in western Hudson Bay in the 1960s and 1970s were either a function of a population increasing from a depleted state and

feeding on a relatively abundant prey base, or density-independent fluctuations in prey population size, or availability due to sea ice variation.” Therefore, declining sea ice is not the only reason reproductive parameters, such as age at weaning, might change. And since the assertion that the proportion of independent yearlings was “almost nonexistent” by the early 2000s is based on unpublished data, we cannot be sure the claimed further decline in proportion of independent yearlings has had any significant impact on population size, since previous changes did not.

In addition, it should be noted the proportion of independent yearlings being approximately zero is the norm for virtually all other polar bear subpopulations studied (Ramsay and Stirling, 1988; Van de Velde *et al.*, 2003). Western Hudson Bay always has been anomalous in this feature. In that respect, in weaning their cubs at 2.5 years rather than 1.5 years, Western Hudson Bay polar bears may simply be returning to normal.

Stirling and Lunn (1997) perhaps put it best:

In the early to mid-1980s, the natality [cub production] of female polar bears in western Hudson Bay was the highest recorded anywhere in polar bear range, and nowhere else did females successfully wean cubs at 1.5 years of age instead of at the normal age of 2.5 years. Subsequently, a long-term decline in condition of adult female polar bears and survival of their cubs was documented from the 1970s through the late 1980s (Derocher and Stirling, 1992), as reflected by a significant decline in condition indices. This decline did not constitute a threat to the population because even when natality was at its lowest in the late 1980s, the rates were still higher than the upper range of values for bears elsewhere in the Arctic (e.g., Stirling *et al.*, 1976, 1980). ... The more important (but unanswered) question is probably not why natality declined from the early 1980s but how could natality have been sustained at a level so much higher than other polar bear populations in the first place, what facilitated the successful weaning of yearlings there but nowhere else in their range, and how could females manage these physiological feats in a habitat where pregnant females must also fast for 8 months or more?”

They did not answer their question.

Rode *et al.* (2014), in their recent study of Chukchi Sea polar bears, found “spring COY litter sizes are among the highest reported for 18 of 19 polar bear populations. ... [S]pring litter sizes of CS yearlings from the study were also higher than other

populations.” The authors note, “the larger body mass of adult females in the CS corresponded not only with larger litter sizes, but also with heavier yearlings (Fig.5) which have a greater chance of survival” and “body size, condition, and reproductive indices of CS polar bears did not decline over time between 1986–1994 and 2008–2011 despite a 44-day increase in the number of reduced-ice days.” In other words, contrary to predictions, reproductive parameters of Chukchi Sea polar bears did not decline, despite marked declines in summer sea ice.

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5.8.4 Effects of more open water

Polar bears use sea ice as a platform for hunting, traveling, and denning. They are known to be excellent swimmers, capable of swimming long distances between ice flows. But what happens during the late summer, when the edge of the pack ice is many kilometers offshore for months at a time? Although some polar bears spend this “open water” period on land, is it because they are incapable of swimming to the ice edge once it gets beyond a certain point? Or are polar bears, particularly females with cubs, able to swim hundreds of kilometers from land to the ice edge during the “open water” season if they choose to do so?

Working from three points along the coast of the Beaufort and Chukchi Seas, Alaska (Barrow, Prudhoe Bay, Kaktovik) between 2004 and 2009, Pagano *et al.* (2012) attached radio collars during March through May (but also in August 2008) to 62 female polar bears, some of which had cubs with them. The number of bears successfully monitored for this study varied each year; as only two collars were deployed in 2007 and one of these failed, data from 2007 were excluded. The authors analyzed global positioning system (GPS) data from the 52 radio collars that successfully transmitted signals between 1 June and 31 October each year and compared these to the position of the sea ice edge determined from satellite imagery. Some additional data from bears collared between 1985 and 2009 were used to assess whether an early cessation of signal transmission during the open water period (July through September), from bears that had been at sea and were not later resighted, could be assumed to indicate the bears had drowned while swimming.

The authors found 50 “long-distance” swimming events (>50 km) were made by 20 of the bears monitored (38% of the total), and 12 of the 20 bears that swam long distances did so multiple times in the same year. The researchers found the majority of the long-distance swims were from unconsolidated sea ice (ice concentration <50%) to the main pack ice (mean distance 155.9 km, range 114.5–197.4 km, 25 swims). Relatively few bears swam from land to another area of land (mean distance 106.2 km, range 53.7–288.3 km, 7 swims) or from unconsolidated sea ice to land (mean distance 169.1 km, range 69.9–302.6 km, 6 swims). Only three swims involved bears moving from land to unconsolidated sea ice (mean distance 102.3 km, range 68.3–113.7 km), and only two were bears moving from land to the main pack ice (mean distance 402.5 km, range 117.9–687.1 km).

There were no long-distance swimming data prior to 2004 with which to compare this study’s data, and sampling differences among years precluded the researchers from determining any trend in their results.

They also found there was no significant difference in the rate of cub mortality between females with cubs that undertook long-distance swims and those that did not. It also appeared premature cessation of radio collar signal transmission did not necessarily indicate a bear had drowned; some bears whose signals stopped prematurely probably drowned, but drowning was not the only explanation for signal failure.

Pagano *et al.* calculated the mean distance between the mainland coast and the sea ice edge at the end of September for each year of the study period. This distance varied from a low of about 200 km (achieved in 2005, 2006, and 2009) and a high of about 430 km (achieved in 2008). Mean distance from the shore to the ice in 2004 was about 300 km, and in 2007 it was about 380 km. Each of these measurements varied somewhat depending on the configuration of the shoreline, but in 2008 the ice edge was definitely farther away than in any other year since 1979. However, the largest number of long-distance swimming events took place in 2009, when the ice edge in this region was about the same distance offshore as in 2005 and 2006. The longest swim was recorded in late August/early September of 2008 at a point where the sea ice was >500 km offshore: a female with a year-old cub swam 687.1 km in just over nine days, as described in detail by Durner *et al.* (2011). This bear was one of only two individuals in the Pagano *et al.* study that swam from land to the main pack ice edge; after a few weeks meandering around at the edge of the pack ice, this bear then walked back to shore on the rapid-forming ice, arriving on land at the end of October. The second-longest swim (366.0 km) was recorded in 2005, when the pack ice edge was about the same distance offshore as in 2009.

Pagano *et al.* state, “we show that both adult female polar bears and their dependent young possess an ability to swim long distances.” They also observe, “most of the long-distance swimming events that we identified involved bears swimming from unconsolidated sea ice to the main pack ice or to land.” In other words, few swims recorded were from land to sea ice, indicating that during the open water season most southern Beaufort and Chukchi Sea polar bears are on the sea ice, not on land—a point also made by Durner *et al.* (2011). In addition, the results of this

Climate Change Reconsidered II: Biological Impacts

study suggest that despite there being little or nothing for female polar bears and their cubs to eat on shore during the late summer months in the southern Beaufort Sea, the few bears that remain on shore are apparently not hungry enough to undertake long-distance swims to the pack ice to relieve their fast, although they appear able to do so. Despite an overall decline in September sea ice levels between 1979 and 2010, this study found no significant correlation between increased long-distance swims and increased amounts of open water in this region over time.

Although polar bears are clearly accomplished swimmers, an anecdotal account of polar bears that apparently drowned in open water, purported to be evidence of global warming and declining sea ice effects, has garnered remarkable media attention. Monnett and Gleason (2006) report what appeared at the time to be four dead polar bears that drowned in open water in 2004. The bodies were observed from aircraft while surveying for bowhead whales (*Balaena mysticetus*) after a September storm. However, like the anecdotal accounts of cannibalism and den collapses attributed to global warming by Stirling and Derocher (2012) discussed previously, no baseline scientific studies have quantified the number of swimming polar bears that have drowned under any conditions vs. those that have not. So while these isolated events continue to be touted as probable effects of global warming, there is no scientific evidence they are anything of the sort. Scientists do controlled, well-designed studies precisely because anecdotes cannot be trusted to give an unbiased picture of events. The inclusion of anecdotal events as supporting evidence of global warming is an appeal to emotions, rather than scientific reasoning.

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5.9 Reptiles

- Studies of the effects of rising temperatures on reptiles find they often are able to tolerate a greater range of environmental conditions than they have been exposed to in the recent past, demonstrate abilities to thermo-regulate to achieve body temperatures close to their preferred temperatures, and often benefit from warmer temperatures.

Many are the predictions of species decline and possible extinction arising from warming-induced changes in the characteristics of regions to which the species are endemic. Concerns over the fate of reptiles are no exception, yet the results of several research studies conducted on this topic suggest these animals are in no such danger.

Chamaille-Jammes *et al.* (2006) studied four discontinuous subpopulations of the common lizard (*Lacerta vivipara*), a small live-bearing lacertid that lives in peat bogs and heath lands across Europe and Asia, concentrating on a small region near the top of Mont Lozere in southeast France, at the southern limit of the species' range. From 1984 to 2001 they monitored several life-history traits of the subpopulations, including body size, reproduction characteristics, and survival rates, while local air temperatures rose by approximately 2.2°C. They found individual body size increased dramatically in all four lizard populations over the 18-year study period, with snout-vent length expanding by roughly 28 percent. This increase in body size occurred in all age classes and, as they describe it, “appeared related to a concomitant increase in temperature experienced during the first month of life (August).” As a result, they found “adult female body size increased markedly, and, as fecundity is strongly dependent on female body size, clutch size and total reproductive output also increased.” In addition, for a population where capture-recapture data were available, they learned “adult survival was positively related to May temperature.”

Since all fitness components investigated responded positively to the increase in temperature, the French researchers state, “it might be concluded that the common lizard has been advantaged by the shift in temperature.” This finding, they write, stands in stark contrast to the “habitat-based prediction that

these populations located close to mountain tops on the southern margin of the species range should be unable to cope with the alteration of their habitat.” They conclude, “to achieve a better prediction of a species persistence, one will probably need to combine both habitat and individual-based approaches.” Furthermore, they note individual responses, such as those documented in their study (which were all positive), represent “the ultimate driver of a species response to climate change.”

Noting tropical species long have been thought to be “especially sensitive to climatic fluctuations because their narrow thermal tolerances and elevational ranges can restrict their ability to persist in, or disperse across, alternate habitats,” Bell *et al.* (2010) compared “responses to historical climate fluctuation in a montane specialist skink, *Lampropholis robertsi*, and its more broadly distributed congener, *L. coggeri*, both endemic to rainforests of northeast Australia.” They combined “spatial modeling of potential distributions under representative palaeoclimates, multi-locus phylogeography and analyses of phenotypic variation.” The seven scientists write, “both species exhibit pronounced phylogeographic structuring for mitochondrial and nuclear genes, attesting to low dispersal and high persistence across multiple isolated regions.” Referring specifically to *L. robertsi*, the researchers state their evidence demonstrates “persistence and isolation” of most populations of the montane species “throughout the strong climate oscillations of the late Pleistocene, and likely extending back to the Pliocene.”

Noting many of the isolated refugia they studied “are particularly rich in narrowly endemic species,” Bell *et al.* state this characteristic has been attributed to “their relative stability during recent episodes of climate change (Williams and Pearson, 1997; Yeates *et al.*, 2002; Graham *et al.*, 2006; VanDerWal *et al.*, 2009).” Furthermore, they say these observations “support the general hypothesis that isolated tropical montane regions harbor high levels of narrow-range taxa because of their resilience to past climate change,” citing Fjeldsa and Lovett (1997) and Jetz *et al.* (2004). Thus, “at first sight, species such as *L. robertsi* would seem especially prone to local extinction and loss of considerable genetic diversity with any further warming; yet, these populations and those of other high-montane endemic species (*Cophixalus* frogs; Hoskin, 2004) have evidently persisted through past warming events.”

Rodder *et al.* (2010) state, “if the climate changes, island endemics may be restricted in their

ability to conduct range shifts depending on the topographic variability and the size of the island,” and “species that inhabit islands characterized by low altitudinal variation may be the ones most strongly affected by climate change due to the lack of possibilities for horizontal or upward range shifts.” However, they note only a small part of the fundamental niche of a species may currently be available to it, and the species may possess a hitherto-unknown ability to tolerate a much greater range of environmental conditions than that to which it may have been exposed in the recent past. Therefore, in determining what climatic conditions a species may be able to tolerate in the future, they state “a comparison between conditions tolerated in the present and in the past may be helpful.”

Focusing on *Phelsuma parkeri*, an endemic gecko species native to the relatively flat (0 to < 100 m elevation) island of Pemba, Tanzania, Rodder *et al.* observed the species and provided information on its current spatial distribution in terms of both physical and environmental space, as well as its adaptability to habitat modification by humans. With respect to past climatic conditions, they employed simulations of the Last Glacial Maximum provided by the Community Climate System Model and the Model for Interdisciplinary Research on Climate, while with respect to the future, they employed climate change predictions based on three other models and the emission scenarios reported in the *Special Report on Emissions Scenarios* by the Intergovernmental Panel on Climate Change.

The three researchers report a comparison of current climatic conditions with those derived from model simulations for 21,000 years ago revealed “no climate conditions analogous to those of today existed during the Last Glacial Maximum,” noting there were “decreases of between 1.4 and 2.8°C in the minimum temperature of the coldest month and of between 2.1 and 3.4°C in the maximum temperature of the warmest month throughout the island” compared to the corresponding temperatures of today. As for the future, the climate models they used suggested “the minimum temperature of the coldest month may increase about 1.2 to 3.8°C and the maximum temperature of the warmest month by about 2.0 to 3.7°C.” Rodder *et al.* say their results suggest “*P. parkeri* is distributed over the largest part of the island, that it is well adapted to current land use, and that it is most likely not threatened by climate change.”

Moreno-Rueda *et al.* (2011) “used data on the distributions of reptiles in Spain during the 20th

century to analyze whether the distributions of these reptiles have changed as climate has changed.” They compared “the distributions of reptile species before 1975”—the year, they say, according to IPCC (2007), the current period of warming began—“with distributions during 1991–2005.” The authors report, “after controlling for sampling effort, geographic bias in sampling, phylogeny, and spatial autocorrelation, the northern limits of the distribution of reptiles in Spain shifted northward between 1940–1975 and 1991–2005,” but “there was no similar shift southward in the southern limits of species’ ranges.” In addition, the mean latitude of the ranges of the species they examined “shifted northward by an equivalent of 0.5 km/year, which is similar to the magnitude of range shifts in other taxonomic groups (Parmesan and Yohe, 2003).”

Noting they were “the first to show there is a correlation between changes in latitudinal distribution and increases in temperature for a wide variety of species of reptiles in Spain,” the four researchers say their “finding that reptiles are expanding their northern ranges, potentially in response to climate change, could mean the probability of extinction associated with increases in temperature may be lower than expected.”

According to Amiel and Shine (2012), a hatchling reptile’s sex, body size, and shape, as well as its locomotor performance, “can be influenced not only by its genes, but also by the temperature that it experiences during incubation.” At the time of their study little was known about whether incubation temperature can also affect a hatchling’s cognitive skills. Amiel and Shine examined “whether incubation temperature affects lizards’ ability to learn the location of a safe retreat site during a predatory attack,” because mastering this cognitive task “is directly relevant to individual survival and therefore fitness,” citing Paulissen (2008).

The pair of Australian researchers worked with the scincid lizard *Bassiana duperreyi*, by first “randomly dividing eggs from each clutch between two incubation treatments (‘hot’ = diel cycle of $22 \pm 7.5^\circ\text{C}$; ‘cold’ = diel cycle of $16 \pm 7.5^\circ\text{C}$),” treatments that “mimic thermal regimes typical of natural nests at low (hot) versus high (cold) elevations.” They then conducted a specific test designed to evaluate the young lizards’ cognitive skills and their abilities to act appropriately to escape the perceived danger. Amiel and Shine report finding “hot-incubated lizards achieved higher learning scores than did cold-incubated lizards,” and “the number of errors they made decreased more from the first to the second half

of the trials than was the case for cold-incubated lizards.” They speculate, based on Ahmad and Zamenhof (1978), Rissman *et al.* (2002), Valenzuela and Lance (2004), and Radder *et al.* (2008), “thermal effects on hormone levels during incubation may induce structural variation in parts of the brain that control behaviors such as learning.” Amiel and Shine conclude, “climate change may simultaneously generate novel challenges for post-hatching organisms, while also modifying their ability to respond flexibly to such challenges.” They specifically opine, “in *B. duperreyi*, hotter natural nests over recent decades (due to climate change) probably have produced hatchling lizards with enhanced learning abilities.”

Clarke and Zani (2012) note observed real-world temperature increases typically have been “asymmetrically distributed over diurnal time frames, with daily minima increasing at a faster rate than daily maxima,” citing Karl *et al.* (1991, 1993), Easterling *et al.* (1997, 2000), and DeGaetano and Allen (2002), whereas most previous studies of the effects of global warming on biological systems have boosted temperatures by the same amount during all hours of the day and night. Clarke and Zani conducted their study of the potential impact of global warming on the common side-blotched lizard (*Uta stansburiana*)—which they collected about 20 km south of Burns, Oregon (USA) at the northern edge of the Great Basin Desert—employing the latter, more-realistic imposed mode of asymmetric nighttime-only warming.

Working at their field laboratory, Clarke and Zani simulated observed trends in the asymmetric alteration of the local diurnal temperature range by increasing the nighttime temperatures in the incubators into which they transferred the female lizards (from their daytime cages) during their ovarian cycle. They treated the eggs the female lizards produced in a similar manner during their incubation period, carefully documenting the differences they detected throughout the entire reproductive process between the female parent and progeny lizards of the warmed and control treatments.

The two U.S. researchers discovered higher nighttime temperatures during the female lizards’ ovarian cycles “increased the probability of reproductive success and decreased the duration of the reproductive cycle.” They found the higher temperatures had neither positive nor negative effects on “embryo stage or size at oviposition, clutch size, egg mass or relative clutch mass.” They also report “higher incubation temperatures increased hatchling

Terrestrial Animals

size and decreased incubation period,” noting “subsequent hatchlings were more likely to survive winter if they hatched earlier.”

Clarke and Zani state, “as our findings confirm that climate warming is likely to increase the rate of development as well as advance reproductive phenology, we predict that warmer nights during the breeding season will increase reproductive output as well as subsequent survival in many temperate ectotherms, both of which should have positive fitness effects.” Thus, they conclude, “these effects are primarily beneficial for this population of northern lizards,” and they predict “future changes will continue to benefit the reproduction, growth and survival of individuals at this site.”

Leal and Gunderson (2012) write, “the general view is that climate change will have a major impact on biodiversity by increasing the extinction risk of many species or changing their distributions,” based on “the implicit assumption that species are relatively fixed entities, unable to respond to rapid changes in ecological conditions, including climatic variables, over an ecological timescale.” They state “evidence that some organisms are able to respond to climatic changes over short timescales has begun to emerge (e.g., Grant and Grant, 2002; Walther *et al.*, 2002; Bradshaw and Holzapfel, 2006).”

Nearly 40 years ago, the tropical Caribbean lizard *Anolis cristatellus*, native to an area of xeric forest in northeastern Puerto Rico, was found in Miami, Florida, by Schwartz and Thomas (1975) in a location where minimum temperatures in winter can average 10°C cooler than in Puerto Rico, but where maximum temperatures in summer are much more similar. Taking advantage of this situation, Leal and Gunderson set about to determine whether the cold tolerance or critical thermal minimum temperature (CT_{min}) of the introduced populations had diverged from that of the source populations of *A. cristatellus* since their physical separation in 1975. As a check on their experimental procedures, they also conducted studies to see whether the critical thermal maximum temperature (CT_{max}) of the two groups of lizards remained about the same.

They found “the introduced population tolerates significantly colder temperatures (by ~3°C) than does the Puerto Rican source population,” while the maximum temperatures tolerated “did not differ.” These observations “demonstrate that changes in thermal tolerance occurred relatively rapidly (~35 generations), which strongly suggests that the thermal physiology of tropical lizards is more labile than previously proposed.” They conclude, “regardless of

the mechanism, the adaptive lability of thermal tolerance in *A. cristatellus* over an ecological timescale” provides “a glimpse of hope for tropical lizards under the current conditions of rapid climate change.”

Valdecantos *et al.* (2013) note “temperature has a great impact on ectotherms, affecting physiological, behavioral and life history traits such as reproductive timing (Zug *et al.*, 2001; Labra and Bozinovic, 2002), reproductive mode (Shine, 2004), growth rate, survivorship (Huey, 1982), locomotion (Hertz *et al.*, 1983; Angilleta *et al.*, 2002) and diet (Espinoza *et al.*, 2004).” They note late twentieth century global warming “has been suggested as a potential threat for lizards at a global scale,” citing Sinervo *et al.* (2010).

The researchers studied four related species—*Liolaemus irregularis*, *L. albiceps*, *L. multicolor*, and *L. yanalcu*—that inhabit high-elevation desert areas in Northwestern Argentina, Northern Chile, and Southwestern Bolivia, working both in the laboratory and at four sites near San Antonio de los Cobres in Salta, Argentina, where they measured body temperatures (T_b), air temperatures (T_a), soil temperatures (T_s), operative temperatures in the field (T_e), and preferred body temperatures (T_{pref}) for all four species.

The four Argentine researchers report their study revealed all four species, “despite living at high elevation and harsh climatic conditions,” were able to “behaviorally or physiologically thermo-regulate to achieve body temperatures close to their preferred temperatures.” They conclude, “as proposed by Labra *et al.* (2009),” “many species are conservative in some aspects (e.g. T_{pref}), yet labile in others (e.g. T_b),” thus “allowing them to inhabit a wide range of environments.”

Moritz *et al.* (2012) note it is often assumed large central populations of a species have higher genetic diversity and, therefore, greater potential for adaptive response to environmental change. But they state “this is not always the case,” and “lineages that have persisted as isolates in peripheral areas through past climate change might well have genotypes that will confer greater resistance to future warming and which could be exploited for genetic translocation,” citing Chown *et al.* (2010).

Moritz *et al.* (2012) tested this hypothesis through comparative assays of minimum and maximum critical thermal limits (CT_{min} and CT_{max}), as well as optimal performance parameters, including CT_{opt}, across central and peripheral lineages of three species of ground-dwelling skinks (scincid lizards) endemic to the rainforests of northeast Australia:

Gnypetoscincus queenslandiae, *Carlia rubrigularis*, and *Saprosincus basiliscus*.

Results of the analysis indicate “peripheral lineages show significantly increased optimal performance temperatures (T_{opt}) relative to central populations, as well as elevated CT_{min} .” Moritz *et al.* conclude the peripheral lineages they examined “appear to have evolved higher thermal optima relative to centrally located lineages,” noting this finding “contrasts with the usual assumption that local adaptation of peripheral populations will be overwhelmed by gene flow from the center of the species range or, in the absence of immigration, will experience higher extinction rates.” Thus the authors state, “long-isolated populations in peripheral rainforests harbor genotypes that confer resilience to future warming.”

Sea turtles, like many other reptiles, have what is called “temperature-dependent sex determination” (TSD), which means the temperature experienced by each developing embryo (within its individual eggshell casing, laid within a nest built by the mother on a terrestrial beach) determines its sex (Janzen, 1994). In turtles, males require somewhat cooler embryonic conditions than females: a temperature of 29°C generates a sex ratio among hatchlings of about 50:50, whereas at higher temperatures, more females are produced (Hawkes *et al.*, 2009). (Strangely enough, in the tuatara, another TSD reptile, the opposite is true: more males are produced at higher temperatures.) As a result, strongly skewed offspring sex ratios are common in TSD reptiles.

The amount of global warming predicted for the next century by some climate scientists is considered a threat to TSD-species because it is feared the higher temperatures will generate such extreme sex ratio biases (e.g. 100% females) that extinction will be inevitable (e.g. Fuentes *et al.*, 2010; Janzen, 1994; Witt *et al.*, 2010). As a highly female-skewed hatchling sex ratio already occurs in marine turtles (Hawkes *et al.* 2009), “predicted increases in global temperatures are expected to exacerbate this trend,” say Wright *et al.*, 2012.

Although living sea turtle species have survived substantial temperature fluctuations in the recent past (Janzen and Paukstis, 1988), Wright *et al.* (2012) investigated whether they will be able to adapt to future warming. Wright *et al.* examined the mating behavior of green sea turtles (*Chelonia mydas*) to see if it was compensating for the extreme female-skewed sex ratios of hatchlings currently produced in the Mediterranean (86–96% female). They undertook genetic typing of tissue samples taken in 2008 from

20 nesting females and 809 of their offspring (from 37 clutches of eggs), from a single rookery beach in northern Cyprus. Paternity analysis of the hatchlings allowed the researchers to determine how many males had mated with the females they sampled. They also put a satellite transmitter on a single male to map his movements during the breeding season.

Sea surface temperatures at the study site rose by, on average, less than 1°C over the past 50 years, and the female bias that exists today in adult green sea turtles is probably the result of a similar extent of female bias among hatchlings produced approximately 30 years ago (due to the late age at sexual maturity in this species)—that is, the authors assumed many more breeding-aged adult turtles in the population were female than were male.

They found, “despite an offspring sex ratio of 95 per cent females, there were at least 1.4 reproductive males to every breeding female”—28 males breeding with 20 females tested. The authors suggest males may breed more often than females (females breed every 2–4 years). In addition, the male they tracked visited a number of rookeries in the region, suggesting males may mate with females on a number of different beaches. Together, the authors suggest, these mating behaviors partially compensate for the lower abundance of males within the population, so “male mating patterns have the potential to buffer the disruptive effects of climate change on marine turtle populations, many of which are already seriously threatened.” Furthermore, Wright *et al.* conclude, “current mating patterns will help to preserve genetic variation that may be critical if marine turtles are to adapt behaviorally or physiologically to a warming climate and have, no doubt, contributed to their persistence through historical climatic upheaval.”

Citing Lavergne *et al.* (2010), Refsnider and Janzen (2012) also studied turtles, writing, “adaptation to climate change may be impossible even when high genetic variation is present if the rate of environmental change is too rapid and the population demography is insufficiently dynamic,” adding, “species with temperature-dependent sex determination may be particularly threatened by climate change, because altered temperatures could skew sex ratios.” Refsnider and Janzen experimentally tested nest-site choice in the long-lived turtle *Chrysemys picta*, to see whether nesting behavior “could compensate for potential skews in sex ratios caused by rapid climate change.” They collected females from five populations spread across the species’ range, housed them in a semi-natural common garden, and waited to see what would

happen.

The two researchers report “females from transplanted populations showed similar choice of shade cover over nests to local females,” which suggests, in their words, “behavioral phenotypic plasticity in female choice of shade cover over the nest site may comprise an immediate mechanism by which long-lived reptiles with temperature-dependent sex determination can avoid skews in sex ratio potentially caused by rapid climate change.”

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Climate Change Reconsidered II: Biological Impacts

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5.10 Worms

- It appears earthworms and soil nematodes respond to increases in the air's CO₂ content, via a number of plant-mediated phenomena, in ways that further enhance the positive effects of atmospheric CO₂ enrichment on plant growth and development, while helping to sequester more carbon more securely in the soil and thereby reducing the potential for CO₂-induced global warming.

“Earthworms,” writes Edwards (1988), “play a major role in improving and maintaining the fertility, structure, aeration and drainage of agricultural soils.” As noted by Sharpley *et al.* (1988), for example, “by ingestion and digestion of plant residue and subsequent egestion of cast material, earthworms can redistribute nutrients in a soil and enhance enzyme activity, thereby increasing plant availability of both soil and plant residue nutrients,” as others also have demonstrated (Bertsch *et al.*, 1988; McCabe *et al.*, 1988; Zachmann and Molina, 1988). Kemper (1988) describes how “burrows opened to the surface by surface-feeding worms provide drainage for water accumulating on the surface during intense rainfall,” noting “the highly compacted soil surrounding the expanded burrows has low permeability to water which often allows water to flow through these holes for a meter or so before it is absorbed into the surrounding soil.”

Hall and Dudas (1988) report the presence of earthworms appears to mitigate the deleterious effects of certain soil toxins. Logsdon and Lindon (1988) describe a number of other beneficial effects of earthworms, including enhancement of soil aeration, since under wet conditions earthworm channels do not swell shut as many soil cracks do; enhancement of soil water uptake, since roots can explore deeper soil layers by following earthworm channels; and enhancement of nutrient uptake, since earthworm casts and channel walls have a more neutral pH and higher available nutrient level than bulk soil.

In light of these observations, there is great interest about what may happen to earthworms as the air's CO₂ content and temperature rise.

With respect to how rising atmospheric CO₂ concentrations might impact earthworms, Edwards (1988) writes, “the most important factor in maintaining good earthworm populations in agricultural soils is that there be adequate availability of organic matter.” Hendrix *et al.* (1988) and Kladvko (1988) report greater levels of plant productivity promote greater levels of earthworm activity. Consequently, since the most ubiquitous and powerful effect of atmospheric CO₂ enrichment is its stimulation of plant productivity (see Chapter 1, this volume), which leads to enhanced delivery of organic matter to soils, it logically follows this aerial fertilization effect of the ongoing rise in the air's CO₂ content should increase earthworm populations and amplify the many beneficial services they provide for plants.

Then there's the second most significant and common impact of atmospheric CO₂ enrichment on plants: its antitranspirant effect, whereby elevated levels of atmospheric CO₂ reduce leaf stomatal apertures and slow the rate of evaporative water loss from the vast bulk of Earth's vegetation. Growth chamber studies and field experiments that have studied this phenomenon provide voluminous evidence it often leads to increased soil water content in many terrestrial ecosystems (see Section 2.33, this volume), which is something earthworms favor.

Zaller and Arnone (1997) fumigated open-top and -bottom chambers they established in a calcareous grassland near Basal, Switzerland with air of either 350 or 600 ppm CO₂ for an entire growing season. They found the mean annual soil moisture content in the CO₂-enriched chambers was 10% greater than that observed in the ambient-air chambers. They note cumulative surface earthworm cast production after only one year was 35% greater in the CO₂-enriched chambers than in the control chambers. In addition, because earthworm casts are rich in organic carbon and nitrogen, the cumulative amount of these important nutrients on a per-land-area basis was found to be 28% greater in the CO₂-enriched chambers than in the ambient-air chambers. In a subsequent study of the same grassland, Zaller and Arnone (1999) report plants growing in close proximity to the earthworm casts produced more biomass than similar plants growing further away from them. They also found the CO₂-induced growth stimulation experienced by the various grasses was greater for those plants growing nearer the earthworm

casts.

These observations show atmospheric CO₂ enrichment sets in motion a self-enhancing cycle of positive biological phenomena whereby increases in the air's CO₂ content stimulate plant productivity and reduce plant evaporative water loss, which results in more organic matter entering the soil and a longer soil moisture retention time and/or greater soil water contents. All of this leads to the development of larger and more active earthworm populations, which enhance many important soil properties, including fertility, structure, aeration, and drainage. These improved properties further enhance the growth of the plants.

There are additional reasons for optimism regarding this process. As Jongmans *et al.* (2003) point out, "the rate of organic matter decomposition can be decreased in worm casts compared to bulk soil aggregates (Martin, 1991; Haynes and Fraser, 1998)." They conducted a micro-morphological investigation of structural development and organic matter distribution in two calcareous marine loam soils on which pear trees had been grown for 45 years. One of the soils exhibited little or no earthworm activity and the other exhibited high earthworm activity, due to different levels of heavy metal contamination of the soils as a consequence of the prior use of different amounts of fungicides. Based on their results and other studies they cite, they 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." That is, atmospheric CO₂ enrichment that stimulates the activity of earthworms also leads to more—and more secure—sequestration of carbon in Earth's soils, thereby reducing the potential for CO₂-induced global warming.

Cole *et al.* (2002) report, "in the peatlands of northern England, which are classified as blanket peat, it has been suggested that the potential effects of global warming on carbon and nutrient dynamics will be related to the activities of dominant soil fauna, and especially enchytraeid worms." Cole *et al.* say they hypothesized warming would lead to increased enchytraeid worm activity, which would lead to higher grazing pressure on microbes in the soil, and since enchytraeid grazing has been observed to enhance microbial activity (Cole *et al.*, 2000), they further hypothesized more carbon would be liberated in dissolved organic form, "supporting the view that

global warming will increase carbon loss from blanket peat ecosystems."

The scientists constructed 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, the former temperature being approximately equal to mean August soil temperature at a depth of 10 cm at the site of soil collection, and the latter being "close to model predictions for soil warming that might result from a doubling of CO₂ in blanket peat environments."

Ten seedlings of an indigenous grass of blanket peat were then transplanted into each of the microcosms, while 100 enchytraeid worms were added to each of half of the mini-ecosystems. These procedures resulted in the creation of four experimental treatments: ambient temperature, ambient temperature + enchytraeid worms, elevated temperature, and elevated temperature + enchytraeid worms. The resulting 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. In addition, throughout the course of the study the microcosms were given distilled water every two days to maintain their original weights.

Contrary to their hypothesis, the scientists found elevated temperature reduced the ability of the enchytraeid worms to enhance the loss of carbon from the microcosms. At the normal ambient temperature, for example, the presence of the worms enhanced dissolved organic carbon (DOC) loss by 16%, and at the elevated temperature expected for a doubling of the air's CO₂ content, the worms had no effect at all on DOC. In addition, Cole *et al.* note, "warming may cause drying at the soil surface, forcing enchytraeids to burrow to deeper subsurface horizons." Hence, since the worms are known to have little influence on soil carbon dynamics below a depth of 4 cm (Cole *et al.*, 2000), the scientists conclude this additional consequence of warming would further reduce the ability of enchytraeids to enhance carbon loss from blanket peatlands.

Summarizing their findings, Cole *et al.* say, "the soil biotic response to warming in this study was negative." That is, it resulted in a reduced loss of carbon to the atmosphere, which would tend to slow

the rate of rise of the air's CO₂ content, as was suggested by the study of Jongmans *et al.*

Maraldo *et al.* (2010) also studied enchytraeids, recognizing their important contribution “to the decomposition processes and nutrient mineralization.” Such activities have been shown to lead to increased nutrient availability and uptake by plants (Laakso and Setälä, 1999; Cragg and Bardgett, 2001). Enchytraeids provide these benefits directly, as Maraldo *et al.* describe it, “by consuming large amounts of organic matter,” and indirectly “by their feeding activity and modifications of soil structure.” They note, “the presence of enchytraeids is especially important in nutrient poor ecosystems” such as “temperate heathland and northern coniferous forests, where their biomass dominates the soil faunal community,” citing Cragg (1961) and Swift *et al.* (1998).

Working on a hilly, nutrient-poor, sandy soil with a dry heath/grassland cover at Brandbjerg, Denmark, Maraldo *et al.* conducted an experiment beginning October 2005 and extending through 2007. The seven scientists studied the individual and combined effects of soil warming, drought, and atmospheric CO₂ enrichment.

They warmed the soil so as to achieve a mean daily temperature increase of 0.3°C in winter and 0.7°C in summer at a depth of 5 cm, using a scaffolding that carried a curtain, which reflected the outgoing infrared radiation from the soil/plant surface back toward the ground, that was automatically pulled over the vegetation at sunset and retracted at sunrise. They achieved drought conditions by reducing peak soil water content by 11 percent and 13 percent compared to control plots in 2006 and 2007, using waterproof curtains that were automatically pulled over the vegetation during rain events. And they used a free-air CO₂ enrichment (FACE) system to increase the air's CO₂ concentration from 382 to 481 ppm.

Maraldo *et al.* report their experimentally imposed warming had no significant impact on enchytraeid biomass production, but their drought treatment decreased it by 40 percent. The extra 99 ppm of CO₂ stimulated enchytraeid biomass by 40 percent. At certain times this latter phenomenon was “especially positive,” as in the summer of 2007, when “the total enchytraeid biomass in the CO₂ plots was increased by 108% compared to ambient plots.” They found no interactions among the three factors, so “the positive effect of increased CO₂ [+40%] and the negative effect of drought [-40%] were cancelled out when applied in combination.”

Bossuyt *et al.* (2005) note “earthworms ingest

large quantities of organic materials that are mixed and excreted as casts (Parmelee *et al.*, 1990; Martin and Marinissen, 1993; Jegou *et al.*, 1998) and improve stable macroaggregation (Guggenberger *et al.*, 1996; Marinissen and Hillenaar, 1996; Scullion and Malik, 2000),” as also has been found by van Rhee (1977), De Vleeschauwer and Lal (1981), and McKenzie and Dexter (1987). In addition, they remark, “the retention of organic C in soil is becoming more important since the rise in atmospheric CO₂ and global warming are recent concerns,” and “earthworms are known to play a role in aggregate formation and soil organic matter (SOM) protection.” However, they say, “it is still unclear at what scale and how quickly earthworms manage to protect SOM.” They conducted a pair of experiments to address that question.

In the first experiment, Bossuyt *et al.* measured soil aggregate size distribution and total C and ¹³C in three treatments—control soil, soil + ¹³C-labeled sorghum leaf residue, and soil + ¹³C-labeled residue + earthworms—after 20 days of incubation, where earthworms were added after the eighth day. In the second experiment, they determined the protected C and ¹³C pools inside the newly formed casts and macro- and micro-soil-aggregates. They found the proportion of large water-stable macroaggregates was on average 3.6 times greater in the soil-residue samples that contained earthworms than in those that lacked earthworms, and the macroaggregates in the earthworm treatment contained approximately three times more sequestered carbon.

Bossuyt *et al.* state, “earthworms were found to form a significant pool of protected C in micro-aggregates within large macroaggregates after 12 days of incubation,” thereby demonstrating the rapidity with which earthworms perform their vital function of sequestering carbon in soils when plant residues become available to them.

Don *et al.* (2008) studied the effects of anecic earthworms—which generally inhabit a single vertical burrow throughout their entire lives that can be as much as five meters in depth but is generally in the range of one to two meters—on soil carbon stocks and turnover at two extensively managed grassland sites in Thuringia, Germany. Analyzing enzyme activity, stable isotopes, nuclear magnetic resonance spectroscopy, and the ¹⁴C age of the earthworm burrow linings, the seven German scientists found “the carbon distribution in soils is changed by anecic earthworms’ activity with more carbon stored in the subsoil where earthworms slightly increase the carbon stocks.” They also state “the translocation of carbon

from [the] organic layer to the subsoil will decrease the carbon vulnerability to mineralization,” because “carbon in the organic layer and the surface soil is much more prone to disturbances with rapid carbon loss than subsoil carbon.”

Don *et al.* note “earthworms are present in almost all ecosystems around the globe with particularly high abundances in grasslands, where they increase productivity (Partsch *et al.*, 2006)” and where “100–800 burrows per square meter have been reported by Lavelle (1988).” The presence and activity of earthworms play important roles in helping Earth’s soils store and preserve carbon—and thereby mitigate the rate of rise of the atmosphere’s CO₂ concentration.

Yeates *et al.* (2003) report a number of results they obtained from a season-long FACE study of a 30-year-old New Zealand pasture, where three experimental plots were maintained at the ambient atmospheric CO₂ concentration of 360 ppm and three others at a concentration of 475 ppm (a CO₂ enhancement of only 32%) for a period of four to five years. The pasture contained about 20 species of plants, including C₃ and C₄ grasses, legumes, and forbs, but the scientists’ attention was focused more on what happened to the microfauna inhabiting the soil in which the plants grew.

Nematode populations increased significantly in response to the 32% increase in the air’s CO₂ concentration. Of the various feeding groups studied, Yeates *et al.* report the relative increase “was lowest in bacterial-feeders (27%), slightly higher in plant (root) feeders (32%), while those with delicate stylets (or narrow lumens; plant-associated, fungal-feeding) increased more (52% and 57%, respectively).” The greatest nematode increases were recorded among omnivores (97%) and predators (105%). Most dramatic, root-feeding populations of the *Longidorus* nematode taxon rose by 330%. Also increasing in abundance were earthworms: *Aporrectodea caliginosa* by 25% and *Lumbricus rubellus* by 58%. Enchytraeids decreased in abundance, by approximately 30%.

Yeates *et al.* note the introduction of lumbricids has been demonstrated to improve soil conditions in New Zealand pastures (Stockdill, 1982), which helps pasture plants grow. Hence, the CO₂-induced increase in earthworm numbers observed in Yeates *et al.*’s study would be expected to do more of the same, and the reduced abundance of enchytraeids they documented in the CO₂-enriched pasture would lead to less carbon being released to the air from the soil, as per the known ability of enchytraeids to promote

carbon loss from British peat lands under current temperatures.

Larsen and Clarke (2002) fed diets with and without coenzyme Q to wild-type nematodes (*Caenorhabditis elegans*) and several mutants during the adult phases of their lives, recording the lengths of time they survived. They found “withdrawal of coenzyme Q (Q) from the diet of wild-type nematodes extends adult life-span by ~60%.” They also report the lifespans of the four mutants they studied were extended by a Q-less diet. More detailed analyses of their results led them to conclude the lifespan extensions were due to reduced generation and increased scavenging of reactive oxygen species.

The results and conclusions of this study are similar to those of Melov *et al.* (2000), who also studied *C. elegans*, testing the theory reactive oxygen species cause aging by examining the effects of two superoxide dismutase-/catalase-like mimetics (EUK–8 and EUK–134) on the lifespans of normal and mutant *C. elegans* worms that ingested various amounts of the mimetics. In every experiment, treatment of normal worms with the antioxidant mimetics significantly increased both mean and maximum lifespan. Treatment of normal worms with but 0.05 mM EUK–134, for example, increased their mean lifespan by fully 54%; in mutant worms whose normal lifespan was genetically shortened by 37%, treatment with 0.5 mM EUK–134 restored their lifespan to normal by increasing their mutation-reduced lifespan by 67%. They also determined these effects were not caused by a reduction in worm metabolism, which could have reduced the production of oxygen radicals, but “by augmenting natural antioxidant defenses without having any overt effects on other traits.”

Melov *et al.* say their results “suggest that endogenous oxidative stress is a major determinant of the rate of aging.” The significance of this statement resides in the fact that antioxidants tend to reduce such stresses in animals, and in the observation atmospheric CO₂ enrichment has been shown to significantly enhance the concentrations of many of these plant constituents (see Antioxidants, Section 7.3.1) as well as the concentrations of several substances that have been proven effective in fighting cancers, viral infections, and other animal maladies (see Health Effects of CO₂, Section 7.3).

It appears earthworms and soil nematodes respond to increases in the air’s CO₂ content, via a number of plant-mediated phenomena, in ways that further enhance the positive effects of atmospheric CO₂ enrichment on plant growth and development,

Terrestrial Animals

while helping to sequester more carbon more securely in the soil and thereby reducing the potential for CO₂-induced global warming.

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Climate Change Reconsidered II: Biological Impacts

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6

Aquatic Life

Key Findings

Introduction

6.1 Ocean Warming

- 6.1.1 Phytoplankton and Macroalgae
- 6.1.2 Corals
- 6.1.3 Crustaceans
- 6.1.4 Fish
- 6.1.5 Other Marine Species

6.2 Freshwater Warming

6.3 Ocean “Acidification”

- 6.3.1 Introduction
- 6.3.2 Effects on Marine Plants
- 6.3.3 Effects on Marine Animals

6.4 Freshwater “Acidification”

- 6.4.1 Algae
- 6.4.2 Macrophytes

6.5 Simultaneous Ocean Warming and “Acidification”

- 6.5.1 Effects on Marine Plants
- 6.5.2 Effects on Marine Animals

Key Findings

The key findings of this chapter, which challenge the alarming and negative projections of United Nations’ Intergovernmental Panel on Climate Change (IPCC), are presented in the bullet points below.

- 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.
- 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.
- 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 of the amount forecast by IPCC.
- 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.

- 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 atmospheric CO₂ levels do not pose a significant threat to aquatic life. Many aquatic species have shown considerable tolerance to declining pH values predicted for the next few centuries, and many have demonstrated a likelihood of positive responses in empirical studies.
- The projected decline in ocean pH levels in the year 2100 (as compared to preindustrial times) may be significantly overstated, amounting to only half of the 0.4 value IPCC predicts.
- The natural variability of oceanic pH is often 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.
- For those aquatic species showing negative responses to pH declines in experimental studies, 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.

Introduction

Some observers have suggested rising atmospheric carbon dioxide (CO₂) concentrations may harm aquatic life via global warming, in which the temperatures of the world's water bodies rise, and through the absorption of additional CO₂ from the air into water, thereby lowering the pH of the waters to which aquatic life is accustomed. IPCC projects

marine and freshwater species will be negatively affected by these processes and will experience future declines, in some instances so severe as to cause species extinctions.

In contrast, the material presented in this chapter, 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 have demonstrated growth and developmental improvements in response to higher temperatures and reduced water pH levels. Other research has illustrated the capability of marine and freshwater species to tolerate and adapt to rising temperature and pH decline of the planet's water bodies. When such observations are considered, the pessimistic projections of IPCC give way to considerable optimism with respect to the future of the planet's marine life.

This chapter begins by summarizing research on the impact of rising ocean temperatures on phytoplankton and macroalgae, corals, crustaceans, fish, and other marine species. Researchers have found repeatedly that many species benefit rather than suffer from rising temperatures, including temperature increases forecast by IPCC. Section 6.2 examines research on the effects of warmer temperatures on freshwater species. Much less research has been conducted in this area, but it too highlights beneficial effects of warming on phytoplankton, several species of fish, and freshwater mussels.

Section 6.3 addresses the threat of so-called "ocean acidification." The phrase is an improper choice because natural seawater is basic (alkaline), with an average pH level typically around 8.1, and the oceans will never become acidic (below 7.0) due to IPCC's worst-case scenarios of future anthropogenic CO₂ emissions. The prospect of oceans and lakes becoming "acidic" is frightening to the general public, and rightly so. While many scientists conducting research in this area use the term, perhaps to attract public attention to their work, more accurate and less judgmental phrases are "lower oceanic pH," "lower seawater pH levels," and "ocean pH reduction." The research summarized in this section makes it clear that rising atmospheric CO₂ levels do not pose as significant a threat to aquatic life as claimed by IPCC. Many aquatic species have shown considerable tolerance to declining pH values predicted for the next few centuries, and many have demonstrated a likelihood of positive responses in empirical studies.

Section 6.4 summarizes research on freshwater

“acidification.” The number of studies examining this topic is dramatically smaller than the number concerning oceans, but those highlighted here reveal findings typically more positive than negative.

Section 6.5 investigates research on the combined effects of rising temperatures and falling pH levels on marine plants and animals. Research in this area is not as plentiful, but what exists is generally reassuring: Many studies show the combination of higher temperatures and falling pH levels to be beneficial, not harmful, to marine life.

6.1 Ocean Warming

According to IPCC, global warming will warm the planet’s oceans, resulting in catastrophic effects on marine plants and animals. In a draft of the Summary for Policymakers of its contribution to IPCC’s Fifth Assessment Report, Working Group II claims “Open-ocean net primary production is projected to redistribute and to fall globally by 2100 under RCP8.5. Climate change adds to threats of over-fishing and other non-climatic stressors, thus complicating marine management regimes (*high confidence*)” (IPCC 2014-II, p. 9). More warnings along these lines appear in Working Group II’s draft full report, as shown by excerpts presented at the beginning of Section 6.1.2 below.

IPCC’s frequent description of the modern rise in global temperature as “unprecedented” suggests there already should be signs of negative impacts on oceanic productivity and marine life, but a review of the scholarly literature on this subject reveals just the opposite: Productivity is rising and species are flourishing, except in cases where human activities such as over-fishing, pollution, generation of silt, and other damaging practices are to blame. The studies highlighted in this section yield little evidence to support IPCC’s point of view.

6.1.1 Phytoplankton and Macroalgae

This section examines research on the impacts of ocean warming on marine phytoplankton and macroalgae. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings.

- Several observation-based analyses reveal phytoplankton productivity has increased over the past several decades in response to the instrumental-era rise in temperature.
 - Evidence suggests marine plants are well-equipped to adapt and evolve to forecasted increases in future temperature, as they have done so in responding to decadal, centennial, and millennial-scale climate oscillations that have persisted for millions of years.
- Sarmiento *et al.* (2004) conducted a massive computational study employing six coupled climate model simulations to determine the biological response of the global ocean to climate warming they simulated from the beginning of the Industrial Revolution to the year 2050. Based on vertical velocity, maximum winter mixed-layer depth, and sea-ice cover, they defined six biomes and calculated how their surface geographies would change in response to their calculated changes in global climate. Next, they used satellite ocean color and climatological observations to develop an empirical model for predicting surface chlorophyll concentrations from the final physical properties of the world’s oceans as derived from their global warming simulations. They then used three primary production algorithms to estimate the response of oceanic primary production to climate warming based on their calculated chlorophyll concentrations. The 13 scientists from Australia, France, Germany, Russia, the United Kingdom, and the United States arrived at a global warming-induced increase in global ocean primary production ranging from 0.7 to 8.1%.
- In addition to Sarmiento *et al.*’s model-based study, a number of real-world observations also suggest IPCC’s concerns about future declines in ocean productivity in response to rising temperatures are unfounded. Goes *et al.* (2005) analyzed seven years (1997–2004) of satellite-derived ocean surface phytoplankton productivity data, as well as associated sea surface temperatures (SSTs) and winds in the Arabian Sea. They report for the region located between 52 to 57°E and 5 to 10°N, “the most conspicuous observation was the consistent year-by-year increase in phytoplankton biomass over the 7-year period.” This change was so significant that by the summer of 2003, they write, “chlorophyll *a* concentrations were >350% higher than those observed in the summer of 1997.” They also report the increase in chlorophyll *a* was “accompanied by an intensification of sea surface winds, in particular of

the zonal (east-to-west) component,” noting these “summer monsoon winds are a coupled atmosphere-land-ocean phenomenon, whose strength is significantly correlated with tropical SSTs and Eurasian snow cover anomalies on a year-to-year basis.” They write, “reduced snow cover over Eurasia strengthens the spring and summer land-sea thermal contrast and is considered to be responsible for the stronger southwest monsoon winds.” They note “the influence of southwest monsoon winds on phytoplankton in the Arabian Sea is not through their impact on coastal upwelling alone but also via the ability of zonal winds to laterally advect newly upwelled nutrient-rich waters to regions away from the upwelling zone.” They conclude, “escalation in the intensity of summer monsoon winds, accompanied by enhanced upwelling and an increase of more than 350% in average summertime phytoplankton biomass along the coast and over 300% offshore, raises the possibility that the current warming trend of the Eurasian landmass is making the Arabian Sea more productive.”

Drinkwater (2006) examined marine ecosystems of the North Atlantic, determining “in the 1920s and 1930s, there was a dramatic warming of the air and ocean temperatures in the northern North Atlantic and the high Arctic, with the largest changes occurring north of 60°N.” This warming “led to reduced ice cover in the Arctic and subarctic regions and higher sea temperatures,” as well as northward shifts of multiple marine ecosystems. This early twentieth century warming “contributed to higher primary and secondary production,” Drinkwater writes, and “with the reduced extent of ice-covered waters, more open water allow[ed] for higher production than in the colder periods.”

McGregor *et al.* (2007) state, “coastal upwelling occurs along the eastern margins of major ocean basins and develops when predominantly along-shore winds force offshore Ekman transport of surface waters, which leads to the ascending (or upwelling) of cooler, nutrient-rich water.” They note these regions of coastal upwelling account for about 20% of the global fish catch while constituting less than 1% of the area covered by the world’s oceans. To better understand this productivity-enhancing phenomenon of great practical and economic significance, they studied its long-term history along the northwest coast of Africa—in the heart of the Cape Ghir upwelling system off the coast of Morocco—by analyzing two sediment cores having decadal-or-better resolution that extend from the late Holocene to the end of the twentieth century—from 520 BC to AD 1998.

The four researchers found an anomalous cooling of sea surface temperatures during the twentieth century, which they say “is consistent with increased upwelling.” They note, the “upwelling-driven sea surface temperatures also vary out of phase with millennial-scale changes in Northern Hemisphere temperature anomalies and show relatively warm conditions during the Little Ice Age and relatively cool conditions during the Medieval Warm Period.”

McGregor *et al.* offer an explanation for how this happens, posing a scenario that starts with an impetus for warming that leads to near-surface air temperatures over land becoming warmer than those over the ocean. The greater warming over the land “deepens the thermal low-pressure cell over land while a higher-pressure center develops over the slower-warming ocean waters.” As this occurs, “winds blow clockwise around the high and anticlockwise around the continental low.” With the coast representing the boundary between the two centers, the resulting wind is “oriented alongshore and southward (equator-ward), which thus drives the upwelling and negative sea surface temperature anomalies.”

McGregor *et al.* say similar anti-phased thermal behavior—the cooling of coastal waters that leads to enhanced coastal upwelling during periods of hemispheric or global warming—has been observed in the Arabian Sea and along the Iberian margin, as well as in parts of the California Current and the Peru-Chile Current. This suggests as global warming enhances the upwelling of cooler nutrient-rich waters along the eastern margins of major ocean basins, it helps to significantly enhance global-ocean primary productivity, which leads to an increase in global-ocean secondary productivity, as represented by the global fish catch.

Boyd *et al.* (2007) reported somewhat analogous findings in their review of iron enrichment experiments conducted between 1993 and 2005. These experiments conclusively demonstrate, they write, “phytoplankton grow faster in warmer open-ocean waters, as predicted by algal physiological relationships.” These findings indicate total ocean productivity should have benefited immensely from twentieth century global warming and likely will continue to benefit from continued global warming.

Marasovic *et al.* (2005) analyzed monthly observations of basic hydrographic, chemical, and biological parameters, including primary production, made since the 1960s at two oceanographic stations, one near the coast of Croatia (Kastela Bay) and one in the middle Adriatic Sea. They found mean annual

primary production in Kastela Bay averaged about $430 \text{ mg C m}^{-2} \text{ d}^{-1}$ over the period 1962–1972, exceeded $600 \text{ mg C m}^{-2} \text{ d}^{-1}$ in 1972–1982, and rose to more than $700 \text{ mg C m}^{-2} \text{ d}^{-1}$ in 1982–1996, accompanied by a similar upward trend in percent oxygen saturation of the surface water. The initial value of primary production in the open sea was much less (approximately $150 \text{ mg C m}^{-2} \text{ d}^{-1}$), but it began to follow the upward trend of the Kastela Bay data after about one decade. Marasovic *et al.* conclude, “even though all the relevant data indicate that the changes in Kastela Bay are closely related to an increase of anthropogenic nutrient loading, similar changes in the open sea suggest that primary production in the Bay might, at least partly, be due to global climatic changes,” which are “occurring in the Mediterranean and Adriatic Sea open waters” and may be directly related to “global warming of air and ocean” because “higher temperature positively affects photosynthetic processes.”

Raitsos *et al.* (2005) investigated the relationship between Sea-viewing Wide Field-of-view Sensor (SeaWiFS) chlorophyll *a* measurements in the Central Northeast Atlantic and North Sea (1997–2002) and simultaneous measurements of the Phytoplankton Color Index (PCI) collected by the Continuous Plankton Recorder survey, an upper-layer plankton monitoring program that has operated in the North Sea and North Atlantic Ocean since 1931. By developing a relationship between the two databases over their five years of overlap, the scientists were able to produce a Chl-*a* history for the Central Northeast Atlantic and North Sea for the period 1948–2002. Of this record they say “an increasing trend is apparent in mean Chl-*a* for the area of study over the period 1948–2002.” They report “there is clear evidence for a stepwise increase after the mid-1980s, with a minimum of 1.3 mg m^{-3} in 1950 and a peak annual mean of 2.1 mg m^{-3} in 1989 (62% increase).” Alternatively, the data may represent a steadier long-term upward trend upon which is superimposed a decadal-scale oscillation. In a final comment on their findings, they note, “changes through time in the PCI are significantly correlated with both sea surface temperature and Northern Hemisphere temperature,” citing Beaugrand and Reid (2003).

Antoine *et al.* (2005) applied revised data-processing algorithms to two ocean-sensing satellites, the Coastal Zone Color Scanner (CZCS) and SeaWiFS, over the periods 1979–1986 and 1998–2002, respectively, to provide an analysis of the decadal changes in global oceanic phytoplankton

biomass. The results showed “an overall increase of the world ocean average chlorophyll concentration by about 22%” over the two decades under study.

Hirawake *et al.* (2005) analyzed chlorophyll *a* data obtained from Japanese Antarctic Research Expedition cruises made on the Southern Ocean by the Fuji and Shirase icebreakers between Tokyo and Antarctica from 15 November to 28 December of nearly every year between 1965 and 2002 in a study of interannual variations of phytoplankton biomass, calculating results for the equatorial region between 10°N and 10°S , the Subtropical Front (STF) region between 35°S and 45°S , and the Polar Front (PF) region between 45°S and 55°S . They found an increase in chl *a* “in the waters around the STF and the PF, especially after 1980 around the PF in particular,” and “in the period between 1994 and 1998, the chl *a* in the three regions exhibited rapid gain simultaneously.” They also found “significant correlations between chl *a* and year through all of the period of observation around the STF and PF, and the rates of increase are 0.005 and $0.012 \text{ mg chl } a \text{ m}^{-3} \text{ y}^{-1}$, respectively.” They report the satellite data of Gregg and Conkright (2002) “almost coincide with our results.” The Japanese scientists note, “simply considering the significant increase in the chl *a* in the Southern Ocean, a rise in the primary production as a result of the phytoplankton increase in this area is also expected.”

Sepulveda *et al.* (2005) presented “the first reconstruction of changes in surface primary production during the last century from the Puyuhuapi fjord in southern Chile, using a variety of parameters (diatoms, biogenic silica, total organic carbon, chlorins, and proteins) as productivity proxies.” Noting the fjord is located in “a still-pristine area,” they state it is “suitable to study changes in past export production originating from changes in both the paleo-Patagonian ice caps and the globally important Southern Ocean.”

They found the productivity of the Puyuhuapi fjord “was characterized by a constant increase from the late 19th century to the early 1980s, then decreased until the late 1990s, and then rose again to present-day values.” For the first of these periods (1890–1980), they report “all proxies were highly correlated ($r > 0.8$, $p < 0.05$)” and “all proxies reveal an increase in accumulation rates.” From 1980 to the present, the pattern differed among the various proxies. The researchers state, “considering that the top 5 cm of the sediment column (~10 years) are diagenetically active, and that bioturbation by benthic organisms may have modified and mixed the sedi-

mentary signal, paleo-interpretation of the period 1980–2001 must be taken with caution.” Their work provides substantial solid evidence that, for the first 90 years of the 111-year record, surface primary production in the Puyuhuapi fjord rose dramatically, and with lesser confidence it appears to have leveled out over the past two decades.

While IPCC worries recent “unprecedented” increases in mean global air temperature and CO₂ concentration have been bad for the biosphere, Sepulveda *et al.* present yet another case of an ecosystem apparently thriving in such conditions. Nevertheless, claims of impending ocean productivity declines have not ceased, and the study of Behrenfeld *et al.* (2006) is often cited as support of such claims. Working with NASA’s Sea-viewing Wide Field-of-view Sensor (SeaWiFS), the team of 10 U.S. scientists calculated monthly changes in net primary production (NPP) from similar changes in upper-ocean chlorophyll concentrations detected from space over the past decade. They report this period was dominated by an initial NPP increase of 1,930 teragrams of carbon per year (Tg C yr⁻¹), which they attributed to the significant cooling of “the 1997 to 1999 El Niño to La Niña transition,” and they note this increase was “followed by a prolonged decrease averaging 190 Tg C yr⁻¹,” which they attributed to subsequent warming.

The researchers’ explanation for the means by which changing temperatures drove the two trends in NPP is based on their presumption a warming climate increases the density contrast between warmer surface waters and cooler underlying nutrient-rich waters. The enhanced stratification that occurs with warming, they say, “suppresses nutrient exchange through vertical mixing,” which decreases NPP by reducing the supply of nutrients to the surface waters where photosynthesizing phytoplankton predominantly live. The scientists suggest “surface cooling favors elevated vertical exchange,” by contrast, which increases NPP by enhancing the supply of nutrients to the ocean’s surface waters, which have a greater concentration of phytoplankton than the underlying waters do because of light requirements for photosynthesis.

Real-world observations raise questions about that explanation. From approximately the middle of 2001 to the end of the data series in early 2006 (which accounts for more than half the data record), there has been, if anything, a slight increase in global NPP. Does this observation mean there has been little or no net global warming since mid-2001? Or does it mean the global ocean’s mean surface temperature declined over that five-year period? Neither alternative accords

with the model-based projections of CO₂-induced climate warming.

The relationship between global warming and oceanic productivity may not be nearly as strong as what Behrenfeld *et al.* suggest. They leave themselves significant wiggle room in this regard, stating, “modeling studies suggest that shifts in ecosystem structure from climate variations may be as [important as] or more important than the alterations in bulk integrated properties reported here,” noting some “susceptible ecosystem characteristics” that might shift include “taxonomic composition, physiological status, and light absorption by colored dissolved organic material.” Given enough time, then, the phenomena Behrenfeld *et al.* describe could result in important “shifts in ecosystem structure” that could compensate, or even overcompensate, for what might initially appear to be negative warming-induced consequences.

Another reason for not concluding too much from the Behrenfeld *et al.* oceanic NPP dataset is that it may be of too short a duration to reveal what might be occurring on a longer timescale throughout the world’s oceans, or its position in time may prevent the detection of greater short-term changes of the opposite sign that may have occurred a few years earlier or might occur in the near future. The central regions of the world’s major oceans were long thought to be essentially vast biological deserts (Ryther, 1969), but several studies of primary photosynthetic production conducted in those regions in the 1980s (Shulenberger and Reid, 1981; Jenkins, 1982; Jenkins and Goldman, 1985; Reid and Shulenberger, 1986; Marra and Heinemann, 1987; Laws *et al.*, 1987; Venrick *et al.*, 1987; Packard *et al.*, 1988) yielded results that suggest marine productivity at that time was at least twice as great as it likely was for a long time before 1969, causing many scientists of that day to speculate “the ocean’s deserts are blooming” (Kerr, 1986).

Of even greater interest, perhaps, the 1970–1988 dataset of Jones *et al.* (1999) indicates Earth underwent a linear-regression-derived global warming of 0.333°C; the database of the Global Historical Climatology Network indicates the planet experienced a similarly calculated global warming of 0.397°C. The mean of these two values (0.365°C) is nearly twice as great as the warming that occurred over the post-1999 period studied by Behrenfeld *et al.*, yet this earlier much larger warming—which Behrenfeld *et al.*’s work suggests should have produced a major decline in ocean productivity—was accompanied by a huge increase in ocean produc-

tivity. It would appear Behrenfeld *et al.* got the cause-and-effect relationship between global warming and ocean productivity exactly backwards.

Since publication of the Behrenfeld *et al.* study, other researchers have found no cause for alarm with respect to ocean productivity and rising global temperatures. Arrigo *et al.* (2008) write, “between the late 1970s and the early part of the 21st century, the extent of Arctic Ocean sea ice cover has declined during all months of the year, with the largest declines reported in the boreal summer months, particularly in September ($8.6 \pm 2.9\%$ per decade),” citing Serreze *et al.* (2007). To “quantify the change in marine primary productivity in Arctic waters resulting from recent losses of sea ice cover,” the authors “implemented a primary productivity algorithm that accounts for variability in sea ice extent, sea surface temperature, sea level winds, downwelling spectral irradiance, and surface chlorophyll *a* concentrations,” and “was parameterized and validated specifically for use in the Arctic (Pabi *et al.*, 2008) and utilizes forcing variables derived either from satellite data or NCEP reanalysis fields.”

Arrigo *et al.* determined “annual primary production in the Arctic increased yearly by an average of 27.5 Tg C per year since 2003 and by 35 Tg C per year between 2006 and 2007.” Thirty percent of the increase was attributable to decreased minimum summer ice extent, and 70% was due to a longer phytoplankton growing season. Arrigo *et al.* conclude if the trends they discovered continue, “additional loss of ice during Arctic spring could boost productivity >3-fold above 1998–2002 levels.” If the 26% increase in annual net CO₂ fixation in the Arctic Ocean between 2003 and 2007 continues, they state, “this would represent a weak negative feedback on climate change.”

Smith and Comiso (2008) employed phytoplankton pigment assessments, surface temperature estimates, modeled irradiance, and observed sea ice concentrations—all derived from satellite data—and incorporated them into a vertically integrated production model to estimate primary productivity trends according to the technique of Behrenfeld *et al.* (2002). The two authors state “the resultant assessment of Southern Ocean productivity is the most exhaustive ever compiled and provides an improvement in the quantitative role of carbon fixation in Antarctic waters.”

Over the nine years (1997–2006) analyzed in the study, “productivity in the entire Southern Ocean showed a substantial and significant increase,” and

this increase can be calculated from the graphical representation of their results as ~17% per decade. The two researchers note “the highly significant increase in the productivity of the entire Southern Ocean over the past decade implies that long-term changes in Antarctic food webs and biogeochemical cycles are presently occurring,” and these changes are positive.

Peck *et al.* (2010) note the loss of glaciers and ice shelves at the Antarctic Peninsula is often thought of as something that “will predominantly increase warming of the Earth because of changes in albedo and heat uptake by newly uncovered ground and ocean.” They state an important opposing effect of this phenomenon “is the opening up of new areas for biological productivity.”

Working with the database of Cook *et al.* (2005), which contains a detailed centennial history of changes in all coastal ice fronts associated with the Antarctic Peninsula compiled from historical accounts, aerial photographs, and satellite imagery, Peck *et al.* developed a time series of changes in the surface ice/water boundary surrounding the Antarctic Peninsula since the early twentieth century. Complementing this information with a 10-year time series of chlorophyll depth profiles (1997–2007) from a near-shore site in northern Marguerite Bay developed by Clarke *et al.* (2008), Peck *et al.* reconstructed the magnitude of new oceanic production that developed around the Antarctic Peninsula as sea ice progressively gave way to open water.

The five researchers with the British Antarctic Survey report as the ice cover along the Antarctic Peninsula has retreated over the past 50 years, “more than 0.5 Mtonnes of carbon has been incorporated into biological standing stock that was not there previously, 3.5 Mtonnes is fixed by phytoplankton blooms and 0.7 Mtonnes deposited to the seabed.” They state if only 15% of the remaining ice-covered areas act in the same way, “over 50 Mtonnes of new carbon would be fixed annually and around 10 Mtonnes of this deposited to the seabed in coastal or adjacent areas,” and “over 9 Mtonnes of carbon would be locked up in biological communities in the water column or on the sea bed.” They suggest over a period of tens, hundreds, or thousands of years, “this process may act as a climate control mechanism.”

Brown *et al.* (2011) investigated the widespread assumption the Bering Sea is “rapidly warming and losing sea ice” by employing “satellite-derived sea ice concentration, sea surface temperature, and ocean color data as input to a primary productivity algorithm to take stock of environmental change and

primary production” in this region. As the three U.S. researchers report, “rather than declining,” they found mean annual sea ice extent in the Bering Sea “has exhibited no significant change over the satellite sea ice record (1979–2009),” because significant warming during the satellite sea surface temperature record (1982–2009) “is mainly limited to the summer months.” In addition, and despite certain hotspots of primary production and a strong pulse in the spring, they also determined “the rate of annual area-normalized primary production in the Bering Sea (124 g C per m² per year) is below the global mean (140 g C per m² per year).” By “comparing warm, low-ice years (2001–2005) with cold, high-ice years (1998–2000 and 2006–2007),” they conclude “Bering Sea primary productivity is likely to rise under conditions of future warming and sea ice loss.” That rise could be substantial, as they report, “basin-wide annual primary production ranged from 233 to 331 Tg C per year under the influence of highly variable sea ice and temperature conditions.”

Chavez *et al.* (2011) reviewed the concepts and methods used to estimate ocean primary production (PP), after which they used the modern global instrumental record of sea surface temperature (SST) to analyze the principal modes of interannual to multidecadal climate and ocean variability. They then compared spatiotemporal patterns derived from *in situ* and satellite time-series of PP with the known time-series of climate and ocean variability, to identify the processes responsible for the observed patterns in PP. They introduced paleoclimate studies into their work to broaden the temporal context and “lead into speculation regarding century-scale variability.”

Based on the first part of their analysis, the three researchers from the Monterey Bay Aquarium Research Institute of Moss Landing, California (USA) write, “general conclusions from the satellite and *in situ* time-series presented here are that PP is increasing globally,” and they note global marine PP appears to have risen over the past several decades in association with multidecadal variations in climate. They report data from Continuous Plankton Recorder surveys conducted in the north Atlantic depict “increases in chlorophyll from the 1950s to the present,” citing McQuatters-Gollop *et al.* (2007).

In the second part of their analysis, Chavez *et al.* report ocean sediment cores containing an “undisturbed history of the past” have been analyzed for variations in PP over timescales that include the Little Ice Age (LIA, ~1400–1800; Gutierrez *et al.*, 2009). Based on reconstructed flux rates of total organic carbon (Sifeddine *et al.*, 2008); diatoms, silica, and

fish scales; bones; and vertebrae, they determined during the LIA the ocean off Peru had “low PP, diatoms and fish,” but “at the end of the LIA, this condition changed abruptly to the low subsurface oxygen, eutrophic upwelling ecosystem that today produces more fish than any region of the world’s oceans (Chavez *et al.*, 2008).” The researchers conclude, “in coastal environments, PP, diatoms and fish and their associated predators are predicted to decrease and the microbial food web to increase under global warming scenarios,” citing Ito *et al.* (2010). However, they write, “present-day trends and the sedimentary record seem to indicate that the opposite might occur.”

Tremblay *et al.* (2011) note the Canadian Beaufort Shelf and adjacent bays make up a small part of the Arctic Ocean but are of “prime social, economical and cultural importance” for coastal communities because they are “hotspots of marine productivity and staging” and “feeding areas for large aggregations of resident and migrant marine birds and mammals,” citing Carmack and MacDonald (2002). Wondering what would happen to the productivity of this important coastal region if it were to warm further, Tremblay *et al.* set out to compare time series of ice cover, wind forcing, and satellite-based assessments of photosynthetic carbon production for the years 2002–2008 with corresponding *in situ* measurements of salinity, nutrients, new production, biological stocks, and biogenic fluxes obtained during overwintering surveys in 2003–2004 and 2007–2008.

In 2007–2008, the 15 researchers report, in areas where ice was no longer present due to enhanced seasonal warming, there was significant wind-induced upwelling of growth-promoting nitrates, which were brought up from deep and dark waters into the euphotic zone, where photosynthesis occurs. As a result of this fertilization effect, the herbivorous copepod *Calanus glacialis*—which they say is “the key link between diatom production and apex consumers on Arctic shelves,” citing Soreide *et al.* (2010)—experienced a total abundance “3 to 33 times higher than in 2003 during mid-fall and 1.6 to 13 fold higher than in 2004 during early summer.”

On the region’s central shelf, they observed “sedimentary chlorophyll *a* was over 20-fold higher than at any station not influenced by upwelling,” and “benthic carbon demand was among the highest ever observed in the Arctic ocean,” citing Clough *et al.* (2005). The end result of these related phenomena was the “repeated instances of ice ablation and upwelling during fall 2007 and summer 2008 multiplied the production of ice algae, phytoplankton,

zooplankton and benthos by 2 to 6 fold.”

Tremblay *et al.* conclude the phenomena they observed are “likely to prevail with the increasingly deep and frequent seaward retreat of the central ice pack and the greater incidence of upwelling-favorable winds,” as described in detail by Yang (2009), and “new production is also bound to rise as winds gain in intensity and upwelling draws deeper into the nutrient-rich, upper Pacific halocline.”

McMinn and Martin (2013) note “most algae regularly experience periods of darkness ranging from a few hours to a few days,” during which time “they are unable to photosynthesize, and so must consume stored energy products.” The scientists note “some organisms such as polar algae and some microalgal cysts and spores are exposed to darkness for months to years, and these must use alternative strategies to survive.” McMinn and Martin—who work at the University of Tasmania’s Institute for Marine and Antarctic Studies—reviewed the scientific literature on this subject and found “some taxa, such as dinoflagellates, form cysts and become dormant,” while “others use physiological methods or adopt mixotrophy,” and “the longest documented survival of more than a century was for dinoflagellates buried in sediments in a Norwegian fjord.” In the future, they opine, polar microalgae will have to survive “the same period of seasonal darkness but at higher temperatures, and this will require a greater drawdown of stored energy.” McMinn and Martin report “recent experimental work has shown that both Arctic [Martin *et al.*, 2012] and Antarctic [Reeves *et al.*, 2011] phytoplankton are able to survive increases of up to 6°C in the dark.” Because such a temperature increase is “unlikely to be experienced in a few centuries as a result of climate change,” polar microalgae should be safe for a long, long time to come.

According to Aberle *et al.* (2012), in places such as the Baltic Sea a “temporal match of zooplankton peaks with the spring phytoplankton bloom is required to provide an efficient energy transfer up the food web at the start of the growing season,” but some scientists have predicted “warming will affect the different trophic levels unequally” and result in a counterproductive “temporal mismatch between predators and their prey.” Aberle *et al.* conducted a set of indoor mesocosm experiments “to analyze time-lags between phytoplankton and micro-zooplankton during the spring succession of Baltic Sea plankton in relation to changing temperature [0 and 6°C above the decadal mean] and light conditions,” along with “model simulations using a

modified Rosenzweig and MacArthur (1963) predator-prey model incorporating temperature-dependent growth, grazing and mortality rates of autotrophic and heterotrophic components.”

The five German scientists say “during the experiments, we observed reduced time-lags between the peaks of phytoplankton and protozoan biomass in response to warming,” adding “warming induced a shift in micro-zooplankton phenology leading to a faster species turnover.” The models they employed also “predicted reduced time-lags between the biomass peaks of phytoplankton and its predators (both micro-zooplankton and copepods) with warming.” Aberle *et al.* conclude their study shows “instead of a mismatch, warming might lead to a stronger match between protist grazers and their prey.”

Renaudie *et al.* (2010) conducted a quantitative micropalaeontological analysis of siliceous phytoplankton remains found in a sediment core extracted from the seabed at an ocean depth of 2,549 meters at ODP Site 1260 (~9.2°N, 54.65°W) on the Demerara Rise, a continental shelf located off the coast of Surinam, focusing on a 200,000-year period of warmth during the Eocene between approximately 40.0 and 40.2 million years ago. The five French scientists found “the pre-warming flora, dominated by cosmopolitan species of the diatom genus *Triceratium*, was replaced during the warming interval by a new and more diverse assemblage, dominated by *Paralia sulcata* (an indicator of high productivity) and two endemic tropical species of the genus *Hemiaulus*.” They found “the critical warming interval was characterized by a steady increase in tropical species of the genus *Hemiaulus*.” They also state, “the microflora preserved above the critical interval was once again of low diversity and dominated by various species of the diatom genus *Hemiaulus*.” Renaudie *et al.*’s findings establish warmer is better, a maxim exemplified in the current case by the greater productivity of the tropical ocean during the warmer period and the ocean’s continuous upward trend in the diversity of phytoplanktonic species throughout the period of warming.

Cermeño (2011) states “micro-organisms dominate terrestrial, aquatic and aerial ecosystems and largely rule our planet’s life by playing pivotal roles in global biogeochemical cycles,” citing Staley and Fuhrman (2002) and Falkowski *et al.* (2008). He declares these facts indicate “life on Earth is microbe dependent.” Cermeño used records of climatic variability and microfossil data from the world’s oceans covering the past 65 million years to “explore the

linkage between the rate of climate change and the probability of extinction, origination and net diversification of marine planktonic diatoms and calcareous nannoplankton,” analyzing the evolutionary dynamics of the two phytoplankton groups throughout the 65-million-year period of study and comparing the results with the climate change record.

Cermeño states his findings demonstrate “the probability of extinction of microbial plankton species did not increase during periods of enhanced climatic instability over the past 65 million years.” He says his results show “exceptional climatic contingencies, such as those occurring across the Late Palaeocene-Eocene and the Eocene-Oligocene boundary transitions, caused substantial morphological diversification.” Cermeño concludes, “to the extent that contemporaneous trends in climate change have analogies with the climates of the geological period analyzed here, my results suggest that these microbial plankton groups will persist in the future ocean, perhaps even expanding their ranges of morphological diversity.”

Cannariato *et al.* (1999) provide additional evidence marine biota are well-equipped to adapt to rising temperatures. They investigated the character, magnitude, and speed of responses of benthic foraminifera to millennial-scale climate oscillations manifest in data obtained from an ocean sediment core in the Santa Barbara Basin of the Northeast Pacific that covered the most recent 60,000 years. Although a number of rapid climatic switches were noted throughout the record, representing periods of “extreme environmental variability,” the scientists found no extinctions, and the benthic ecosystems “appear to be both resilient and robust in response to rapid and often extreme environmental conditions.” Although faunal turnovers occurred within decades, they did so “without extinction or speciation.”

Ladah *et al.* (1999) examined the density and population structure of giant kelp “forests” located near Bahia Tortugas, Baja California, Mexico, before, during, and after the 1998 El Niño. At the height of the extreme warming event, sea surface temperatures (SSTs) were 3°C higher than the previous 10-year average for this region, and they led to the complete disappearance of the giant kelp that historically had inhabited the area. However, when the SST anomalies subsided, the giant kelp were once again found to be growing there, and from evidence derived from population structure data and the rapidity with which the plants reestablished themselves, Ladah *et al.* deduced “a microscopic stage that was not visible during dive surveys survived the stressful conditions

of ENSO and caused the recruitment event, supporting the hypothesis that a bank of microscopic forms can survive conditions stressful to macroscopic algae.” They note there was independent evidence to suggest “microscopic stages may subsist in nature under low light intensities in a semi-dormant state until conditions become favorable.”

In a follow-up study published several years later, Ladah and Zertuche-Gonzalez (2004) found a second and more likely predominant means by which the return of the giant kelp was made possible. Although all giant kelp growing at 15 m depth or shallower died during the peak warmth of the El Niño, the pair of researchers discovered there were numerous large fertile adults located between 25 and 40 m depth unaffected by the high surface water temperatures. Although the upper 15 meters of these plants died and sloughed off, regenerated fronds reached the surface of the sea by the fall of 1998.

The two scientists write, “survival in deep water during this extreme El Niño may have been due to local hydrography, such as internal waves bringing cool nitrate-rich water into the deeper regions of the shelf from below the thermocline, providing a refugium against the warm temperatures, low nutrients, and heavy wave action associated with warming events.” They also note “the increased light that often occurs after canopy removal apparently resulted in ... recruitment events ... from newly produced spores from nearby fertile individuals surviving in deeper waters.” They conclude “deep-water populations may regularly survive El Niño warming in this region due to internal wave activity, and go undetected due to the depth at which they occur and the sloughing of the shallow (<15 m) biomass.”

Zheng *et al.* (2012) state dinoflagellates “are generally believed to prefer warm temperatures and presumably may do better in the face of temperature increases,” noting *Prorocentrum donghaiense* was able to grow at temperatures ranging from 10 to 27°C and achieved its maximum specific growth rate at the latter temperature (Xu *et al.*, 2010). For *P. minimum*, they note, “growth rates increased from 0.25/day at 4°C to 0.98/day at 20°C,” citing Lomas and Gilbert (1999a,b). They report the composition of phytoplankton exposed to a temperature rise in the vicinity of a nuclear power plant’s thermal effluent “tipped toward dinoflagellates both in terms of species number and cell abundance (Li *et al.*, 2011),” probably because “some dinoflagellates were found to produce heat-shock proteins to stabilize protein secondary structure in response to thermal stress

(Alexandrov, 1994).” They further note, “heat shock protein 70 was induced in *Alexandrium tamarense* when subjected to a 10°C jump from its acclimated temperature of 20°C (Kobiyama *et al.*, 2010).”

Zheng *et al.* studied the effects of temperature shock on the growth of the dinoflagellate *Polarella glacialis*, “by monitoring its physiological and biochemical responses to temperature rises from 4°C to 10 and 15°C” while examining the growth rate and expression of two important genes for this alga. The three researchers state, “it is noteworthy that in the present study the cultures were directly transferred from 4°C to 10 and 15°C without progressive intermediate steps,” and in response to these sudden temperature shifts, “the cultures first experienced a period of declination, then cell density tended to become stable, a sign that a part of the cell population survived.” Zheng *et al.* conclude, “if the species can survive such heat shock in the long term, there is good opportunity that it can be transported from polar regions to temperate or even warmer waters,” which perhaps explains why “taxa closely related to this species occur in temperate aquatic environments (Lin *et al.*, 2009, 2010).” If *P. glacialis* and related species can do that, they should have no problem coping with projected global warming.

Clark *et al.* (2013) used “a quantitative genetic breeding design to establish whether there is a heritable variation in thermal sensitivity in two populations of a habitat-forming intertidal macroalga, *Hormosira banksii* (Turner) Descaisne,” in which “gametes from multiple parents were mixed and growth and photosynthetic performance were measured in the resulting embryos, which were incubated under control and elevated temperatures (20°C and 28°C).” The four researchers report “significant interactions between male genotype and temperature in one population indicated the presence of genetic variation in thermal sensitivity,” such that “selection for more tolerant genotypes thus has the ability to result in the evolution of increased thermal tolerance.” They found “genetic correlations between embryos grown in the two temperatures were positive, indicating that those genotypes that performed well in elevated temperature also performed well in control temperature.” Clark *et al.* conclude their “finding of genetic variation in thermal tolerance of *H. banksii* embryos suggests resilience to thermal stresses.”

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6.1.2 Corals

Perhaps no other species of marine life is projected by IPCC to experience as much hardship and degradation in response to rising temperatures as corals. Several statements from a draft of Working Group II's contribution to IPCC's *Fifth Assessment Report* illustrate these concerns:

The frequency and magnitude of coral bleaching and mortality will increase in the next few decades (*very high confidence*).

Under the A1B CO₂ emission scenario, 99% of the grid cells experience at least one severe bleaching event over 2090–2099.

Half of the coral reefs may avoid high frequency bleaching through 2100 assuming hypothetical

acclimation and/or adaptation (*limited evidence, low agreement*).

— Chapter 5, Coastal Systems and Low-Lying Areas, Working Group II, IPCC *Fifth Assessment Report*, draft dated March 28, 2013, p. 19.

It is *very likely* that coral reef ecosystems will not survive changes in sea temperature beyond an additional increase of 1°C.

Combining the known sensitivity of coral reefs within the Caribbean and Coral Triangle sub-regions, with the exposure to higher temperatures that are projected under medium (RCP4.5) to high (RCP8.5) scenarios, reveals that both coral reef rich regions are *virtually certain* to experience levels of thermal stress that cause coral bleaching every 1–2 years by the mid to late part of this century (*robust evidence, high levels of agreement, very high confidence*).

The frequency of mass mortality events (DHM > 5; Figure 30–11 A,C) climbs towards events that occur every 1–2 years by mid to late of this century under low to high climate change scenarios (*robust evidence, high levels of agreement, very high confidence*).

Mass mortality events that impact coral reefs will result in changes to community composition in the short term (2010–2039) and a continuing downward trend in reef building coral stocks in the longer term.

— Chapter 30, The Ocean, Working Group II, IPCC *Fifth Assessment Report*, draft dated March 28, 2013, p. 35.

There is *robust evidence* and *high agreement* that coral reefs are one of the most vulnerable marine ecosystems.

Even under optimistic assumptions regarding corals being able to rapidly adapt to thermal stress, one-third (9–60%, 68% uncertainty range) of the world's coral reefs are projected to be subject to long-term degradation under the RCP3-PD scenario. Under the RCP4.5 scenario, this fraction increases to two-thirds (30–88%, 68% uncertainty range).

If present day corals have residual capacity to acclimatize and/or adapt, half of the coral reefs may avoid high frequency bleaching through 2100 (*limited evidence, limited agreement*). Evidence of

corals adapting rapidly, however, to climate change is missing or equivocal.

— Technical Summary, Working Group II, IPCC *Fifth Assessment Report*, draft dated March 28, 2013, pp. 67–68.

This section examines the future of Earth's corals in response to possible global warming, beginning with a review of the literature on the many suspected causes of coral bleaching, almost all of which have been attributed (often implausibly) to CO₂-induced global warming. Thereafter, the discussion turns to the possibility corals can adapt to the various environmental threats they face, followed by an examination of whether the widespread bleaching events seen in recent decades are indeed caused by global warming. The discussion concludes with a brief examination of an indirect temperature-related threat to corals—rising sea levels—which IPCC predicts will occur to a significant degree over the twenty-first century and beyond as global warming melts large portions of the ice presently stored in the world's glaciers and ice sheets.

This survey offers a much different perspective on the future of Earth's corals than that predicted by IPCC. Though rising temperatures have challenged and may continue to challenge Earth's corals, a large body of evidence indicates many corals can adapt to and even overcome the temperature-related challenges they are projected to face in response to CO₂-induced global warming. In reaching its overly pessimistic conclusions about corals, IPCC has clearly and improperly ignored the weight of the many research findings summarized here.

6.1.2.1 Causes of Coral Bleaching

This section reviews studies examining the causes of coral bleaching. The key findings are as follows:

- Many studies attribute high sea water temperatures as the primary cause of coral bleaching. However, the crucial link between temperature and coral reef bleaching may not reside in the absolute temperature of the water surrounding the corals but in the rapidity with which the temperature either rises above or falls below the temperature regime to which the corals are normally adapted.
- A number of studies have provided evidence inconsistent with the global-warming-induced coral

bleaching hypothesis, pointing to other important factors and causes of coral bleaching, including solar irradiance, a solar radiation-temperature stress synergism, changes in salinity, bacterial infections, increased sedimentation, and exposure to toxicants.

- Many sources of coral stress and survival have little or nothing to do with rising CO₂ concentrations or temperatures.

Coral bleaching ranks among the more frequently cited negative consequences projected to result from CO₂-induced global warming. A loss of color in certain reef-building corals occurs when algal symbionts, or zooxanthellae, living within the host corals are subjected to various stresses and expelled from them, resulting in a loss of photosynthetic pigments from the coral colony. If the stress is mild, or short in duration, the affected corals often recover and regain their normal complement of zooxanthellae. If the stress is prolonged, or extreme, the corals eventually die, being deprived of their primary food source.

One of the most frequently cited causes of coral bleaching is anomalously high water temperature (Linden, 1998). The origin of this attribution can be traced to the strong El Niño event of 1982–1983, in which widespread bleaching was reported in corals exposed to unusually high surface water temperatures (Glynn, 1988). Since then, a number of other such observations have been made (Cook *et al.*, 1990; Glynn 1991; Montgomery and Strong, 1994; Brown *et al.*, 1996), and several laboratory studies have demonstrated elevated seawater temperatures can indeed induce bleaching in corals (Hoegh-Guldberg and Smith, 1989; Jokiel and Coles, 1990; Glynn and D'Croz, 1990).

Anomalously low seawater temperatures also have been identified with coral bleaching (Walker *et al.*, 1982; Coles and Fadlallah, 1990; Muscatine *et al.*, 1991; Gates *et al.*, 1992; Saxby *et al.*, 2003; Hoegh-Guldberg and Fine 2004; Yu *et al.*, 2004; Kemp *et al.*, 2011). These observations suggest the crucial link between temperature and coral reef bleaching may not be in the absolute temperature of the water surrounding the corals, but in the rapidity with which the temperature varies from the temperature regime to which the corals are normally adapted.

Winter *et al.* (1998), for example, studied relationships between coral bleaching and nine temperature indices, concluding, although “prolonged heat stress may be an important precondition for

bleaching to occur,” sharp temperature changes act as the “immediate trigger.” Jones (1997) reported coral bleaching on a portion of Australia’s Great Barrier Reef just after average daily sea water temperature rose by 2.5°C over a brief period of eight days. Kobluk and Lysenko (1994) observed severe coral bleaching after an 18-hour *decline* of 3°C in seawater temperature. Because the corals studied by the latter researchers had experienced massive bleaching two years earlier as a result of an anomalous 4°C *increase* in water temperature, the authors conclude coral bleaching is more a function the rapidity of a temperature change than of the absolute magnitude or sign of the change, of heating or cooling.

Podesta and Glynn (1997) provided further evidence seawater temperatures *per se* are not the critical factors in coral bleaching. They examined a number of temperature-related indices of surface waters near Panama over the period 1970–1994. Their analysis revealed for the two years of highest maximum monthly sea surface temperature, 1972 and 1983, coral bleaching was reported only in 1983; 1972 produced no bleaching whatsoever, even though water temperatures that year were just as high as they were in 1983.

Another prominent cause of coral bleaching is solar radiation, a link dating back more than a century to when MacMunn (1903) postulated ultraviolet radiation could damage corals. It wasn’t until half-a-century later that scientists began to confirm this suspicion (Catala-Stucki, 1959; Siebeck, 1988; Gleason and Wellington, 1995).

Many investigators of the solar irradiance-coral reef bleaching link have studied the phenomenon by transplanting reef corals from deep to shallow waters. Gleason and Wellington (1993), for example, transplanted samples of the reef-building coral *Montastrea annularis* from a depth of 24 meters to depths of 18 and 12 meters. Using sheets of acrylic plastic to block out ultraviolet radiation on some of the coral samples, they found the shielded corals experienced less bleaching than the unshielded corals, and the unshielded corals at the 12-meter depth had significantly lower amounts of zooxanthellae and chlorophyll per square centimeter than all other treatment and control groups. Similarly, Hoegh-Guldberg and Smith (1989) reported bleaching in the corals *Stylophora pistillata* and *Seriatopora hystrix* when they were moved from a depth of 6 meters to 1.2 meters. Vareschi and Fricke (1986) obtained similar results when moving *Plerogyra sinuosa* from a depth of 25 meters to 5 meters. As in the case of temperature stress, Glynn (1996) notes artificially

reduced light levels also have been observed to cause coral bleaching.

A number of laboratory studies have provided additional evidence for a link between intense solar irradiance and coral reef bleaching, but identifying a specific wavelength or range of wavelengths as the cause of the phenomenon has proven difficult. Fitt and Warner (1995), for example, reported the most significant decline in symbiont photosynthesis in the coral *Montastrea annularis* occurred when it was exposed to ultraviolet and blue light, but other studies have reported coral bleaching to be most severe at shorter ultraviolet wavelengths (Droller *et al.*, 1994; Gleason and Wellington, 1995). Still others have found it to be most strongly expressed at longer photosynthetically active wavelengths (Lesser and Shick, 1989; Lesser *et al.*, 1990; Brown *et al.*, 1994).

As additional studies provided evidence for a solar-induced mechanism of coral reef bleaching (Brown *et al.*, 1994; Williams *et al.*, 1997; Lyons *et al.*, 1998), some also provided evidence for a synergism of solar radiation and temperature stress (Gleason and Wellington, 1993; Rowan *et al.*, 1997; Jones *et al.*, 1998). Researchers have found a number of situations, for example, in which corals underwent bleaching when changes in both of these parameters combined to produce particularly stressful conditions (Lesser *et al.*, 1990; Glynn *et al.*, 1992; Brown *et al.*, 1995), such as during periods of low wind velocity and calm seas, which favor the intense heating of shallow waters and concurrent strong penetration of solar radiation.

This two-parameter interaction has much to recommend it as a primary cause of coral bleaching. It is the mechanism favored by Hoegh-Guldberg (1999), who claimed, in one of the strongest attempts made to that point in time to portray global warming as the cause of bleaching in corals, “coral bleaching occurs when the photosynthetic symbionts of corals (zooxanthellae) become increasingly vulnerable to damage by light at higher than normal temperatures.”

The story is considerably more complicated than that. In a review paper on coral bleaching, Brown (1997) listed several potential causes, including elevated seawater temperature, decreased seawater temperature, intense solar radiation, the combination of intense solar radiation and elevated temperature, reduced salinity, and bacterial infections. In a similar review, Meehan and Ostrander (1997) added increased sedimentation and exposure to toxicants.

With respect to seawater salinity, Meehan and Ostrander (1997) note, as with temperature, both high and low values have been observed to cause coral

bleaching. Low values typically occur as a result of seawater dilution caused by high precipitation or storm runoff; high values are much rarer, typically occurring only near desalinization plants.

A number of studies also have described the role of bacterial infections in causing coral reef bleaching (Ritchie and Smith, 1998). This phenomenon, too, may have a connection to high seawater temperatures. In a study of the coral *Oculina patagonica* and the bacterial agent *Vibrio* AK-1, for example, Kushmaro *et al.* (1996, 1997) conclude bleaching of colonies of this coral along the Mediterranean coast has its origin in bacterial infection, and that warmer temperatures may lower the resistance of the coral to infection and/or increase the virulence of the bacterium. In subsequent studies of the same coral and bacterium, Toren *et al.* (1998) and Kushmaro *et al.* (1998) further demonstrated this high temperature effect may operate by enhancing the ability of the bacterium to adhere to the coral.

Kushmaro *et al.* (1998) comment on the “speculation that increased seawater temperature, resulting from global warming or El Niño events, is the direct cause of coral bleaching.” Against this presumption, they cite several studies of coral bleaching events not associated with any major sea surface temperature anomalies, and they explicitly state, “it is not yet possible to determine conclusively that bleaching episodes and the consequent damage to reefs is due to global climate change.” Likewise, Toren *et al.* (1998) note the extensive bleaching that occurred on the Great Barrier Reef during the summer of 1982 was not associated with any major sea surface temperature increase, and “several authors have reported on the patchy spatial distribution and spreading nature of coral bleaching.” They note this observation conflicts with the global-warming-induced coral bleaching hypothesis. Instead, they write, “the progression of observable changes that take place during coral bleaching is reminiscent of that of developing microbial biofilms,” a point that will later be seen to be of great significance.

High rates of sedimentation have been demonstrated to lead to coral bleaching (Wesseling *et al.*, 1999), and most historical increases in sedimentation rates are clearly human-induced. Umar *et al.* (1998), for example, listed such contributing anthropogenic activities as deforestation, agricultural practices, coastal development, construction, mining, drilling, dredging, and tourism. Nowlis *et al.* (1997) discussed “how land development can increase the risk of severe damage to coral reefs by sediment runoff during storms.” However, it has been difficult to

determine just how much these phenomena have varied over the past few centuries.

McCulloch *et al.* (2003) recreated a 250-year record of sediment transfer to Havannah Reef—a site on the inner Great Barrier Reef of northern Queensland, Australia—by flood plumes from the Burdekin River. They found sediments suspended in the Burdekin River contain barium (Ba), which is desorbed from the particles that carry it as they enter the ocean, where growing corals incorporate it into their skeletons along with calcium (Ca). When more sediment is carried to the sea by periodic flooding and more gradual longer-term changes in land use that exacerbate soil erosion, the resultant increases in sediment load are recorded in the Ba/Ca ratio of coral skeleton material. McCulloch *et al.* measured Ba/Ca ratios in a 5.3-meter-long coral core from Havannah Reef that covered the period from about 1750 to 1985, as well as in some shorter cores from Havannah Reef and nearby Pandora Reef that extended the proxy sediment record to 1998.

The results revealed before the time of European settlement, which began in the Burdekin catchment in 1862, there was “surprisingly little evidence for flood-plume related activity from the coral Ba/Ca ratios.” Soon after, land clearance and domestic grazing intensified, and the soil became more vulnerable to monsoon-rain-induced erosion. By 1870, baseline Ba/Ca ratios had risen by 30%, and “within one to two decades after the arrival of European settlers in northern Queensland, there were already massive impacts on the river catchments that were being transmitted to the waters of the inner Great Barrier Reef.” During subsequent periods of flooding, the transport of suspended sediment to the reef increased by five- to ten-fold over what had been characteristic of pre-European settlement times.

In a companion article, Cole (2003) report corals from East Africa “tell a similar tale of erosion exacerbated by the imposition of colonial agricultural practices in the early decades of the twentieth century.” There, similar coral data from Malindi Reef, Kenya, indicate “a low and stable level of barium before about 1910 which rises dramatically by 1920, with a simultaneous increase in variance,” which was also evident in the Australian data.

Cole concludes “human activity, in the form of changing land use, has added sedimentation to the list of stresses experienced by reefs.” As land-use intensification is a widespread phenomenon, she notes, “many reefs close to continents or large islands are likely to have experienced increased delivery of sediment over the past century,” which suggests the

stress levels produced by this phenomenon are likely to have increased over the past century as well. Cole concludes as coastal populations continue to rise, “this phenomenon is likely to expand.”

A number of poisonous substances are known to induce coral bleaching. Some—such as herbicides, pesticides, and even excess nutrients that make their way from farmlands to the sea (Simkiss, 1964; Pittock, 1999)—are of human origin. Other poisons originate in the sea itself, many the result of metabolic waste products of other creatures (Crossland and Barnes, 1974) and some a by-product of the coral host itself (Yonge, 1968). Each of these toxicants presents the coral community with its own distinct challenge.

Taken together, these findings identify a number of sources of stress on coral survival and growth that have little or nothing to do with rising CO₂ concentrations or temperatures. They also clearly indicate human population growth and economic development have predisposed coral reefs to incidences of bleaching and subsequent mortality via a gradual intensification of near-coastal riverine sediment transport rates.

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6.1.2.2 Responses to Temperature-Related Stresses

Considering the many threats to the health of corals outlined in the previous section, many have questioned how these repositories of underwater biodiversity could possibly escape irreversible bleaching and death. In response to such concerns, Glynn (1996) noted, “numerous reef-building coral species have endured three periods of global warming, from the Pliocene optimum (4.3–3.3 million years ago) through the Eemian interglacial (125 thousand years ago) and the mid-Holocene (6000–5000 years ago), when atmospheric CO₂ concentrations and sea tem-

peratures often exceeded those of today.” Glynn observed “an increase in sea warming of less than 2°C would result in a greatly increased diversity of corals in certain high latitude locations.”

Living organisms are resilient. Various life forms can tolerate temperatures from below freezing to the boiling point of water; others inhabit niches where light intensity varies from complete darkness to full sunlight. Given time to adapt, nearly all living organisms can learn to survive in conditions well outside their normal zones of environmental tolerance. As Gates and Edmunds (1999) note, numerous studies indicate “corals routinely occupy a physically heterogeneous environment,” which “suggests they should possess a high degree of biological flexibility.” Their successful responses to the different threats that cause coral bleaching prove that flexibility and are examined in the subsections below.

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6.1.2.2.1 Thermal Adaptation

The studies reviewed in this section examine the concept of thermal adaptation, which refers to the ability of corals to adapt to temperature stresses in the future of similar or even greater magnitude than what they have experienced in the past. The key findings are presented in the bullet points below followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- As living entities, corals are not only affected by the various elements of their environment, they also react or respond to them. When changes in environmental factors pose a challenge to their continued existence, they sometimes take major defensive or adaptive actions, including thermal adaptation, to ensure their survival.
- Multiple studies demonstrate corals are thermally adapting to rising sea water temperatures. Bleaching at many reefs is either reduced or no longer occurs at temperatures that previously caused it.

- Cold water coral species also have been shown to display resilience in adapting to temperature increases as large as 5°C.
- Coral genera most susceptible to thermal stress sometimes display the greatest increase in thermal tolerance.
- Genotypic analyses suggest “the physiological plasticity of the host and/or symbiotic components” plays an important role in thermal adaptation.
- There is “a growing body of evidence to support the notion that corals inhabiting more thermally unstable habitats outperform conspecifics from reefs characterized by more stable temperatures when exposed to elevated temperatures.”
- “Previous exposure to an environmentally variable microhabitat adds substantially to coral-algal thermal tolerance, beyond that provided by heat-resistant symbionts alone.” Similarly, the thermal adaptive capacity of some corals “is likely facilitated by a combination of short-term acclimation in individuals during acute environmental conditions (e.g., recurrent bleaching events) and long-term adaptation among coral populations to chronic environmental conditions (e.g., extreme temperatures).”
- “It is premature to suggest that widespread reef collapse is a certain consequence of ongoing bleaching, or that this will inevitably lead to fisheries collapses.”

Fang *et al.* (1997) experimented with samples of *Acropora grandis* taken from the hot water outlet of a nuclear power plant near Nanwan Bay, Taiwan. In 1988, the year the power plant began full operation, the coral samples were completely bleached within two days of exposure to a temperature of 33°C. Two years later, however, “samples taken from the same area did not even start bleaching until six days after exposure to 33°C temperatures,” illustrating their ability to thermally adapt.

Middlebrook *et al.* (2008) reported similar findings. They collected multiple upward-growing branch tips of the reef-building coral *Acropora aspera* from three large colonies at the southern end of Australia’s Great Barrier Reef and placed them on racks immersed in running seawater within four 750-liter tanks maintained at the mean local ambient tem-

perature (27°C) and exposed to natural reef-flat summer daily light levels. Two weeks before a simulated bleaching event—where water temperature was raised to a value of 34°C for six days—they boosted the water temperature in one of the tanks to 31°C for 48 hours, and in another tank they boosted it to 31°C for 48 hours one week before the simulated bleaching event. In the third tank they had no pre-heating treatment, and in the fourth tank they used no pre-heating nor any simulated bleaching event. At different points throughout the study, they measured photosystem II efficiency, xanthophyll and chlorophyll *a* concentrations, and *Symbiodinium* densities.

Middlebrook *et al.* found the symbionts of the corals exposed to the 48-hour pre-bleaching thermal stress “were found to have more effective photo-protective mechanisms,” including “changes in non-photochemical quenching and xanthophyll cycling.” They determined “these differences in photo-protection were correlated with decreased loss of symbionts, with those corals that were not pre-stressed performing significantly worse, losing over 40% of their symbionts and having a greater reduction in photosynthetic efficiency,” whereas “pre-stressed coral symbiont densities were unchanged at the end of the bleaching.” Middlebrook *et al.* say their study “conclusively demonstrates that thermal stress events two weeks and one week prior to a bleaching event provide significantly increased thermal tolerance to the coral holobiont, suggesting that short time-scale thermal adaptation can have profound effects on coral bleaching.”

In another laboratory-based study, Bellantuono *et al.* (2012) “tested the response of *Acropora millepora* to thermal preconditioning by exposing coral nubbins to 28°C (3°C below bleaching threshold) for 10 days, prior to challenging them with water temperatures of 31°C for 8 days,” while “in another treatment (non-preconditioned), corals were exposed to 31°C without prior exposure to the 28°C treatment.” They conducted these procedures in a set of “transparent tanks plumbed into flowing sea water, with four replicate tanks for each treatment.”

The three researchers discovered short-term preconditioning to higher-than-ambient temperatures (but still 3°C below the experimentally determined bleaching threshold) for 10 days provided thermal tolerance for the scleractinian coral and its symbionts. Based on various genotypic analyses they conducted, they determined “the acclimatization of this coral species to thermal stress does not come down to simple changes in *Symbiodinium* symbiont shuffling and/or the bacterial communities that associate with

reef-building corals bacterial shuffling.” These findings, Bellantuono *et al.* write, suggest “the physiological plasticity of the host and/or symbiotic components appears to play an important role in responding to ocean warming.” They describe real-world examples of this phenomenon possibly playing a crucial role in preserving corals exposed to extreme warm temperatures in the past (Fang *et al.*, 1997; Middlebrook *et al.*, 2008; Maynard *et al.*, 2008b).

South of Malta in the Mediterranean Sea, Naumann *et al.* (2013) collected live specimens of two scleractinian cold-water coral (CWCs) species, *Dendrophyllia cornigera* and *D. dianthus*. They transferred the specimens into two identically equipped and darkened 100-L flow-through aquaria through which Mediterranean subsurface seawater was continuously pumped from a 50-meter depth and supplied to the tanks at a rate of about one liter per minute. They maintained this water at a temperature of $12.5 \pm 0.1^\circ\text{C}$ for approximately 30 months before initiating the primary phase of their experiment, which was to increase the temperature of one of the aquariums by 0.5°C per day up to $17.5 \pm 0.1^\circ\text{C}$, thereafter maintaining it for a further 87 days, while conducting “daily visual assessments of coral health (i.e. tentacle protrusion, suspension feeding and mortality/survival) and monthly growth measurements by the buoyant weight technique (Davies, 1989),” ultimately translating the latter into coral dry weight data.

The three researchers write, “over the entire experimental period, both CWC species showed neither differences in tentacle protrusion and suspension feeding nor mortality at ambient (12.5°C) or elevated (17.5°C) seawater temperatures.” They state, “*D. cornigera* specimens developed a non-quantified number of new polyps at both temperatures suggesting efficient thermal acclimatization.” They report “*D. dianthus* exhibited growth rates for ambient and elevated temperatures of $0.23 \pm 0.08\%$ per day and $0.19 \pm 0.06\%$ per day, whereas *D. cornigera* grew at $0.05 \pm 0.01\%$ per day under ambient and $0.14\% \pm 0.07\%$ per day under elevated temperature conditions.” Their findings “suggest that *D. dianthus* and *D. cornigera* may be capable of surviving in warmer environments than previously reported, and thus challenge temperature as the paramount limiting environmental factor for the occurrence of some CWC species.”

Multiple researchers have confirmed the phenomenon of thermal adaptation in corals in response to real-world temperature-related stresses. Brown *et al.* (2002) conducted a 17-year study of

coral reef flats at Ko Phuket, Thailand, assessing reef changes in response to elevated sea temperatures in 1991, 1995, 1997, and 1998. Although the authors state many corals bleached “during elevated sea temperatures in May 1991 and 1995,” they report “no bleaching was recorded in 1997.” In addition, they write, “in May 1998 very limited bleaching occurred although sea temperatures were higher than previous events in 1991 and 1995 (Dunne and Brown, 2001).” When bleaching did take place, they note, “it led only to partial mortality in coral colonies, with most corals recovering their color within 3–5 months of initial paling.”

Riegl (2003) reviewed what was known at the time about the responses of coral reefs to high-temperature-induced bleaching, focusing primarily on the Arabian Gulf, which they note “has recently experienced high-frequency recurrences of temperature-related bleaching (1996, 1998, 2002).” Riegl reports in each of the three high-temperature years, sea surface temperature (SST) anomalies of 2 to 2.5°C above average *in situ* measured summer maximum SSTs persisted from April to September, and local maxima of *in situ* measured SSTs were 35.5°C in 1996 and 37°C in 2002. In response to these high-temperature events, *Acropora*, which during the 1996 and 1998 events always bleached first and suffered heaviest mortality, bleached less than all other corals in 2002 at Sir Abu Nuair (an offshore island of the United Arab Emirates) and recovered along the coast of Dubai between Jebel Ali and Ras Hasyan. Riegl states, “the unexpected resistance of Sir Abu Nuair *Acropora* to bleaching in 2002 might indicate support for the hypothesis of Baker (2001) and Baker *et al.* (2002) that the symbiont communities on recovering reefs of the future might indeed be more resistant to subsequent bleaching,” and “the Arabian Gulf perhaps provides us with some aspects which might be described as a ‘glimpse into the future,’ with ... hopes for at least some level of coral/zooxanthellae adaptation.”

Jimenez and Cortes (2003a) documented coral cover variability in the Pacific between 1992 and 2001, when the El Niño warming events of 1991–1992 (weak) and 1997–1998 (“the strongest in recorded history”) affected coral communities along the Costa Rican central Pacific coast, after which they reported their observations and those of other scientists pertaining to these and earlier warming events caused by the El Niños of 1982–1983 (very strong) and 1986–1987 (moderate). The authors report there was a “paucity of bleaching and mortality in the study area in 1987 despite sea temperature

anomalies similar to or higher than in other years in which bleaching and mortality occurred,” and this situation “may have been the result of the higher cloud cover and runoff which, in combination, decreased solar radiation stress.” They suggest “similar atmospheric conditions during 1998 may explain the considerably small number of corals that bleached that year in the upwelling area of [Costa Rica’s] Golfo de Papagayo,” where they report “few corals bleached, even though sea temperature anomalies were higher than in autumn 1997.”

As to the 1997–1998 El Niño, considered to be “the strongest event on record (McPhaden, 1999; Enfield, 2001),” the authors report “mortality of entire colonies associated with this event was remarkably low in Costa Rica, less than 6% (Jimenez *et al.*, 2001),” and “only one coral species, *Psammocora stellata*, disappeared at one locality (Cambutal) after the 1997–1998 warming event.” This disappearance “did not have an effect on the percent of total cover, which was not significantly dissimilar to previous years.” They report “this species was not affected in Mexico by the 1997–1998 warming episode (Carriquiry *et al.*, 2001).”

Jimenez and Cortes note conspecific corals “have shown differences in susceptibility to bleach, mortality rates and recovery capabilities (Brown, 1997; Hoegh-Guldberg, 1999; Marshall and Baird, 2000; Fitt *et al.*, 2001; Glynn *et al.*, 2001),” which may “reflect corals’ adaptation to local conditions, different warming intensities at each locality, thermal acclimation, and presence of several clades of symbionts.” They state moderate warming events “may positively affect coral reef communities,” noting “increases in growth rates, reproductive activity and recruitment pulses have been observed after some El Niño episodes (Glynn *et al.*, 1991, 1994; Feingold, 1995; Guzman and Cortes, 2001; Vargas-Angel *et al.*, 2001; Jimenez and Cortes, 2003b).”

Guzman and Cortes (2007) note coral reefs of the eastern Pacific Ocean “suffered unprecedented mass mortality at a regional scale as a consequence of the anomalous sea warming during the 1982–1983 El Niño.” At Cocos Island (5°32’N, 87°04’W), in particular, where they conducted a survey of three representative reefs in 1987, they found remaining live coral cover was only 3% of what it had been before the great El Niño four years earlier (Guzman and Cortes, 1992). Based on this finding and the similar observations of other scientists at other reefs, they predicted “the recovery of the reefs’ framework would take centuries, and recovery of live coral

cover, decades.” In 2002, nearly 20 years after the disastrous coral-killing warming, they returned to see how correct they were after their initial assessment of the El Niño damage, quantifying “the live coral cover and species composition of five reefs, including the three previously assessed in 1987.”

Regarding thermal tolerance, the most interesting aspect of their study was the occurrence of a second major El Niño between the two assessment periods. Guzman and Cortes state “the 1997–1998 warming event around Cocos Island was more intense than all previous El Niño events,” noting temperature anomalies “above 2°C lasted 4 months in 1997–1998 compared to 1 month in 1982–83.” Nevertheless, they report, “the coral communities suffered a lower and more selective mortality in 1997–1998, as was also observed in other areas of the eastern Pacific (Glynn *et al.*, 2001; Cortes and Jimenez, 2003; Zapata and Vargas-Angel, 2003),” indicating some type of thermal adaptation occurred after the 1982–1983 El Niño.

Maynard *et al.* (2008a) question the wisdom of “popularizing predictions based on essentially untested assumptions,” among which they list IPCC-held claims, “all corals live close to their thermal limits” and “corals cannot adapt/acclimatize to rapid rates of change.”

In discussing the first of these “untested assumptions,” the three Australian researchers say “predictions that reefs will disappear as a result of global warming are based, at least in part, on the assumption corals are living close to their maximum thermal limits.” However, they note, “the severity of bleaching responses varies dramatically within and among taxa,” citing McClanahan *et al.* (2009), and “such variable bleaching susceptibility implies that there is a considerable variation in the extent to which coral species are adapted to local environmental conditions.”

The three scientists report little is known about the sensitivity of coral population response to climate-induced changes in growth, mortality, and fecundity, but they state a large body of evidence “supports temperature tolerance varying among species, populations, communities, and reef regions (Marshall and Baird, 2000; Coles and Brown, 2003).” They conclude, “even in the absence of an adaptive response, a change in the relative abundance of species is a far more likely outcome of climate change than the disappearance of reef corals,” citing Loya *et al.* (2001), McClanahan (2002), and Hughes *et al.* (2003).

The three researchers clearly accept there is “an

adaptive response,” in contradiction of the second untested assumption Maynard *et al.* (2008a) discuss, stating “a number of studies suggest that bleaching mortality rates have declined and thermal tolerance has increased in some regions.” They report, for example, “mortality rates in the Eastern Pacific were significantly lower in 1998 when compared with 1982 and 1983 (Glynn *et al.*, 2001),” and “Maynard *et al.* (2008b) found thermal tolerance of three common coral genera on the Great Barrier Reef to be greater in 2002 than that expected from the relationship between temperature stress and bleaching severity observed in 1998.”

The Australian scientists say there is “circumstantial evidence for ongoing evolution of temperature tolerance between both species and reefs,” citing Coles and Brown (2003). In addition, they suggest “symbiont shuffling from less to more stress-resistant clades is another mechanism by which corals may increase the thermal tolerance of the holobiont.” And they declare “there is growing evidence that such shuffling can increase thermal tolerance, at least in the short term (Berkelmans and van Oppen, 2006).” Thus Maynard *et al.* (2008a) conclude, “it is premature to suggest that widespread reef collapse is a certain consequence of ongoing bleaching, or that this will inevitably lead to fisheries collapses.”

Adjeroud *et al.* (2009) observed coral reefs of the Tiahura outer reef sector at the western end of the north shore of Moorea, French Polynesia, a region they say is “largely free of direct anthropogenic disturbances.” They describe the results of detailed observations made there periodically since the early 1970s and annually since 1991. This history, they write, “constitutes one of the longest records of coral reef dynamics.” Concentrating on the period of detailed annual observations (1991 onward), the 10 researchers report a significant decline in coral cover followed the two disturbances of 1991 (a major bleaching event and a cyclone), when “coral cover (pooled among genera) declined from $51.0 \pm 9.5\%$ in early 1991 to $24.2 \pm 14.4\%$ in 1992, and $22.5 \pm 9.3\%$ in 1993.” This decline, they write, was “among the most rapid of this magnitude recorded following natural disturbances.” In contrast, they found “the bleaching events of 1994, 2002 and 2003 had no detectable effects on coral cover, even though the thermal anomalies causing these events and their short-term impacts in terms of bleaching prevalence were similar to the 1991 bleaching event.”

Adjeroud *et al.* say their results reveal “corals can recover rapidly following a dramatic decline,” noting

similar recoveries of coral cover have been documented at several other locations, citing Connell (1997), Halford *et al.* (2004), Emslie *et al.* (2008), and Sheppard *et al.* (2008). They state their work “supports the hypothesis that some reefs will undergo gradual changes in structure of their coral communities in response to major stress rather than collapse abruptly,” citing Loya *et al.* (2001), Hughes *et al.* (2003), and Wakeford *et al.* (2008).

Maynard *et al.* (2008b) analyzed the bleaching severity of three genera of corals (*Acropora*, *Pocillopora*, and *Porites*) along five sites in the central section of Australia’s Great Barrier Reef in late February and March of 1998 and 2002. Regarding the influence of temperature, the four researchers report “the amount of accumulated thermal stress (as degree heating days) in 2002 was more than double that in 1998 at four of the five sites,” and “average surface irradiance during the 2002 thermal anomaly was 15.6–18.9% higher than during the 1998 anomaly.” They found “in 2002, bleaching severity was 30–100% lower than predicted from the relationship between severity and thermal stress in 1998, despite higher solar irradiances during the 2002 thermal event.” In addition, “coral genera most susceptible to thermal stress (*Pocillopora* and *Acropora*) showed the greatest increase in tolerance.”

Maynard *et al.* state their findings are “consistent with previous studies documenting an increase in thermal tolerance between bleaching events (1982–1983 vs. 1997–1998) in the Galapagos Islands (Podesta and Glynn, 2001), the Gulf of Chiriqui, the Gulf of Panama (Glynn *et al.*, 2001), and on Costa Rican reefs (Jimenez *et al.*, 2001).” They also note “Dunne and Brown (2001) found similar results ... in the Andaman Sea, in that bleaching severity was far reduced in 1998 compared to 1995 despite sea-temperature and light conditions being more conducive to widespread bleaching in 1998.”

The Australian scientists say “the range in bleaching tolerances among corals inhabiting different thermal realms suggests that at least some coral symbioses have the ability to adapt to much higher temperatures than they currently experience in the central Great Barrier Reef,” citing Coles and Brown (2003) and Riegl (1999, 2002). They note, “even within reefs there is a significant variability in bleaching susceptibility for many species (Edmunds, 1994; Marshall and Baird, 2000), suggesting some potential for a shift in thermal tolerance based on selective mortality (Glynn *et al.*, 2001; Jimenez *et al.*, 2001) and local population growth alone.” Their results suggest “a capacity for acclimatization or

adaptation.” Maynard *et al.* (2008b) conclude “there is emerging evidence of high genetic structure within coral species (Ayre and Hughes, 2004),” suggesting “the capacity for adaptation could be greater than is currently recognized.” As Skelly *et al.* (2007) state, “on the basis of the present knowledge of genetic variation in performance traits and species’ capacity for evolutionary response, it can be concluded that evolutionary change will often occur concomitantly with changes in climate as well as other environmental changes.”

Focusing more on such evolutionary possibilities, Meyer *et al.* (2009) “performed controlled crosses between three genetically distinct colonies of the branching coral *Acropora millepora*,” and then “compared the families of larvae (which in this species naturally lack symbionts) for several physiological traits.” They conducted this work at two water temperatures—the standard culturing temperature of 28°C and an elevated temperature of 32°C—as well as an even higher temperature of 34°C maintained for two full days.

Results of the U.S., Canadian, and Australian researchers’ analysis confirmed the existence of phenotypic variance for several pertinent thermal and dispersive factors among the families of coral they studied. This finding, they write, “suggests the existence of considerable heritable variation in natural coral populations,” and this in turn supports “the possibility of effective adaptive responses to climate change.” In addition, they report other analyses of the species they studied have found “high levels of genetic diversity both within and between reefs (Smith-Keune and van Oppen, 2006),” and “studies in other coral species have also uncovered substantial genetic diversity within populations (Ayre and Hughes, 2000; Underwood, 2009; Wang *et al.*, 2009).” Myer *et al.* conclude “additive genetic variance exists within coral populations for several traits that might reasonably be expected to have fitness consequences during global climate change,” which “supports the possibility of effective adaptive responses to climate change.”

Grimsditch *et al.* (2010) say “it has been shown that it is possible for colonies to acclimatize to increased temperatures and high irradiance levels so that they are able to resist bleaching events when they occur.” They note “threshold temperatures that induce coral bleaching-related mortality vary worldwide—from 27°C in Easter Island (Wellington *et al.*, 2001) to 36°C in the Arabian Gulf (Riegl, 1999)—according to the maximum water temperatures that are normal in the area, implying a capacity of corals and/or

zooxanthellae to acclimatize to high temperatures depending on their environment.”

Grimsditch *et al.* examined “bleaching responses of corals at four sites (Nyali, Mombasa Marine Park, Kanamai and Vipingo) representing two distinct lagoon habitats on the Kenyan coast (deeper and shallower lagoons).” This was done for the coral community as a whole, and zooxanthellae densities and chlorophyll levels were monitored for three target species (*Pocillopora damicornis*, *Porites lutea*, and *Porites cylindrica*) during a non-bleaching year (2006) and a mild bleaching year (2007). They found “during the 2007 bleaching season, corals in the shallow lagoons of Kanamai and Vipingo were more resistant to bleaching stress than corals in the deeper lagoons of Mombasa Marine Park and Nyali.” This result suggests, they write, “corals in the shallower lagoons have acclimatized and/or adapted to the fluctuating environmental conditions they endure on a daily basis and have become more resistant to bleaching stress.”

Osborne *et al.* (2011) note “coral decline is frequently described as ongoing with the integrity and persistence of the reef system threatened by a number of different stressors,” citing Bellwood *et al.* (2004), and “climate change is widely regarded as the single greatest threat to coral reef ecosystems.” They also note “the scale and extent of bleaching on the GBR [Great Barrier Reef] since 1998 is unprecedented (Oliver *et al.*, 2009),” “coral disease is an emerging stressor that was first recorded on the GBR in the early 1990s (Willis *et al.*, 2004; Lough, 2007),” and various harmful environmental disturbances “appear to be increasing in frequency and severity.”

To quantify the trend in live coral cover of the Great Barrier Reef between 1995 and 2009, which IPCC contends was the warmest decade-and-a-half experienced by the planet in the past millennium, the scientists surveyed coral communities annually on 47 reefs in six latitudinal sectors across 1300 km of the GBR, surveying between two and five reefs in each sub-region. They did so at three sites on the northeast flank of each reef, with each site consisting of five 50-m transects marked by steel rods at depths between six and nine meters. They note “percent cover of live hard coral was estimated from a randomly selected sequence of images taken along the transects using a point-sampling technique in a quincunx pattern (Adbo *et al.*, 2004).”

They found “coral cover increased in six sub-regions and decreased in seven sub-regions,” with some of the changes “being very dynamic and others changing little.” With respect to the entire reef

system, they report “overall regional coral cover was stable (averaging 29% and ranging from 23% to 33% across years) with no net decline between 1995 and 2009.” They state they found “no evidence of consistent, system-wide decline in coral cover since 1995.” In spite of the purportedly unprecedented negative influences arrayed against them over the past decade-and-a-half, GBR corals appear to have held their own, adapting to the purported onslaught of stresses and maintaining a stable presence.

According to Oliver and Palumbi (2011), “the vast majority of studies that investigate the effects of fluctuating thermal regimes on thermal tolerance have examined daily thermal cycles in which the hottest temperatures lasted on the timescale of hours,” and in eight of 10 such studies—performed on taxa as diverse as corals, crustaceans, fish, and amphibians—“organisms that were acclimated to a daily fluctuating thermal regime showed thermal tolerance or tolerance-relevant gene expression (e.g., heat shock proteins) that was equal to, or greater than, that of organisms acclimated to a thermal regime held constant at the maximum temperature of the fluctuating regime,” citing Hutchison and Ferrance (1970), Otto (1974), Sastry (1979), Thorp and Wineriter (1981), Thresher and Houston (1983), Podrabsky and Somero (2004), Schaefer and Ryan (2006), and Putnam *et al.* (2010).

Studying back-reef pools in American Samoa that differ in diurnal thermal variation, Oliver and Palumbi experimentally heat-stressed *Acropora hyacinthus* corals from a thermally moderate lagoon pool and a more thermally variable pool that naturally experienced two- to three-hour high temperature events during summer low tides. They compared coral mortality and photosystem II photochemical efficiency of colony fragments collected from each of these lagoons that they exposed to either ambient (28.0°C) or elevated (31.5°C) water temperatures. The two researchers report in the heated treatment, “moderate pool corals showed nearly 50% mortality whether they hosted heat-sensitive or heat-resistant symbionts,” whereas “variable pool corals, all of which hosted heat-resistant symbionts, survived well, showing low mortalities statistically indistinguishable from controls held at ambient temperatures.” Also in the heated treatment, they state, “moderate pool corals hosting heat-sensitive algae showed rapid rates of decline in algal photosystem II photochemical efficiency,” whereas those “hosting heat-resistant algae showed intermediate levels of decline.” They found “variable pool corals hosting heat-resistant algae showed the least decline.”

Oliver and Palumbi say their results suggest “previous exposure to an environmentally variable microhabitat adds substantially to coral-algal thermal tolerance, beyond that provided by heat-resistant symbionts alone,” indicating a latent potential of Earth’s corals to adapt to warmer temperatures than scientists believed possible in the past, should they gradually begin to experience recurring daily episodes of greater warmth in a gradually warming world.

In a study designed to investigate how coral assemblages in the Persian Gulf might cope with global warming via reproductive biology, Bauman *et al.* (2011) examined six locally common coral species on two shallow reef sites in Dubai, United Arab Emirates, in 2008 and 2009, to investigate their patterns of reproduction, focusing primarily on the timing and synchrony of spawning. They found the reproductive biology of the six coral species in the southern Persian Gulf “appears to be well adapted to extreme annual environmental fluctuations” and is “remarkably similar to conspecifics elsewhere in the Indo-Pacific (Baird *et al.*, 2009a,b).” They also found “the adaptive capacity of corals in the Persian Gulf is likely facilitated by a combination of short-term acclimation in individuals during acute environmental conditions (e.g., recurrent bleaching events) and long-term adaptation among coral populations to chronic environmental conditions (e.g., extreme temperatures).”

Bauman *et al.* state their work “confirms that corals are capable of reproductive activities under extreme environmental conditions,” as Coles and Fadlallah (1991) and Coles and Brown (2003) also found. They conclude “coral populations can survive and proliferate in extreme conditions that are projected to occur in many other regions of the world by the end of this century,” noting, “the recovery of these coral assemblages following mortality induced by a number of recent temperature-related bleaching events (1996, 1998 and 2002) suggests these assemblages are also resilient to extreme fluctuations in water temperature,” citing Riegl (1999, 2003) and Burt *et al.* (2008).

Serrano *et al.* (2013) investigated the adaptation of corals to temperature-related stresses through range expansion or migration. The team of researchers state, “despite the evidence that some coral species appear to be responding to climatic warming by expanding their distributions toward the poles (Wooddroffe, 2011), it has been argued that latitudinal migration is unlikely to occur rapidly enough to respond to the current projected temperature change (3–6°C over the next 100 years (IPCC, 2007)) due to the significant

distance involved (i.e., the latitudinal temperature gradient is $\sim 1.5^{\circ}\text{C}/1000\text{ km}$), the effects of temperature on reproduction, and the decrease in carbonate ion concentrations at high latitudes.” Serrano *et al.* analyzed a long-term, large-scale observational dataset to characterize the dynamics of a hermatypic coral (*Oculina patagonica*) in regard to its “recent northward range shift along the coast of Catalonia,” while examining “the main factors that could have influenced this spread,” which they did “by monitoring 223 locations including natural and artificial habitats along $>400\text{ km}$ of coastline over the last 19 years (1992–2010).”

The six Spanish scientists report *Oculina patagonica* “increased from being present in one location in 1992 to occur on 19% of the locations in 2010, and exhibited an acceleration of its spreading over time driven by the joint action of neighborhood and long-distance dispersal.” They further note the “northward expansion has occurred at the fastest rate (22 km per year) reported for a coral species thus far.” Serrano *et al.* write, “a coral species with particular biological characteristics that allow it to withstand the temperature challenge that accompanies northward migration as well as the natural and anthropogenic side effects that this type of migration involves (i.e., competition with macroalgae, high sediment loads, turbidity, water chemistry) has accomplished a successful northward expansion and may be able to keep pace with the global warming prediction of $\sim 3^{\circ}\text{C}$ over the next 100 years.”

Yamano *et al.* (2011) report “although most studies of climate change effects on corals have focused on temperature-induced coral bleaching in tropical areas, poleward range shifts and/or expansions may also occur in temperate areas, as suggested by geological records and present-day eyewitnesses in several localities,” citing Greenstein and Pandolfi (2008) and Precht and Aronson (2004). Yamano *et al.* collected records of coral species occurrence from eight temperate regions of Japan along a latitudinal gradient, where they obtained what they describe as “the first large-scale evidence of the poleward range expansion of modern corals, based on 80 years of national records ... where century-long measurements of *in situ* sea-surface temperatures have shown statistically significant rises.”

They found “four major coral species categories, including two key species for reef formation in tropical areas, showed poleward range expansions since the 1930s, whereas no species demonstrated southward range shrinkage or local extinction,” adding “the speed of these expansions reached up to

14 km per year,” which they say “is far greater than that for other species.” They note, “in regions with poleward current flows (east coast of the United States [Precht and Aronson, 2004], east coast of South America, east coast of Africa and east coast of Australia [Figueira and Booth, 2010]) the speed would be much greater.”

The Japanese scientists conclude their results, “in combination with recent findings suggesting range expansions of tropical coral-reef associated organisms, strongly suggest that rapid, fundamental modifications of temperate coastal ecosystems could be in progress.” They suggest “temperate areas may serve as refugia for tropical corals in an era of global warming.”

Van Woesik *et al.* (2012) examined the response of more than 30,000 coral colonies at 80 sites in Palau during a regional thermal-stress event in 2010, to determine “whether any habitats were comparatively resistant to thermal stress.” The six scientists discovered “bleaching was most severe in the northwestern lagoon, in accordance with satellite-derived maximum temperatures and anomalous temperatures above the long-term averages,” noting corals there “suffered the most extensive bleaching and the highest mortality.” But “in the bays where temperatures were higher than elsewhere, bleaching and mortality were low.” They suggest “constant exposure to high temperatures, and high vertical attenuation of light caused by naturally high suspended particulate matter buffered the corals in bays from the 2010 regional thermal-stress event.” Van Woesik *et al.* conclude their study shows “reefs around bays were more resistant to regional thermal stress than patch and outer reefs,” and “nearshore reefs in the bays are therefore valuable refuges to buffer coral-reef ecosystems against climate change-induced disturbances.” Those bays “should be given high conservation status because they provide refugia for coral populations as the oceans continue to warm.”

Carilli *et al.* (2012) note “observations indicating that mass bleaching events have recently become more common, combined with projected increases in heat stress, have prompted dire predictions for the future of coral reefs under unabated greenhouse gas emissions scenarios,” citing Hoegh-Guldberg (1999) and Donner *et al.* (2005). They point out, “there is evidence that corals may adapt to better withstand heat stress via a number of mechanisms,” as “corals might acquire more thermally-resistant symbionts (Buddemeier and Fautin, 1993; Rowan, 2004), or might increase their own physiological mechanisms

to reduce bleaching susceptibility by producing oxidative enzymes (Coles and Brown, 2003) or photoprotective compounds (Salih *et al.*, 2000).” They emphasize there is evidence suggesting the susceptibility of a given coral or reef to bleaching depends on the thermal history of that coral or reef (Thompson and Van Woesik, 2009; Donner, 2011; Brown *et al.*, 2002).

Carilli *et al.* “collected cores from massive *Porites* sp. corals in the Gilbert Islands of Kiribati to determine how corals along a natural gradient in temperature variability responded to recent heat stress events” and “examined changes in coral skeletal growth rates and partial mortality scars (Carilli *et al.*, 2010) to investigate the impact of the bleaching event in 2004 (Donner, 2011) on corals from different temperature variability regimes.”

The three researchers—from Australia, Canada, and the United States—discovered the spatial patterns in skeletal growth rates and partial mortality scars found in corals from the central and northern islands suggest “corals subject to larger year-to-year fluctuations in maximum ocean temperature were more resistant to a 2004 warm-water event,” and “a subsequent 2009 warm event had a disproportionately larger impact on those corals from the island with lower historical heat stress.” Carilli *et al.* conclude, “coral reefs in locations with more frequent warm events may be more resilient to future warming.”

Penin *et al.* (2013) “compared variations in spatial and taxonomic patterns between two bleaching events at the scale of an island (Moorea Island, French Polynesia),” where “nine stations involving three locations (Haapiti, Tiahura, and Viapahu) and three depths (6, 12, and 18 m) have been routinely surveyed for various scientific purposes since 2001,” as described by Penin *et al.* (2007a, 2010). They measured bleaching intensity “two weeks following the first signs of bleaching (Penin *et al.*, 2007b)” for six coral genera (*Acropora*, *Montipora*, *Montastrea*, *Pavona*, *Pocillopora*, and *Porites*) at each of the nine stations in 2002 and 2007. The six coral genera accounted for 88% of the total coral assemblage.

Their measurements showed the “thermal stress was similar between the two years studied,” but “the bleaching intensity was lower in 2007 (25–49%) than in 2002 (39–72%)” and “the response to elevated temperature was delayed in the latter year.” They note “the outer slopes at Moorea Island are located in an oligotrophic oceanic environment and are not under terrestrial influence, which makes it unlikely that there was any effect of nutrients on the response of the corals, as has been proposed for other reef eco-

systems (Wooldridge and Done, 2009).” The three researchers conclude “it is likely that the observed decrease in stress response was the result of acclimatization of the coral/algal holobionts (Berkelmans *et al.*, 2004; Maynard *et al.*, 2008) or an influx of thermo-tolerant colonies between 2002 and 2007.” They note several “similar decreases in susceptibility to thermal stress have been documented between successive bleaching events, including between 1991 and 1994 at Moorea Island (Adjeroud *et al.*, 2002), between 1998 and 2002 on the Great Barrier Reef in Australia (Maynard *et al.*, 2008b), and between 1982–83 and 1997–98 in Panama (Glynn *et al.*, 2001), Costa Rica (Jimenez *et al.*, 2001), and at the Galapagos Islands (Podesta and Glynn, 2001).”

Mayfield *et al.* (2013) write, “recent work has found that pocilloporid corals from regions characterized by unstable temperatures, such as those exposed to periodic upwelling, display a remarkable degree of phenotypic plasticity,” and “some recent works have shown that not all corals bleach, or even manifest signs of stress, at elevated temperatures predicted to characterize reefs in the coming decades (Barshis *et al.*, 2013).” They also note “corals from highly variable temperature environments of both American Samoa (Oliver and Palumbi, 2011) and southern Taiwan (Mayfield *et al.*, 2011, 2013) have previously been shown to withstand exposure to temperatures (e.g., 30–31°C) that induce bleaching or even mortality in conspecifics from other regions (Jokiel and Coles, 1990; Brown, 1997).”

To “uncover the long-term impacts of elevated temperature exposure to corals from reefs that experience episodic upwelling,” Mayfield *et al.* conducted a mesocosm-based experiment in which *P. damicornis* specimens collected from an upwelling coral reef on Houbihu (a small embayment within Nanwan Bay, southern Taiwan) were exposed for nine months to nearly 30°C, a temperature that the corals normally encounter *in situ* for just a few hours per year (Mayfield *et al.*, 2012). The three researchers write, “upon nine months of exposure to nearly 30°C, all colony (mortality and surface area), polyp (*Symbiodinium* density and chlorophyll *a* content), tissue (total thickness), and molecular (gene expression and molecular composition)-level parameters were documented at similar levels between experimental corals and controls incubated at 26.5°C, suggesting that this species can readily acclimate to elevated temperatures that cause significant degrees of stress, or even bleaching and mortality, in conspecifics of other regions of the Indo-Pacific.”

Mayfield *et al.* state, “there is now a growing

body of evidence to support the notion that corals inhabiting more thermally unstable habitats outperform conspecifics from reefs characterized by more stable temperatures when exposed to elevated temperatures,” citing Coles (1975), Castillo and Helmuth (2005), and Oliver and Palumbi (2011). They also report, “in other systems, provocative gene expression changes, such as the constitutive up-regulation of genes involved in thermotolerance (e.g., *hsp*s; Heath *et al.*, 1993; Feder, 1996), underlie the capacity for organisms to inhabit high and/or variable temperature environments,” as Barshis *et al.* (2013) also documented in corals.

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Climate Change Reconsidered II: Biological Impacts

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6.1.2.2.2 Symbiont Shuffling

The studies reviewed in this section examine symbiont shuffling, the ability of corals to replace the zooxanthellae expelled during a stress-induced bleaching episode with one or more varieties of zooxanthellae more tolerant of that particular stress. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings.

- Zooxanthellae that reside within the cells of host corals are highly diverse, comprising perhaps hundreds of species, of which several are typically found in each species of coral.
- Many corals respond to stress by replacing the zooxanthellae expelled during a stress-induced bleaching episode with one or more varieties of zooxanthellae more tolerant of that stress.
- Coral bleaching is an adaptive strategy for “shuffling” symbiont genotypes to create associations better adapted to new environmental conditions, as opposed to “a breakdown of a stable relationship that serves as a symptom of degenerating environmental conditions.”
- Multiple studies confirm the strategy of symbiont shuffling is occurring in nature.
- Symbiont shuffling “represents a mechanism for rapid acclimatization of the holobiont to environmental change.”

Although once considered to be members of the single species *Symbiodinium microadriaticum*, the zooxanthellae that reside within membrane-bound vacuoles in the cells of host corals are highly diverse, comprising perhaps hundreds of species, with each species of coral typically possessing several of these species (Trench, 1979; Rowan and Powers, 1991; Rowan *et al.*, 1997). One way corals respond to stress is to replace the zooxanthellae expelled by the coral host during a stress-induced bleaching episode with one or more varieties of zooxanthellae more tolerant of that particular stress.

Rowan *et al.* (1997) suggest this phenomenon

occurs in many of the most successful Caribbean corals that act as hosts to dynamic multispecies communities of symbionts, and “coral communities may adjust to climate change by recombining their existing host and symbiont genetic diversities,” thereby reducing the amount of damage that might be expected from another occurrence of anomalously high temperatures. Buddemeier and Fautin (1993) propose coral bleaching is an adaptive strategy for “shuffling” symbiont genotypes to create associations better adapted to new environmental conditions. Kinzie (1999) suggests coral bleaching “might not be simply a breakdown of a stable relationship that serves as a symptom of degenerating environmental conditions,” but also “may be part of a mutualistic relationship on a larger temporal scale, wherein the identity of algal symbionts changes in response to a changing environment.”

The findings of Rowan and Knowlton (1995) and Gates and Edmunds (1999) provide additional evidence of this process of replacing less-stress-tolerant symbionts with more-stress-tolerant ones. The process seems to be successful, for as Glynn (1996) observed, “despite recent incidences of severe coral reef bleaching and mortality, no species extinctions have yet been documented.”

These observations accord well with the experimental findings of Fagoonee *et al.* (1999), who suggest coral bleaching events “may be frequent and part of the expected cycle.” Gates and Edmunds (1999) report “several of the prerequisites required to support this hypothesis have now been met”; after describing them in some detail, they conclude “there is no doubt that the existence of multiple *Symbiodinium* clades, each potentially exhibiting a different physiological optima, provide corals with the opportunity to attain an expanded range of physiological flexibility which will ultimately be reflected in their response to environmental challenge.” This phenomenon may explain the paradox posed by Pandolfi (1999): “a large percentage of living coral reefs have been degraded, yet there are no known extinctions of any modern coral reef species.” This result is exactly what would be expected if periods of stress lead to the acquisition of more-stress-resistant zooxanthellae by coral hosts.

Hoegh-Guldberg (1999) challenged the symbiont shuffling hypothesis by noting the stress-induced replacement of less-stress-tolerant varieties of zooxanthellae by more-stress-tolerant varieties “has never been observed.” Although that was true at the time it was written, subsequent studies have produced the long-sought proof that transforms the hypothesis

into fact.

Baker (2001) transplanted corals of different combinations of host and algal symbiont from shallow (2–4 m) to deep (20–23 m) water and vice versa. After eight weeks, nearly half of the corals transplanted from deep to shallow water had experienced partial or severe bleaching, whereas none of the corals transplanted from shallow to deep water bleached. After one year, and despite even more bleaching at shallow depths, upward transplants showed no mortality, but nearly 20% of downward transplants had died.

The symbiont shuffling hypothesis explains Baker’s results as follows. The corals transplanted upwards were presumed to have adjusted their algal symbiont distributions, via bleaching, to favor more-tolerant species, whereas the corals transplanted downward were assumed to have not done so, since they did not bleach. Baker suggests these findings “support the view that coral bleaching can promote rapid response to environmental change by facilitating compensatory change in algal symbiont communities.” Without bleaching, he continues, “sub-optimal host-symbiont combinations persist, leading eventually to significant host mortality.” Baker proposed coral bleaching may “ultimately help reef corals to survive.” It may also explain why reefs, though depicted by IPCC as environmentally fragile, have survived the large environmental changes experienced throughout geologic time.

Adjeroud *et al.* (2002) provided additional evidence for the veracity of the symbiont shuffling hypothesis through their study of the interannual variability of coral cover on the outer slope of the Tiahura sector of Moorea Island, French Polynesia, between 1991 and 1997, which focused on the impacts of bleaching events caused by thermal stress when sea surface temperatures rose above 29.2°C. Soon after the start of their study, they observed a severe decline in coral cover following a bleaching event that began in March 1991, which was followed by another bleaching event in March 1994. They report the latter bleaching event “did not have an important impact on coral cover,” even though “the proportion of bleached colonies ... and the order of susceptibility of coral genera were similar in 1991 and 1994 (Gleason, 1993; Hoegh-Guldberg and Salvat, 1995).” Between 1991 and 1992 total coral cover dropped from 51.0 to 24.2%, but “coral cover did not decrease between 1994 and 1995.”

Adjeroud *et al.* note a “possible explanation of the low mortality following the bleaching event in 1994 is that most of the colonies in place in 1994

were those that survived the 1991 event or were young recruits derived from those colonies,” and “one may assume that these coral colonies and/or their endosymbiotic zooxanthellae were phenotypically and possibly genotypically resistant to bleaching events,” exactly what the symbiont shuffling hypothesis would predict. They say “this result demonstrates the importance of understanding the ecological history of reefs (i.e., the chronology of disturbances) in interpreting the specific impacts of a particular disturbance.”

Brown *et al.* (2002) published the results of a 17-year study of coral reef flats at Ko Phuket, Thailand, in which they assessed coral reef changes in response to elevated water temperatures in 1991, 1995, 1997, and 1998. They write, “many corals bleached during elevated sea temperatures in May 1991 and 1995, but no bleaching was recorded in 1997.” They report, “in May 1998 very limited bleaching occurred although sea temperatures were higher than previous events in 1991 and 1995 (Dunne and Brown, 2001)”; when bleaching did take place, “it led only to partial mortality in coral colonies, with most corals recovering their color within 3–5 months of initial paling.

Riegl (2003) reviewed what is known about the responses of real-world coral reefs to high-temperature-induced bleaching, focusing primarily on the Arabian Gulf, which experienced high-frequency recurrences of temperature-related bleaching in 1996, 1998, and 2002. *Acropora*, which during the 1996 and 1998 events always bleached first and suffered heaviest mortality, bleached less than all other corals in 2002 at Sir Abu Nuair (an offshore island of the United Arab Emirates) and recovered along the coast of Dubai between Jebel Ali and Ras Hasyan. Riegl writes, “the unexpected resistance of Sir Abu Nuair *Acropora* to bleaching in 2002 might indicate support for the hypothesis of Baker (2001) and Baker *et al.* (2002) that the symbiont communities on recovering reefs of the future might indeed be more resistant to subsequent bleaching,” and “the Arabian Gulf perhaps provides us with some aspects which might be described as a ‘glimpse into the future,’ with ... hopes for at least some level of coral/zooxanthellae adaptation.”

Kumaraguru *et al.* (2003) assessed the damage inflicted on a number of coral reefs within Palk Bay (located on the southeast coast of India just north of the Gulf of Mannar) by a major warming event that produced monthly mean sea surface temperatures of 29.8 to 32.1°C from April through June 2002, after which they studied the degree of recovery of the

reefs. They determined “a minimum of at least 50% and a maximum of 60% bleaching were noticed among the six different sites monitored.” They continue, “the corals started to recover quickly in August 2002 and as much as 52% recovery could be noticed.” By comparison, they note, “recovery of corals after the 1998 bleaching phenomenon in the Gulf of Mannar was very slow, taking as much as one year to achieve similar recovery.” The Indian scientists state, “the process of natural selection is in operation, with the growth of new coral colonies, and any disturbance in the system is only temporary.” They conclude, “the corals will resurge under the sea.”

Rowan (2004) described how he measured the photosynthetic responses of two zooxanthellae genotypes or clades—*Symbiodinium C* and *Symbiodinium D*—to increasing water temperature and found the photosynthetic prowess of the former decreased at higher temperatures whereas that of the latter increased. He notes “adaptation to higher temperature in *Symbiodinium D* can explain why *Pocillopora* spp. hosting them resist warm-water bleaching whereas corals hosting *Symbiodinium C* do not,” and “it can also explain why *Pocillopora* spp. living in frequently warm habitats host only *Symbiodinium D*, and, perhaps, why those living in cooler habitats predominantly host *Symbiodinium C*.” These observations, he concludes, “indicate that symbiosis recombination may be one mechanism by which corals adapt, in part, to global warming.”

Baker *et al.* (2004) “undertook molecular surveys of *Symbiodinium* in shallow scleractinian corals from five locations in the Indo-Pacific that had been differently affected by the 1997–98 El Niño-Southern Oscillation (ENSO) bleaching event.” Along the coasts of Panama, they surveyed ecologically dominant corals in the genus *Pocillopora* before, during, and after ENSO bleaching, finding “colonies containing *Symbiodinium* in clade D were already common (43%) in 1995 and were unaffected by bleaching in 1997, while colonies containing clade C bleached severely.” They found “by 2001, colonies containing clade D had become dominant (63%) on these reefs.”

After describing similar observations in the Persian (Arabian) Gulf and the western Indian Ocean along the coast of Kenya, Baker *et al.* summarize say their results indicate “corals containing thermally tolerant *Symbiodinium* in clade D are more abundant on reefs after episodes of severe bleaching and mortality, and that surviving coral symbioses on these reefs more closely resemble those found in high-temperature environments,” where clade D predom-

inates. They conclude by noting the symbiont changes they observed “are a common feature of severe bleaching and mortality events,” and they predict “these adaptive shifts will increase the resistance of these recovering reefs to future bleaching.”

Lewis and Coffroth (2004) described a controlled experiment in which they induced bleaching in a Caribbean octocoral (*Briareum* sp.) and then exposed it to exogenous *Symbiodinium* sp. containing rare variants of the chloroplast 23S ribosomal DNA (rDNA) domain V region (cp23S-genotype), after which they documented the symbionts’ repopulation of the coral, whose symbiont density had been reduced to less than 1% of its original level by the bleaching. In an analogous study, Little *et al.* (2004) investigated the acquisition of symbionts by juvenile *Acropora tenuis* corals growing on tiles they attached to different portions of reef at Nelly Bay, Magnetic Island (an inshore reef in the central section of Australia’s Great Barrier Reef).

Lewis and Coffroth state their results show “the repopulation of the symbiont community involved residual populations within *Briareum* sp., as well as symbionts from the surrounding water,” noting “recovery of coral-algal symbioses after a bleaching event is not solely dependent on the *Symbiodinium* complement initially acquired early in the host’s ontogeny,” but “these symbioses also have the flexibility to establish new associations with symbionts from an environmental pool.” Similarly, Little *et al.* report, “initial uptake of zooxanthellae by juvenile corals during natural infection is nonspecific (a potentially adaptive trait),” and “the association is flexible and characterized by a change in (dominant) zooxanthella strains over time.”

Lewis and Coffroth conclude “the ability of octocorals to reestablish symbiont populations from multiple sources provides a mechanism for resilience in the face of environmental change.” Little *et al.* conclude the “symbiont shuffling” observed by both groups “represents a mechanism for rapid acclimatization of the holobiont to environmental change.”

Chen *et al.* (2005) reported on their study of the seasonal dynamics of *Symbiodinium* algal phylotypes via bimonthly sampling over an 18-month period of *Acropora palifera* coral on a reef flat at Tantzel Bay, Kenting National Park, southern Taiwan, in an attempt to detect real-world symbiont shuffling. They found two levels of symbiont shuffling in host corals: between *Symbiodinium* phylotypes C and D, and among different variants within each phylotype. The most significant changes in symbiont composition occurred at times of significant increases in seawater

temperature during late spring and early summer, perhaps as a consequence of enhanced stress experienced at that time, leading Chen *et al.* to state their work revealed “the first evidence that the symbiont community within coral colonies is dynamic ... involving changes in *Symbiodinium* phylotypes.”

Van Oppen *et al.* (2005) sampled zooxanthellae from three common species of scleractinian corals at 17 sites along a latitudinal and cross-shelf gradient in the central and southern sections of the Great Barrier Reef four to five months after the major bleaching event of 2002, recording the health status of each colony at the time of its collection and identifying its zooxanthella genotypes, of which there are eight distinct clades (A-H) with clade D being the most heat-tolerant. They found “there were no simple correlations between symbiont types and either the level of bleaching of individual colonies or indicators of heat stress at individual sites.” They write, “there was a very high post-bleaching abundance of the heat tolerant symbiont type D in one coral population at the most heat-stressed site.”

The Australian researchers say they suspect the post-bleaching abundance of clade D zooxanthellae at the high heat-stress site was due to “a proliferation in the absolute abundance of clade D within existing colonies that were previously dominated by clade C zooxanthellae.” In the four to five months before sampling them, the writers note, “mixed C-D colonies that had bleached but survived may have shifted (shuffling) from C-dominance to D-dominance, and/or C-dominated colonies may have suffered higher mortality during the 2002 bleaching event” and subsequently been repopulated by a predominance of clade D genotypes.

Berkelmans and van Oppen (2006) investigated the thermal acclimatization potential of *Acropora millepora* corals at Australia’s Great Barrier Reef to rising temperatures through transplantation and experimental manipulation. They found the adult corals “are capable of acquiring increased thermal tolerance and that the increased tolerance is a direct result of a change in the symbiont type dominating their tissues from *Symbiodinium* type C to D.” Two years later, working with an expanded group of authors (Jones *et al.*, 2008), the two researchers reported similar findings following the occurrence of a natural bleaching event.

Before that bleaching event, Jones *et al.* report, “*A. millepora* at Miall reef associated predominantly with *Symbiodinium* type C2 (93.5%) and to a much lesser extent with *Symbiodinium* clade D (3.5%) or mixtures of C2 and D (3.0%).” During the bleaching

event, they report, “the relative difference in bleaching susceptibility between corals predominated by C2 and D was clearly evident, with the former bleaching white and the latter normally pigmented,” whereas corals harboring a mix of *Symbiodinium* C2 and D were “mostly pale in appearance.” Three months after the bleaching event, they observed “a major shift to thermally tolerant type D and C1 symbiont communities ... in the surviving colonies”; the latter types had not been detected in any of the corals before bleaching. They report, “this shift resulted partly from a change of symbionts within coral colonies that survived the bleaching event (42%) and partly from selective mortality of the more bleaching-sensitive C2-predominant colonies (37%).” All of the colonies that harbored low levels of D-type symbionts before the bleaching event survived and changed from clade C2 to D predominance.

Jones *et al.* write, “as a direct result of the shift in symbiont community, the Miall Island *A. millepora* population is likely to have become more thermo-tolerant,” as they note “a shift from bleaching-sensitive type C2 to clade D increased the thermal tolerance of this species by 1–1.5°C.” They say their results “strongly support the reinterpreted adaptive bleaching hypothesis of Buddemeier *et al.* (2004), which postulates that a continuum of changing environmental states stimulates the loss of bleaching-sensitive symbionts in favor of symbionts that make the new holobiont more thermally tolerant.” They state their observations “provide the first extensive colony-specific documentation and quantification of temporal symbiont community change in the field in response to temperature stress, suggesting a population-wide acclimatization to increased water temperature.”

Lien *et al.* (2007) examined the symbiont diversity in a scleractinian coral, *Oulastrea crispata*, throughout its entire latitudinal distribution range in the West Pacific, from tropical peninsular Thailand (<10°N) to high-latitudinal outlying coral communities in Japan (>35°N). Those results convincingly demonstrate, the six scientists write, “that phylotype D is the dominant *Symbiodinium* in scleractinian corals throughout tropical reefs and marginal outlying non-reefal coral communities.” They learned this particular symbiont clade “favors ‘marginal habitats’ where other symbionts are poorly suited to the stresses, such as irradiance, temperature fluctuations, sedimentation, etc.” As a major component of the symbiont repertoire of most scleractinian corals in most places, the apparent near-universal presence of *Symbiodinium* phylotype D thus provides, Lien *et al.*

write, “a flexible means for corals to routinely cope with environmental heterogeneities and survive the consequences (e.g., recover from coral bleaching).”

Also in 2007, Mieog *et al.* (2007) utilized a newly developed real-time polymerase chain reaction assay, which they say “is able to detect *Symbiodinium* clades C and D with >100-fold higher sensitivity compared to conventional techniques,” to test 82 colonies of four common scleractinian corals (*Acropora millepora*, *Acropora tenuis*, *Stylophora pistillata*, and *Turbinaria reniformis*) from 11 locations on Australia’s Great Barrier Reef for evidence of the presence of background *Symbiodinium* clades. They found “ninety-three percent of the colonies tested were dominated by clade C and 76% of these had a D background.” The latter symbionts, they write, “are amongst the most thermo-tolerant types known to date,” being found “on reefs that chronically experience unusually high temperatures or that have recently been impacted by bleaching events, suggesting that temperature stress can favor clade D.” Mieog *et al.* conclude the clade D symbiont backgrounds detected in their study may act as a safety net, “allowing corals to become more thermo-tolerant through symbiont shuffling as seawater temperatures rise due to global warming.” They suggest symbiont shuffling is likely to play a role in the way “corals cope with global warming conditions,” leading to new competitive hierarchies and, ultimately, “the coral community assemblages of the future.”

Despite the hope symbiont shuffling provides—that corals will be able to cope with any future global warming, whether anthropogenic or natural—some researchers have claimed few coral symbioses host more than one type of symbiont, which has led some commentators to argue symbiont shuffling is not an option for most coral species to survive the coming thermal onslaught of global warming. That claim has been shown to be incorrect.

Working with samples of the widely distributed massive corals *Porites lobata* and *Porites lutea*—collected from Kaneohe Bay, Hawaii—Apprill and Gates (2007) compared the identity and diversity of *Symbiodinium* symbiont types obtained using cloning and sequencing of internal transcribed spacer region 2 (ITS2) with those obtained using the more commonly applied downstream analytical techniques of denaturing gradient gel electrophoresis (DGGE). The results revealed “a total of 11 ITS2 types in *Porites lobata* and 17 in *Porites lutea* with individual colonies hosting from one to six and three to eight ITS2 types for *P. lobata* and *P. lutea*, respectively.” The two authors

report, “of the clones examined, 93% of the *P. lobata* and 83% of the *P. lutea* sequences are not listed in GenBank,” noting they resolved “sixfold to eightfold greater diversity per coral species than previously reported.”

In a “perspective” that accompanied Apprill and Gates’ paper, van Oppen (2007) wrote, “the current perception of coral-inhabiting symbiont diversity at nuclear ribosomal DNA is shown [by Apprill and Gates] to be a significant underestimate of the wide diversity that in fact exists.” These findings, in her words, “have potentially far-reaching consequences in terms of our understanding of *Symbiodinium* diversity, host-symbiont specificity and the potential of corals to acclimatize to environmental perturbations through changes in the composition of their algal endosymbiont community.”

Baird *et al.* (2007) also discount the argument symbiont shuffling is not an option for most coral species, because it is the sub-clade that must be considered within this context, citing studies that indicate “there are both heat tolerant and heat susceptible sub-clades within both clades C and D *Symbiodinium*.” Hence, the more relevant question becomes: How many coral species can host more than one sub-clade? The answer is that most, if not all, likely do. As Baird *et al.* note, “biogeographical data suggest that when species need to respond to novel environments, they have the flexibility to do so.”

Although most prior research into how and when such sub-clade changes might occur has been on adult colonies switching symbionts in response to warming-induced bleaching episodes, Baird *et al.* suggest “change is more likely to occur between generations,” because initial coral infection typically occurs in larvae or early juveniles, which are much more flexible than adults. They note, “juveniles of *Acropora tenuis* regularly harbor mixed assemblages of symbionts, whereas adults of the species almost invariably host a single clade,” and larvae of *Fungia scutaria* ingest symbionts from multiple hosts, although they generally harbor but one symbiont as adults.

The Australian researchers say there is no need for an acute disturbance, such as bleaching, to induce clade or sub-clade change. Instead, if ocean temperatures rise in the future, they foresee juveniles naturally hosting more heat-tolerant sub-clades and maintaining them into adulthood.

In a further assessment of the size of the symbiont diversity reservoir, especially among juvenile coral species, Pochon *et al.* (2007) collected more than 1,000 soritid specimens over a depth of 40 meters on

a single reef at Gun Beach on the island of Guam, Micronesia, throughout an entire year. They studied the specimens by means of molecular techniques to identify unique internal transcribed spacer-2 (ITS-2) types of ribosomal DNA (rDNA), in a project self-described as “the most targeted and exhaustive sampling effort ever undertaken for any group of *Symbiodinium*-bearing hosts.”

Pochon *et al.* identified 61 unique symbiont types in only three soritid host genera, making the Guam *Symbiodinium* assemblage the most diverse derived to date from a single reef. They report, “the majority of mixed genotypes observed during this survey were usually harbored by the smallest hosts.” The authors speculate “juvenile foraminifera may be better able to switch or shuffle heterogeneous symbiont communities than adults,” so as juveniles grow, “their symbiont communities become ‘optimized’ for the prevailing environmental conditions,” suggesting this phenomenon “may be a key element in the continued evolutionary success of these protests in coral reef ecosystems worldwide.”

The work of Mumby (1999), who analyzed the population dynamics of juvenile corals in Belize both before and after a massive coral bleaching event in 1998, supports that statement. Although 70 to 90% of adult coral colonies were severely bleached during the event, only 25% of coral recruits exhibited signs of bleaching. One month after the event, they concluded “net bleaching-induced mortality of coral recruits ... was insignificant,” demonstrating the ability of juvenile corals to successfully weather such bleaching events.

Fitt *et al.* (2009) note the various *Symbiodinium* clades that comprise the algal symbiont found in their coral host have been thought “to exert a major influence on the ability of reef-building corals to survive high-temperature stress.” They add that if the host itself plays a role in this process, “the hypothesis that corals simply shuffle or swap their *Symbiodinium* for clades that are more thermally tolerant does not tell the whole story.” In fact, it suggests corals may be even more adept at coping with rising temperatures than scientists previously believed.

Fitt *et al.* studied a number of coral host and *Symbiodinium* properties and processes in two ubiquitous Indo-Pacific reef corals known to be either very susceptible (*Stylophora pistillata*) or resistant (*Porites cylindrica*) to heat stress, exposing them to seawater temperatures of either 28°C (normal ambient) or 32°C (elevated) for five days before returning them to the normal ambient temperature. The 16 scientists report finding “both physiological

and biochemical differences of both symbiont and host origin in the response to high-temperature stress.” They say “hypotheses that talk only in terms of the thermal characteristics of the symbiont may miss critical information concerning questions surrounding the thermal tolerance of corals in the coming century.” They note “there are dynamic photoprotective mechanisms in both the host and zooxanthellae that include ultraviolet radiation absorbing mycosporine-like amino acids (Shick and Dunlap, 2002; Lesser, 2004), excess excitation energy dissipation in photosystem II via the xanthophyll cycle (Brown *et al.* 1999; Gorbunov *et al.*, 2001), the expression of heat-shock proteins and other stress markers (Black *et al.*, 1995; Downs *et al.*, 2000; Lesser and Farrell, 2004), the up-regulation of antioxidant enzymes (Lesser, 1996; Lesser and Farrell, 2004; Lesser, 2006), host energy reserve utilization (Porter *et al.*, 1989; Grottooli *et al.*, 2004, 2006), and heterotrophic plasticity (Grottooli *et al.*, 2006).” All of these phenomena, they write, “presumably have underlying influences on any response to thermal stress, and hence, contribute to the overall differences within and between species in regard to their bleaching sensitivity.” This diverse group of phenomena that can help both the coral host and its algal symbionts adjust to rising temperatures indicate Earth’s corals are well-equipped to deal with whatever further warming may come their way.

Silverstein *et al.* (2012) state many reef-building corals “have been shown to respond to environmental change by shifting the composition of their algal symbiont (genus *Symbiodinium*) communities,” and “these shifts have been proposed as a potential mechanism by which corals might survive climate stressors, such as increased temperatures.” They say “conventional molecular methods suggest this adaptive capacity may not be widespread because few (~25%) coral species have been found to associate with multiple *Symbiodinium* clades.” They hasten to add, “these methods can fail to detect low abundance symbionts (typically less than 10–20% of the total algal symbiont community).”

To determine whether additional *Symbiodinium* clades might be present but undetected in various corals using conventional discovery and identification techniques, Silverstein *et al.* “applied a high-resolution, real-time PCR [polymerase chain reaction] assay to survey *Symbiodinium* (in clades A-D) from 39 species of phylogenetically and geographically diverse scleractinian corals.” This survey, they write, “included 26 coral species thought to be restricted to hosting a single *Symbiodinium* clade,” referring to the

latter corals as symbiotic specialists.

The three U.S. scientists say they “detected at least two *Symbiodinium* clades (C and D) in at least one sample of all 39 coral species tested,” and “all four *Symbiodinium* clades were detected in over half (54%) of the 26 symbiotic specialist coral species.” They report, “on average, 68% of all sampled colonies within a given coral species hosted two or more symbiont clades.” Silverstein *et al.* conclude, “the ability to associate with multiple symbiont clades is common in scleractinian (stony) corals,” and in regard to coral-algal symbiosis, “specificity is rarely absolute.” They conclude “the potential for reef corals to adapt or acclimatize to environmental change via symbiont community shifts may therefore be more phylogenetically widespread than has previously been assumed.”

Cumbo *et al.* (2013) note “coral reefs thrive in part because of the symbiotic partnership between corals and *Symbiodinium*,” but “the point at which symbiosis is established (i.e., larva vs. juvenile) remains uncertain, as does the source of free-living *Symbiodinium* in the environment.” They investigated “the types of symbionts taken up by *Acropora* larvae exposed to sediments collected from three different locations on the Great Barrier Reef, and compared this to the *Symbiodinium* types within adult cnidarians for each location.” In addition, they “tested whether the *Symbiodinium* types changed during ontogeny by comparing types within the larvae, juvenile and adults of the same species at each location.”

The three researchers report, “*Symbiodinium* clearly reside in the sediments of shallow reef communities and are capable of initiating symbiosis with aposymbiotic coral larvae,” and “the larvae of many species of corals are promiscuous, associating with multiple *Symbiodinium* types independent of coral species or location.” Cumbo *et al.* say their findings suggest “as sea surface temperatures rise, the promiscuity of larvae could benefit corals by allowing them to acquire symbionts with the greatest heat tolerance in each new generation (LaJeunesse *et al.*, 2004; Baird *et al.*, 2007).” In addition, although “this mechanism of acclimatization will most likely be restricted to species that show horizontal transmission of symbionts,” they note such species account for approximately 85% of all species.

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Climate Change Reconsidered II: Biological Impacts

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6.1.2.2.3 Other Stress Response Strategies

The studies reviewed in this section examine other stress response strategies known to operate in corals under stressful conditions. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings.

- Some corals increase their expression of heat shock proteins that help repair heat-damaged constituents of their bodies as another strategy to cope with heat stress.
- The coral probiotic hypothesis, or bacterial shuffling, posits that many corals rearrange their bacterial populations in a manner akin to symbiont shuffling as another response to environmental stress.
- Corals employ other strategies of coping with and adapting to environmental stresses, further suggesting they will be able to continue to cope with the many environmental threats they face now and may face in the future.

In addition to thermal acclimation and symbiont shuffling, corals have other means to cope with and adapt to environmental stresses. One such mechanism is the production of heat shock proteins that help repair heat-damaged constituents of their bodies (Black *et al.*, 1995; Hayes and King, 1995; Fang *et al.*, 1997). Sharp *et al.* (1997), for example, demonstrated sub-tidal specimens of *Goniopora djiboutiensis* typically have much lower constitutive levels of a 70-kD heat shock protein than do their intertidal conspecifics, and they have shown corals transplanted from subtidal to intertidal locations (where temperature extremes are greater and more common) typically increase their expression of this heat shock protein.

Roberts *et al.* (1997) reported similar results in field work with *Mytilus californianus*. Gates and Edmunds (1999) observed an increase in the 70-kD heat shock protein after six hours of exposure of *Montastraea franksi* to a 2–3°C increase in temperature, followed by another heat shock protein increase at the 48-hour point of exposure to elevated water temperature. They state the first of these protein increases “provides strong evidence that changes in protein turnover during the initial exposure to elevated temperature provides this coral with the biological flexibility to acclimatize to the elevation in sea water temperature,” and the second increase “indicates another shift in protein turnover perhaps associated with an attempt to acclimatize to the more chronic level of temperature stress.”

Reshef *et al.* (2006) discussed another adaptive bleaching mechanism, developing a case for what they call the coral probiotic hypothesis, which might also be referred to as bacterial shuffling. This concept, they write, “posits that a dynamic relation-

ship exists between symbiotic microorganisms and environmental conditions which brings about the selection of the most advantageous coral holobiont.” It is analogous to the adaptive bleaching hypothesis of Buddemeier and Fautin (1993), or what was referred to in the preceding section as symbiont shuffling, in which corals exposed to some type of stress—such as that induced by exposure to unusually high water temperatures or solar irradiance—first lose their dinoflagellate symbionts (bleach) and then regain a new mixture of zooxanthellae better suited to the stress conditions. The two phenomena work in precisely the same way, in one case by the corals rearranging their zooxanthellae populations (symbiont shuffling) and in the other by the corals rearranging their bacterial populations (bacterial shuffling).

The team of Israeli researchers looked for examples of corals developing resistance to emerging diseases. Corals lack an adaptive immune system—they possess no antibodies (Nair *et al.*, 2005)—and therefore can protect themselves against specific diseases in no other way than to adjust the relative sizes of the diverse bacterial populations associated with their mucus and tissues so as to promote the growth of those types of bacteria that tend to mitigate most effectively against the specific disease that happens to be troubling them.

Reshef *et al.* described the discovery that bleaching of *Oculina patagonica* corals in the Mediterranean Sea was caused by the bacterium *Vibrio shiloi*, together with the finding that bleaching of *Pocillopora damicornis* corals in the Indian Ocean and Red Sea was the result of an infection with *Vibrio coralliilyticus*. They report “during the last two years *O. patagonica* has developed resistance to the infection by *V. shiloi*,” “*V. shiloi* can no longer be found on the corals,” and “*V. shiloi* that previously infected corals are unable to infect the existing corals.” They write, “by some unknown mechanism, the coral is now able to lyse the intracellular *V. shiloi* and avoid the disease.” Because corals lack the ability to produce antibodies and have no adaptive immune system, the only logical conclusion to be drawn from these observations is that bacterial shuffling must be at work.

The Israeli scientists note “Hoegh-Guldberg (1999, 2004) has predicted that coral reefs will have only remnant populations of reef-building corals by the middle of this century,” based on “the assumption that corals cannot adapt rapidly enough to the predicted temperatures in order to survive.” They report considerable evidence has been collected in support of the adaptive bleaching hypothesis, and

they emphasize the hundreds of different bacterial species associated with corals “give the coral holobiont an enormous genetic potential to adapt rapidly to changing environmental conditions.” They state, “it is not unreasonable to predict that under appropriate selection conditions, the change could take place in days or weeks, rather than decades required for classical Darwinian mutation and selection,” and “these rapid changes may allow the coral holobiont to use nutrients more efficiently, prevent colonization by specific pathogens and avoid death during bleaching by providing carbon and energy from photosynthetic prokaryotes,” of which they say there is “a metabolically active, diverse pool” in most corals.

Another example of adaptation to stress comes from studies of corals that exhibit a “zonation” of their symbiont taxa with depth, where symbiont algae that are less tolerant of intense solar radiation grow on corals at greater depths below the ocean surface (Rowan and Knowlton, 1995; Rowan *et al.*, 1997). Researchers also have demonstrated zooxanthellae in corals possess a number of light-quenching mechanisms that can be employed to reduce the negative impacts of excess light (Hoegh-Guldberg and Jones, 1999; Ralph *et al.*, 1999). Both the coral host and its symbionts also have the capacity to produce amino acids that act as natural “sunscreens” (Hoegh-Guldberg, 1999); and they can regulate their enzyme activities to enhance internal scavenging systems that remove noxious oxygen radicals produced in coral tissues as a result of high light intensities (Dyken and Shick, 1984; Lesser *et al.*, 1990; Matta and Trench, 1991; Shick *et al.*, 1996).

Another means corals can use to lessen the stress of solar irradiance is coral tissue retraction. Brown *et al.* (1994) studied the phenomenon in the scleractinian coral *Coeloseris mayeri* at coral reefs in Phuket, Thailand by examining the retraction and recovery of coral tissues over a tidal cycle. They found extreme tissue retraction occurred approximately 85 minutes after initial sub-aerial coral exposure. Tissue retraction did not involve any reduction in chlorophyll concentration or algae symbiont abundance; the tissues expanded over the coral skeletons to pre-retraction conditions following the return of the tide. The adaptive benefits of tissue retraction, the authors write, “include increased albedo, leading to a reduction in absorbed solar energy of 10%, ... and possible avoidance of photochemical damage or photoinhibition at high solar irradiance.”

Nakamura and van Woesik (2001) evaluated the bleaching of large and small coral colonies along the

western coast of Okinawa, Japan during the summers of 1998 and 2001, arguing small coral colonies should survive thermal and light stress more readily than large coral colonies based on mass transfer theory, which suggests rates of passive diffusion are more rapid for small colonies than for large colonies. Bena and van Woesik (2004) offer still another reason why large coral colonies may suffer more than small colonies during environmental conditions conducive to bleaching: Small *Acropora* recruits “contain high concentrations of fluorescent proteins (Papina *et al.*, 2002), which have photoprotective properties (Salih *et al.*, 2000),” and “a high concentration of photoprotective pigments in early life, when planulae are near the surface and as newly settled recruits, may facilitate survival during this phase as well as during stress events involving both high irradiance and thermal anomalies (van Woesik, 2000).”

In addition to the adaptive phenomena described above, Earth appears to possess a natural “heat vent” over the tropics that suppresses the intensity of temperature and/or solar radiation to which corals are exposed whenever dangerously high water temperatures are approached. According to Hoegh-Guldberg (1999), 29.2°C is the threshold water temperature above which significant bleaching can be expected to occur in many tropical corals. As Sud *et al.* (1999) have demonstrated, deep atmospheric convection is typically initiated whenever sea surface temperatures (SSTs) reach a value of about 28°C, so that an upper SST on the order of 30°C is rarely exceeded. As SSTs reach 28–29°C, the cloud-base air mass is charged with sufficient moist static energy for the clouds to reach the upper troposphere. At this point, the billowing cloud cover reduces the amount of solar radiation received at the surface of the sea, while cool and dry downdrafts produced by the moist convection tend to promote ocean surface cooling by increasing sensible and latent heat fluxes at the air-sea interface that cause temperatures there to decline. This “thermostat-like control,” as Sud *et al.* describe it, tends “to ventilate the tropical ocean efficiently and help contain the SST between 28–30°C,” which is essentially a fluctuating temperature band of $\pm 1^\circ\text{C}$ centered on the bleaching threshold temperature of 29.2°C identified by Hoegh-Guldberg.

Other intriguing observations indicate a natural phenomenon of this nature. Satheesh and Ramanathan (2000), for example, determined polluted air from south and southeast Asia absorbs enough solar radiation over the northern Indian Ocean during the dry monsoon season to heat the atmosphere there by 1–3°C per day at solar noon, thereby greatly reducing

the intensity of solar radiation received at the surface of the sea. Ackerman *et al.* (2000), however, calculated this atmospheric heating would decrease cloud-layer relative humidity and reduce boundary-layer mixing, thereby leading to a 25 to 50% drop in daytime cloud cover relative to that of an aerosol-free atmosphere, which could negate the surface cooling effect suggested by Satheesh and Ramanathan. In a test of this hypothesis based on data obtained from the Extended Edited Cloud Report Archive, Norris (2001) determined daytime low-level ocean cloud cover (which tends to cool the water surface) not only did not decrease from the 1950s to 1990s, it increased, in both the Northern and Southern Hemispheres and at essentially all hours of the day.

Norris remarks, “the observed all-hours increase in low-level cloud cover over the time period when soot aerosol has presumably greatly increased argues against a dominant effect of soot solar absorption contributing to cloud ‘burn-off.’” He says “other processes must be compensating,” one of which could be the phenomenon Sud *et al.* described.

Another process is the “adaptive infrared iris” phenomenon Lindzen *et al.* (2001) described. Working with upper-level cloudiness data from the Japanese Geostationary Meteorological Satellite and SST data from the National Centers for Environmental Prediction, the atmospheric scientists found a strong inverse relationship between upper-level cloud area and the mean SST of cloudy regions, such that the area of cirrus cloud coverage (which tends to warm the planet) normalized by a measure of the area of cumulus coverage (which tends to cool the planet) decreased about 22 percent for each 1°C increase in the SST of the cloudy regions.

“Essentially,” the scientists write, “the cloudy-moist region appears to act as an infrared adaptive iris that opens up and closes down the regions free of upper-level clouds, which more effectively permit infrared cooling, in such a manner as to resist changes in tropical surface temperatures.” So powerful is this phenomenon, Lindzen *et al.* say they are confident it could “more than cancel all the positive feedbacks in the more sensitive current climate models” routinely used to predict the climatic consequences of projected increases in atmospheric CO₂ concentration.

Is there any real-world evidence the natural thermostat discovered by Sud *et al.* and Lindzen *et al.* has been instrumental in preventing coral bleaching? Mumby *et al.* (2001) examined long-term meteorological records from the vicinity of the Society Islands, which provide what they call “the first empirical evidence that local patterns of cloud

cover may influence the susceptibility of reefs to mass bleaching and subsequent coral mortality during periods of anomalously high SST.” Regarding the great El Niño of 1998, Mumby and his colleagues determined SSTs in the Society Islands sector of French Polynesia were above the 29.2°C bleaching threshold for a longer period of time (two months) than in all prior bleaching years of the historical record. Mass coral bleaching, which was extensive in certain other areas, was found to be “extremely mild in the Society Islands” and “patchy at a scale of 100s of km.”

What provided the coral relief from extreme sun and heat? As Mumby and his associates write, “exceptionally high cloud cover significantly reduced the number of sun hours during the summer of 1998,” much as one would have expected Earth’s natural thermostat to have done in the face of such anomalously high SSTs. The marine scientists also note extensive spotty patterns of cloud cover, besides saving most of the coral they studied, “may partly account for spatial patchiness in bleaching intensity and/or bleaching-induced mortality in other areas.”

Although the natural thermostat cannot protect all of Earth’s corals from life-threatening bleaching during all periods of anomalously high SSTs, it apparently protects enough of them enough of the time to ensure sufficiently large numbers of corals survive and grow, since living reefs have persisted over the eons in spite of the continuing recurrence of ever-present environmental threats. That may be how it has always been, although a host of unprecedented anthropogenic forces of site-specific origin might be weakening the abilities of some species to tolerate the thermal and solar stresses they have successfully weathered in the past.

Smith *et al.* (2005) note “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).” They also 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.”

These facts resonate with other findings presented in this volume (see Section 7.3, Health Effects of CO₂) and suggest the ongoing rise in the air’s CO₂

content may ultimately provide the solution to the worldwide problem of heat-induced coral bleaching. This concept originates from research conducted in the terrestrial realm, which reveals, Ren *et al.* (2001) write, “elevated CO₂ can enhance the capacity of plants to resist stress-induced oxidative damage.”

In the case of ozone pollution, the primary problems occur in the leaf mesophyll, where ozone dissolves into the wet surfaces of exposed cell walls. There, reactions of ozone with water and solutes in the apoplast lead to the formation of several ROS, including hydrogen peroxide (H₂O₂), hydroperoxide, superoxide, hydroxyl radicals, and singlet oxygen (Foyer *et al.*, 1994; Kangasjarvi *et al.*, 1994; Wohlgemuth *et al.*, 2002), all of which promote oxygen toxicity (Podila *et al.*, 2001).

In a free-air CO₂ enrichment (FACE) study of this phenomenon in aspen and paper birch seedlings exposed to ambient air, ozone-enriched air, CO₂-enriched air, or air enriched with both ozone and CO₂, Oksanen *et al.* (2003) found H₂O₂ accumulation occurred only “in ozone-exposed leaves and not in the presence of elevated CO₂,” adding “CO₂ enrichment appears to alleviate chloroplastic oxidative stress.” Similarly, in a study of mature holm and white oak trees that had been growing near natural CO₂ springs in central Italy for 30 to 50 years, Schwanz and Polle (1998) found they exhibited significant reductions in their amounts of lipid peroxidation.

Yu *et al.* (2004) sought to ascertain whether the ROS-fighting properties of elevated CO₂ might also operate in the aquatic realm. They grew the marine microalgae *Platymonas subcordiformis* in the laboratory at ambient levels of atmospheric CO₂ and UV-B radiation flux density, and at elevated levels of 5,000 ppm CO₂ and/or UV-B radiation characteristic of what would result from a 25% stratospheric ozone depletion under clear sky conditions in summer. They found the elevated UV-B treatment significantly decreased microalgal dry weight and photosynthetic rate, whereas the elevated CO₂ treatment enhanced dry weight and photosynthetic rate. They also report elevated UV-B significantly increased the production of the toxic superoxide anion and hydrogen peroxide, as well as malonyldialdehyde, which is an end product of lipid peroxidation, whereas elevated CO₂ did just the opposite. In the treatment consisting of both elevated UV-B and elevated CO₂, the concentrations of these three substances were lower than those observed in the elevated UV-B and ambient CO₂ treatment.

Yu *et al.* say their results suggest “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*.” They note, “CO₂ enrichment showed a protective effect against the oxidative damage of UV-B-induced stress,” and, therefore, elevated CO₂ can enhance “the capacity of stress resistance.” They conclude, “algae grown under high CO₂ would better overcome the adverse impact of environmental stress factors that act via generation of activated oxygen species.”

Smith *et al.* (2005) write, “thermal bleaching of many corals is ultimately the result of the destruction of photosynthetic pigments by ROS,” and as Oksanen *et al.* (2003) observe, “CO₂ enrichment appears to alleviate chloroplastic oxidative stress.” It is thus clear some as-yet-undefined level of atmospheric CO₂ enrichment could completely counter coral thermal bleaching. In addition, since the presence of hydrogen peroxide, as Smith *et al.* (2005) write, “may be a signal that triggers a response in the host cell to eject the zooxanthellae or shed the host cell from the coral,” and as Yu *et al.* (2004) write, “CO₂ enrichment could reduce ... lipid peroxidation damage,” it readily follows some degree of atmospheric CO₂ enrichment should cause host cells not to eject their zooxanthellae.

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Climate Change Reconsidered II: Biological Impacts

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6.1.2.3 Resilience of Corals

The studies reviewed in this section examine observational evidence for the resilience of corals in responding to stress events that routinely occur in nature. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings.

- Corals have been around for a very long time, experiencing climatic conditions that have changed dramatically, from conditions both warmer and colder than the present.
- Many researchers have documented rapid recoveries of corals following recent mass bleaching/mortality events, and such recoveries have occurred on time scales previously assumed to be nearly impossible.
- A growing body of research indicates coral resilience is the rule, not the exception, and these findings are at odds with IPCC's projections of future coral demise.

As illustrated in the preceding section (6.1.2.2 Responses to Temperature-Related Stresses), numerous studies attest to the ability of corals to adapt and evolve in response to temperature-related stresses. Nevertheless, there have been many recorded instances where the severity of coral bleaching from temperature-related stresses was great enough to cause mass mortality of corals, and these occurrences have led IPCC to conclude corals are among the most vulnerable species of marine life, saying it “is very likely that coral reef ecosystems will not survive changes in sea temperature beyond an additional increase of 1°C.” (p. 35 of Chapter 30. The Ocean, Working Group II, IPCC *Fifth Assessment Report*, dated March 28, 2013).

Corals, however, have been around for a very long time, experiencing climatic conditions that have changed dramatically, from conditions both warmer and colder than the present, suggesting they are much more resilient than IPCC claims.

The earliest coral reefs date to the Palaeozoic Era, more than 450 million years ago (Hill, 1956). The scleractinian corals, the major builders of the reefs of today (Achtuv and Dubinsky, 1990), appeared in the mid-Triassic some 240 million years later (Hill, 1956), when Earth was considerably warmer than it is today (Chadwick-Furman, 1996). Although reef-building ceased for a time after the extinctions at the

end of the Triassic, the Scleractinia came back during the Jurassic (Newell, 1971; Veron, 1995) and continued to exhibit great robustness throughout the Cretaceous, even when temperatures were as much as 8–15°C higher (Chadwick-Furman, 1996; Veizer *et al.*, 1999), and atmospheric CO₂ concentrations two to seven times higher (Berner and Kothavala, 2001), than they are today.

At the end of the Cretaceous, 70% of the genera and one-third of the families of scleractinian corals disappeared (Veron, 1995) in the greatest biospheric extinction event in geological history, which may have been caused by a large asteroid impact (Alvarez *et al.*, 1980; 1984). They developed again, however, throughout the Cenozoic, particularly during the Oligocene and Miocene (Chadwick-Furman, 1996). Throughout the past two million years of the Pleistocene, they survived at least 17 glacial-interglacial cycles of dramatic climate change and sea-level fluctuation, successfully adapting, over and over again, to these enormous environmental challenges (Pandolfi, 1999). According to Benzie (1999), this evidence suggests “coral reef communities are relatively resilient, have survived previous global climate change, and appear likely to survive future changes.”

Such resilience helps explain why many researchers have documented rapid recoveries of corals following recent mass bleaching/mortality events, on time scales previously assumed to be nearly impossible. As more research is conducted on this topic, it appears coral resilience is the rule, not the exception. These findings are vastly at odds with IPCC’s projections of future coral demise.

An early example of such resilience was observed after the widespread bleaching of corals in the Indian and Pacific Oceans during the peak warmth of the 1998 El Niño, the deadly effects of which were described at the time as the most extensive ever seen. Many of the devastated corals were not expected to recover (Normile, 2000). But barely a year later many of the reefs were in fact recovering, with large amounts of new coral found in what had been made to look like “graveyards” by the prior year’s marine heat wave. Normile quotes Terry Done of the Institute of Marine Science in Cape Ferguson as saying these real-world observations forced many people to admit coral reefs are indeed “more resilient than we had thought.” Since that admission, many more studies have illustrated similar recoveries as scientists have investigated and tracked coral recoveries.

Kayanne *et al.* (2002) assessed coral cover within the reef flat of Shiraho Reef, Ishigaki Island (situated

at the southernmost end of the Ryukyus Islands of Japan) just before, during, and six times after an unprecedented bleaching event that began in early July 1998 and ended in early October of that year. They note “massive *Porites* were susceptible to bleaching, but regained their algae after the bleaching and sustained their coverage.” Branching *Porites*, *Montipora*, and *Acropora* corals experienced significant mortality of 41.1%, 55.4%, and 82.4%, respectively, and approximately two-thirds of the surviving corals were completely or partly bleached. Nevertheless, coverage of large patches of the branching *Montipora* coral, initially reduced by 66%, recovered to pre-bleaching levels after two years.

Kayanne *et al.* note “the recovery of corals to their pre-bleaching levels has been inferred to take from 10 to 30 years for damaged coral populations and from 5 to 10 years for bleached corals that do not die (Hoegh-Guldberg, 1999; Wilkinson *et al.*, 1999).” Shiraho Reef, they report, “is recovering at an unexpectedly fast rate.” The authors conclude, “even susceptible species have a high potential to regain zooxanthellae after bleaching or to recover after mortality.”

Adjeroud *et al.* (2005) initiated a monitoring program on 13 islands (eight atolls and five high volcanic islands) in four of the five archipelagoes of French Polynesia, to document the effects of natural perturbations on coral assemblages. For the period covered by their report (1992–2002), these reefs were subjected to three major coral bleaching events (1994, 1998, 2002) and three cyclones (1997), and before this period the sites had experienced an additional seven bleaching events and 15 cyclones as well as several *Acanthaster planci* outbreaks.

They found the impacts of the bleaching events varied among the different study locations. They observed three temporal trends: “(1) ten sites where coral cover decreased in relation to the occurrence of major disturbances; (2) nine sites where coral cover increased, despite the occurrence of disturbances affecting seven of them; and (3) a site where no significant variation in coral cover was found.” They report, “an interannual survey of reef communities at Tiahura, Moorea, showed that the mortality of coral colonies following a bleaching event was decreasing with successive events, even if the latter have the same intensity (Adjeroud *et al.*, 2002).”

The seven French scientists say the “spatial and temporal variability of the impacts observed at several scales during the present and previous surveys may reflect an acclimation and/or adaptation of local populations,” and “coral colonies and/or their

endosymbiotic zooxanthellae may be phenotypically (acclimation) and possibly genotypically (adaptation) resistant to bleaching events,” citing Rowan *et al.* (1997), Hoegh-Guldberg (1999), Kinzie *et al.* (2001), and Coles and Brown (2003) in support of this conclusion.

Pratchett *et al.* (2013) developed a history of variations in coral bleaching among four key genera of reef-building corals (*Acropora*, *Montipora*, *Pocillopora*, and *Porites*) in Moorea, focusing on four mass-bleaching events that occurred there in 1991, 1994, 2002, and 2007. They documented the history of the bleaching susceptibility of each of the four coral genera in each of the four events, finding “*Acropora* and *Montipora* consistently bleached in far greater proportions than *Pocillopora* and *Porites*.” They also found “an apparent and sustained decline in the proportion of colonies that bleached during successive bleaching events, especially for *Acropora* and *Montipora*.” In 2007, for example, only 77% of *Acropora* colonies bleached compared with 98% in 1991. They acknowledge “temporal variation in the proportion of coral colonies bleached may be attributable to differences in environmental conditions among years” but also state, “alternately, the sustained declines in bleaching incidence among highly susceptible corals may be indicative of acclimation or adaptation.” Pratchett *et al.* suggest it may be “that gradual removal of highly susceptible genotypes (through selective mortality of individuals, populations, and/or species) is producing a coral assemblage that is more resistant to sustained and ongoing ocean warming,” which further suggests “there is some capacity for adaptation, which will delay devastating effects of global climate change.”

Golbuu *et al.* (2007) examined recovery rates of coral communities on the Palauan reef complex of Micronesia (7°30'N, 134°30'E) at two depths (3 and 10 m) at several sites (nine outer-reef wave-exposed sites, four on the east coast and five on the west coast; two patch reef sites; and two sheltered-bay sites) three, four, and seven years after the 1998 El Niño-Southern Oscillation (ENSO)-induced bleaching event. The nine researchers report, “coral populations recovered rapidly on the reefs of Palau,” but “recovery trajectories changed over time and were habitat and depth-dependent,” noting “seven years after the bleaching event, some reefs supported >30% coral cover, and some habitats supported >40% coral cover.” They observe “recovery within the bays at 3 m was mostly a consequence of growth of remnant (surviving) coral colonies, while recovery on the exposed slopes was mostly likely a consequence of

both remnant regrowth and sexual recruitment events at 10 m, and more a consequence of recruitment at 3 m.”

Guzman and Cortes (2007) studied coral reefs of the eastern Pacific Ocean that “suffered unprecedented mass mortality at a regional scale as a consequence of the anomalous sea warming during the 1982–1983 El Niño.” At Cocos Island (5°32'N, 87°04'W), they found in a survey of three representative reefs, which they conducted in 1987, the remaining live coral cover was only 3% what it had been before the great El Niño four years earlier (Guzman and Cortes, 1992). Based on this finding and the similar observations of other scientists at other reefs, they predicted “the recovery of the reefs’ framework would take centuries, and recovery of live coral cover, decades.”

In 2002, nearly 20 years after the disastrous coral-killing warming, they returned to see how accurate their prediction had been, quantifying “the live coral cover and species composition of five reefs, including the three previously assessed in 1987.” The two researchers report overall mean live coral cover increased nearly fivefold, from 2.99% in 1987 to 14.87% in 2002, at the three sites studied during both periods, and the mean live coral cover of all five sites studied in 2002 was 22.7%. They found “most new recruits and adults belonged to the main reef building species from pre-1982 ENSO, *Porites lobata*, suggesting that a disturbance as outstanding as El Niño was not sufficient to change the role or composition of the dominant species.”

The 1998 El Niño-induced bleaching episode severely affected most Indian Ocean reefs, with the Maldives suffering 90% coral mortality in their central atolls. Before this mass mortality, Lasagna *et al.* (2008) write, “hard coral cover was generally between 30 and 60%, often reaching 100% in shallow water.” One year later, they report, “coral cover had decreased to less than 8%, and reefs were dominated by algae.”

In April 2006, Lasagna *et al.* “re-examined the status of the Maldivian reefs, focusing on their benthic composition to evaluate the possible change in dominance from hard corals to non-structural organisms such as soft corals, algae or sponges,” which have been predicted to replace hard corals after major bleaching episodes. The seven Italian scientists report, “eight years after the 1998 coral mass mortality, hard coral cover varied from 12% to 37%,” and “cover of soft corals, algae and sponges was comparatively low (approximately 7% on average).” They say “a recent inventory of coral species showed

that their number is larger than that known before 1998 (Pichon and Benzoni, 2007)."

McClanahan *et al.* (2009) conducted surveys of coral reefs in northern Tanzania "in 2004/5 with the aim of comparing them over an ~8-year period during a time of increased efforts at fisheries management and the 1998 El Niño Southern Oscillation (ENSO) and Indian Ocean Dipole coral mortality event that caused 45% mortality in northern Tanzania and much of the Indian Ocean." The Kenyan, Swedish, Tanzanian, and U.S. researchers report their repeated surveys "indicate general stability of these reefs over time," and "in the context of the high bleaching and mortality of western Indian Ocean reefs after 1998 (Goreau *et al.*, 2000; McClanahan *et al.*, 2007), the general stability and improvement of these reefs six to seven years after the largest ENSO in recent history (McPhaden, 1999) indicates reefs with considerable resilience to climate change."

Because "all reefs exhibited some resilience and ecological stability and even improvements during this time of climate and management change," McClanahan *et al.* conclude this observation "creates considerably more optimism for poor countries, such as Tanzania, to effectively manage their reefs in an environment of climate change." They conclude, "Tanzanian and possibly many other reefs that exhibit similar environmental conditions have the ability to recover from large-scale climatic and human disturbances."

Scopelitis *et al.* (2009) sought to determine the responses of corals of Saint-Leu Reef on la Reunion (a mountainous volcanic island of the Mascarene Archipelago in the Southwest Indian Ocean) to major devastating events that occurred there over the prior 35 years (between 1973 and 2007), including a category 5 cyclone (Firinga, of 29 January 1989). These events "caused 99% coral cover loss (Naim *et al.*, 1997)." A severe coral bleaching event in March 2002 followed on the heels of cyclone Dina of January 2002, and other bleaching episodes occurred in 1983, March–April 1987, and February 2003.

Scopelitis *et al.* studied vertical images of the reef provided by five aerial photographs taken in 1973, 1978, 1989, 1997, and 2003, along with two Quick-bird satellite images taken in 2002 and 2006, as well as periodic quantitative *in situ* observations of parts of the reef-top that could be used to document ecological and substratum characteristics that produce the color and texture observable in the photos and satellite images. From these observations they constructed a history of changes in the reef's coral community over a period of 35 years (1973–2007).

"Despite the multiple disturbance events," the six scientists write, "the coral community distribution and composition in 2006 on Saint-Leu Reef did not display major differences compared to 1973." This pattern of recurrent recovery is truly remarkable, especially since "in the wake of cyclone Firinga, Saint-Leu Reef phase-shifted and became algae-dominated for a period of five years," and even more impressive given that no corals had survived an unnamed cyclone of 27 January 1948. Such findings, the Australian and French researchers write, indicate "a high degree of coral resilience at the site, led by rapid recovery of compact branching corals."

According to Crabbe (2009), "coral reefs throughout the world are under severe challenges from a variety of environmental factors including overfishing, destructive fishing practices, coral bleaching, ocean acidification, sea-level rise, algal blooms, agricultural run-off, coastal and resort development, marine pollution, increasing coral diseases, invasive species, and hurricane/cyclone damage."

Crabbe employed a number of tools to analyze the resilience of the fringing reefs around Discovery Bay, Jamaica, documenting the responses of their populations "to a number of environmental stressors, in particular hurricanes and the mass bleaching event of 2005," which he describes as "by far the major acute influence on the reef sites." The UK researcher reports "there was a reduction in numbers of colonies in the smallest size class for all the species at all the sites in 2006, after the mass bleaching of 2005, with subsequent increases for all species at all sites in 2007 and 2008." At Dairy Bull Reef, he notes, "live coral cover increased from $13 \pm 5\%$ in 2006 to $20 \pm 9\%$ in 2007 and $31 \pm 7\%$ in 2008," and "live *Acropora* species increased from $2 \pm 2\%$ in 2006 to $10 \pm 4\%$ in 2007 and $22 \pm 7\%$ in 2008."

The UK researcher concludes his results "indicate good levels of coral resilience on the fringing reefs around Discovery Bay in Jamaica," even after having "suffered from long term human-induced chronic stressors, such as overfishing and land development," along with "die-off of the long-spined sea urchin" and "coral disease." Crabbe states he and a colleague "found a variety of clades of zooxanthellae, including clade C, in corals at Dairy Bull Reef (Crabbe and Carlin, 2007)," and "the potential for symbiont shuffling, as we have found in 111 colonies of *Acropora* species from the Ningaloo Reef, Australia (Crabbe and Carlin, 2009), may be a factor in their recovery," citing Stat *et al.* (2008).

In early 2006, mass bleaching of corals on

inshore reefs of the Keppel Islands in the southern Great Barrier Reef (GBR) caused high coral mortality, with severe bleaching affecting 77–95% of coral colonies (Weeks *et al.*, 2008; Jones *et al.*, 2008). This event, Diaz-Pulido *et al.* (2009) write, was followed by “an extraordinary bloom of the brown seaweed *Lobophora variegata*,” which was “unprecedented in magnitude on the GBR” and “exacerbated coral mortality by overgrowing stressed coral tissue.” After the natural seasonal decline in *L. variegata*, which in some places had increased its cover by 200–300% by August 2006, “the cover of branching *Acropora* corals at most sites showed an extremely rapid recovery,” the Australian researchers write, “reaching pre-bleaching levels by December 2006–April 2007 ca 12–14 months after the onset of bleaching.”

“Unexpectedly,” as they describe it, “this rapid reversal did not involve reestablishment of corals by recruitment of coral larvae, as often assumed, but depended on several ecological mechanisms previously underestimated.” Most interesting in this regard was “the ‘phoenix effect’ in which apparently dead coral branches regenerate live tissue (Krupp *et al.*, 1993; Jokiel *et al.*, 1993; Riegl and Piller, 2001).” This “remnant surviving coral tissue,” Diaz-Pulido *et al.* continue, “rapidly expanded upwards along the dead coral branches and actively overgrew *L. variegata*, as well as a range of other algal types, including filamentous algal turfs, fleshy seaweeds and crustose coralline algae,” resulting in “a ‘seaweed sandwich’ with algae engulfed between new and old layers of [coral] skeleton.”

Noting reefs of the Keppel Islands “have shown rapid recovery of coral dominance, despite repeated coral bleaching events (1998, 2002, and 2006), severe flood plumes (e.g. 1991, 2008), and dense algal overgrowth,” Diaz-Pulido *et al.* conclude these and other reefs that are “able to rapidly recover abundant corals may serve as key refugia, or sources of larvae for reef recovery at broader scales,” and the phenomena they document in their research “may well be critical to the overall resilience and persistence of coral reef ecosystems globally.”

Bruno *et al.* (2009) recognized additional resilience of corals against algal growth that often ensues after a bleaching event, noting one of the great concerns of marine scientists is “coral reefs are moving toward or are locked into a seaweed-dominated state.” Bruno *et al.* “analyzed 3,581 quantitative surveys of 1,851 reefs performed between 1996 and 2006 to determine the frequency, geographical extent, and degree of macroalgal dominance

of coral reefs and of coral to macroalgal phase shifts around the world.”

The five marine researchers found “the replacement of corals by macroalgae as the dominant benthic functional group is less common and less geographically extensive than assumed,” noting “only 4% of reefs were dominated by macroalgae (i.e., >50% cover).” Across the Indo-Pacific, where regional averages of macroalgal cover were 9–12%, they found “macroalgae only dominated 1% of the surveyed reefs.” In addition, “between 1996 and 2006, phase shift severity decreased in the Caribbean, did not change in the Florida Keys and Indo-Pacific, and increased slightly on the Great Barrier Reef.”

Bruno *et al.* state “coral reef ecosystems appear to be more resistant to macroalgal blooms than assumed,” and “the mismatch between descriptions of reef degradation in the literature and patterns in nature was caused by the generalization of a relatively small number of examples.” They conclude their analysis suggests “the macroalgae problem has been exaggerated,” and “overall,” there has been “no general recent trend (i.e., post-1995) toward macroalgal dominance.” They write, “macroalgal cover may currently be close to the historical baseline across most of the world.”

Zapata *et al.* (2010) developed an extended history from data they obtained over the period 1998–2004 from 20 permanent transects at two sites on one of the largest and best developed coral reefs in the Colombian Pacific (La Azufrada reef on Gorgona Island), plus data obtained there even earlier by others. The four Colombian researchers report comparisons with previous studies showed the reef at La Azufrada returned to “pre-disturbance (1979) levels of coral cover within a 10-year period after the 1982–83 El Niño, which caused 85% mortality,” and subsequently, “the effects of the 1997–98 El Niño, indicated by the difference in overall live coral cover between 1998 and 1999, were minor (<6% reduction).” They report “despite recurrent natural disturbances, live coral cover in 2004 was as high as that existing before 1982 at La Azufrada.” Zapata *et al.* conclude “the recent history of La Azufrada reef since coral reef studies began at Gorgona Island three decades ago (Prahl *et al.*, 1979; Glynn *et al.*, 1982) suggests a remarkable ability of this reef to recover from past perturbations,” which are of the type (extreme El Niño-driven temperature increases leading to coral bleaching) IPCC claims should be especially deadly and from which coral recovery should not be expected.

According to van Woesik *et al.* (2011), “over the

past three decades, thermal stress events have damaged corals globally,” but few studies “have tracked the recovery process or assessed whether winners in the short term are also winners in the long term.” They repeatedly evaluated (1997, 1999, 2000, 2001, 2004, 2007, 2010) a coral assemblage on the southeastern reef of Sesoko Island at the Tropical Biosphere Research Center of the University of the Ryukyus, Okinawa, Japan (26°38’N, 127°52’E), which experienced significant thermal stress events in 1998 and 2001.

The four researchers report, “by 2007, species richness had recovered to ~13 species per m², which was similar to species richness in 1997,” and “hard coral cover increased from 3% in 2001 to 47% in 2010.” They also found “species composition had undergone change,” as “some species were thermally tolerant and increased in relative abundance through time,” some “increased in relative abundance through the thermal stress and remained constant thereafter,” and some “were neither winners nor losers through time.”

Van Woesik *et al.* conclude the ecosystem they studied was “able to absorb the thermal stressors without undergoing change to a less desirable state,” citing the similar findings of Holling (1973) and Scheffer and Carpenter (2003). They note “*Acropora* populations had fully recovered seven years after an extreme thermal-stress event in Palau (Golbuu *et al.*, 2007),” and in the Arabian Gulf, “Riegl and Purkis (2009) showed that *Acropora* assemblages could recover from thermal-stress cycles occurring every fifteen years.”

Marimuthu *et al.* (2013) investigated the recovery of the corals in the Andaman and Nicobar Islands in the eastern part of the Bay of Bengal following a significant warming event in summer 2010. At the time, sea surface temperatures (SSTs) rose to about 34°C, resulting in the bleaching of 74 to 77% of the corals surrounding Havelock Island and Port Blair Bay, respectively. Marimuthu *et al.* utilized pre-bleaching population data obtained by the line intercept transect (LIT) method of English *et al.* (1997) in July 2010, along with post-bleaching data they collected in January 2011 for the most severely affected corals, which included *Acropora cerealis*, *A. humilis*, *Montipora* sp., *Favia pallida*, *Diploastrea* sp., *Goniopora* sp., *Fungia concinna*, *Gardineroseries* sp., *Porites* sp., *Favites abdita*, and *Lobophyllia robusta*. They found “the observed post bleaching recovery [January 2011] of coral cover was 21.1% at Port Blair Bay and 13.29% at Havelock Island,” and “once the sea water temperature resumed

back to the normal condition, most of the corals where found recovered.”

Gilmour *et al.* (2013) note, “coral reef recovery from major disturbance is hypothesized to depend on the arrival of propagules from nearby undisturbed reefs,” and, therefore, “reefs isolated by distance or current patterns are thought to be highly vulnerable to catastrophic disturbance.” In a test of this hypothesis, Gilmour *et al.* set out to “document the recovery of coral assemblages at Australia’s largest oceanic reef system, where changes in assemblage structure and key demographic parameters were quantified for 16 years, through a regime of disturbances beginning with a catastrophic mass bleaching event in 1998.” The authors focused on “the Scott system of reefs, which is surrounded by oceanic waters on the edge of Western Australia’s continental shelf” and is “more than 250 km from the mainland and other reefs in the region, and more than 1000 km from a major center of urbanization.”

The five Australian researchers report finding “for 6 years, recruitment rates were <6% of those prior to the disturbance,” and “on the basis of these rates of change,” they say “recovery was projected to take decades.” Within just 12 years, “coral cover, recruitment, generic diversity, and community structure were again similar to the pre-bleaching years.” The coral recovery “may have been even faster if not for a series of more moderate disturbances, including two cyclones, an outbreak of disease, and a second bleaching.”

Gilmour *et al.* say their results demonstrate “even corals with a negligible supply of larvae from outside can recover relatively quickly from disturbances in the absence of chronic human pressures.” They suggest “addressing local pressures, such as pollution and overfishing, is as important to the recovery of coral reefs as the establishment of networks of marine protected areas.” They conclude, “managing local pressures to promote resilience will be critical to preventing the global degradation of coral reefs,” which is true of several other damaging phenomena, many of which have particular application to Australia’s Great Barrier Reef. These include rising nutrient levels caused by runoff from agricultural activity on land; outbreaks of the coral-devouring crown-of-thorns starfish; the barbed hooks and scything nets used in fishing; tourists and the developers who build resorts and marinas for them; increased sediment levels; the nets of prawn trawlers stirring up the growing load of sediments; the 6–10 tons of “bycatch” for each ton of prawns netted that are caught and die, which dramatically changes the

composition of reef life; sea life depleted to the point of exhaustion by over-fishing; huge catamarans and dive boats that take thousands of visitors to the Barrier Reef each day and dump their sewage in the sea on the way home; the live reef-fish trade; fishermen using dynamite and cyanide; coral diseases; and pollution.

Mondal *et al.* (2013) studied the fringing reefs off Little Andaman Island at the juncture of the Bay of Bengal and the Andaman Sea. A number of such reefs were essentially destroyed when a 2004 tsunami swept across them with devastating consequences. Five years later in 2009, however, 34 species of scleractinian corals had reappeared (Sawall *et al.*, 2010). But the next year brought a massive bleaching event caused by a dramatic increase in sea surface temperatures above their normal average ranges (Mondal and Raghunathan, 2011), after which Mondal *et al.* (2013) found “the bleached corals were transformed mostly into dead ones.”

In February 2012 the three Indian researchers dove to depths of up to 35 meters to identify and record what species of scleractinian corals they encountered at three locations around Little Andaman Island. They employed the line intercept transect method (Bradbury *et al.*, 1886) with a series of 20-meter transects randomly placed at intervals of 10 meters, with three replicates of the procedure carried out at depths of 5, 10, 15, 20, 25, 30, and 35 meters. They discovered 124 species of youthful scleractinian corals, 90 more than the 34 species detected by Sawall *et al.* in 2009. Mondal *et al.* report the minimum value of the Shannon-Weaver Diversity Index was 5.09, which they state “is above the optimum hypothetical value,” whereas the minimum value of Simpson’s Density Index was 0.94, which they report “is very near to the maximum value which is most advantageous.”

In light of these observations and because “bleaching was the only physiological process which happened in between 2009 and 2012,” Mondal *et al.* conclude “bleaching is a prime regulator for the settlement of new recruitment of scleractinian corals which leads to diversified reef area,” further noting “the adaptive features of bleaching can be seen as a mechanism that enables the exchange of symbionts in a better fit of the holobiont to a changed environment,” citing Graham *et al.* (2011).

According to Miranda *et al.* (2013), sub-lethal bleaching effects “occur when corals do not experience mortality after bleaching, but rather undergo a temporary loss of zooxanthellae and/or of their photosynthetic pigments, with later recovery.” This

implies, they write, “corals have an adaptive capacity or resistance to seasonal changes in environmental conditions,” as suggested by Buddemeir and Fautin (1993), Hennige *et al.* (2010), and Hughes *et al.* (2011).

The three Brazilian researchers note “thermal anomalies on the Brazilian coast have been monitored by NOAA satellite imaging since 1998.” They also observe, “there have been many reports of bleaching events occurring in association with ocean warming events,” but “only Dutra *et al.* (2000) reported observations of the reefs after the occurrence of the beaching phenomenon.” They studied the effects of bleaching in the corals of Caramuanas reef—comprised of three main flat reef banks (13°07’S, 38°43’W; 13°07’S, 38°44’W; 13°08’S, 38°44’W)—by comparing them during and immediately after the thermal anomalies related to the ENSO event of 2010 in terms of “frequency and severity of bleaching, live coral cover, number of colonies, class size, disease occurrence and mortality rate,” based on samples taken at 12 fixed transects in three reef locations.

Miranda *et al.* found, “after this bleaching event, neither the rate of mortality nor the number of colonies with disease increased; the size class structure of the most abundant species did not vary; and the number of live colonies and live coral cover also remained the same.” They report, “the reef showed certain resilience to the perturbations caused by the 2010 ENSO event.” In further support of their findings, they write, “the sub-lethal effects of bleaching in Brazilian corals have been observed previously,” noting, “in 1998, the northern littoral of Bahia experienced a bleaching event that affected up to 60% of the coral community, which after one year have completely recovered,” as reported by Dutra *et al.* (2000).

Miranda *et al.* point out, “the Brazilian zooxanthellate coral fauna is characterized by endemic species, with some reminiscent of a Tertiary coral fauna that may be adapted to these inhospitable environment conditions,” citing Leao *et al.* (2003). They cite as some examples various species of the genus *Mussismilia*, as these species had “the lowest percent of bleached colonies,” adding, “those that bleached completely recovered during this investigation.” With respect to potential policy implications of their findings, the Brazilian biologists suggest “eliminating or reducing anthropogenic effects on this reef may increase its resistance and resilience to bleaching, allowing its maintenance,” so “the Caramuanas reef could then act as a reserve of species and genes for this geographic region.”

Earth's corals likely will be able to cope with any further increases in water temperatures, anthropogenic or natural. Corals have survived such warmth and worse many times in the past, including the Medieval Warm Period, Roman Warm Period, and Holocene Optimum, as well as numerous times during prior interglacial periods. There is no reason to think they cannot do so again if the need arises.

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6.1.2.4 Sea-level Rise

The studies reviewed in this section examine the threat potentially large increases in sea level may pose to corals. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- The warming-induced sea-level rise predicted for the coming century—which could be greatly exaggerated if predictions of CO₂-induced global warming are wrong—falls well within the range of typical coral vertical extension rates and can be less than half the rate of certain branching corals.
- Most coral reefs are known to have responded successfully to the sea-level rises that occurred between 14,000 and 6,000 years ago, which were more than twice as rapid as what is being predicted for the coming century.
- Earth’s oceans have undergone, and their coral reefs survived, at least 17 major cycles of sea-level rise and fall during the Pleistocene, the most recent low phase of which ended 18,000 years ago with a global sea level some 120–135 meters below where it is today.
- Even if reef vertical growth rates could not keep up with rising sea levels, that would not spell their doom, as “propagules of the species could keep pace and settle at suitable depths each generation.”
- Rising sea levels likely would benefit many coral reefs. Over the past 6,000 years, relatively stable sea levels have limited upward reef growth, resulting in the development of extensive reef flats. Rising sea levels likely would release them from this vertical constraint.

Some researchers claim CO₂-induced global warming will melt large portions of planetary ice, thereby raising sea levels at a rate faster than corals can adjust to, while reducing the amount of life-sustaining light

that reaches coral algal symbionts. Such concerns are overblown and unlikely to occur, as discussed in the studies reviewed below.

The approximate 30- to 60-cm warming-induced sea-level rise that is predicted for the coming century—which could turn out to be greatly exaggerated if predictions of CO₂-induced global warming are wrong—falls well within the range (2 to 6 mm per year) of typical coral vertical extension rates, which exhibited a modal value of 7 to 8 mm per year during the Holocene and can be more than double that value in certain branching corals (Hopley and Kinsey, 1988; Done, 1999). Moreover, most coral reefs are known to have responded successfully to the sea-level rises that occurred between 14,000 and 6,000 years ago, which were accompanied by large changes in “CO₂ concentrations, ... rainfall, cloud cover, storms and currents” (Wilkinson, 1996), and which were more than twice as rapid as what is being predicted for the coming century (Digerfeldt and Hendry, 1987).

Earth's oceans have undergone, and their coral reefs have survived (Chadwick-Furman, 1996), at least 17 major cycles of sea-level rise and fall during the Pleistocene, the most recent low phase of which ended 18,000 years ago with a global sea level some 120–135 meters below where it is now (Grigg and Epp, 1989). And most coral reefs handle increases in sea level, even rapid increases, much better than decreases (White *et al.*, 1998).

Even if reef vertical growth rates could not keep up with rising sea levels, that would not spell their doom. One of the important characteristics of essentially all reef cnidarians is their ability to produce free-swimming planulae, spores, or dispersive larval stages. Kinzie (1999) notes, “no matter how quickly sea level might rise, propagules of the species could keep pace and settle at suitable depths each generation,” thereby creating what he calls jump-up reefs that “might well contain most of the species present in the original community.” Done (1999) notes “coral communities have a history of tracking their preferred environmental niche which may suggest that as an entity, they will be predisposed to ‘adapt’ to prospective changes in environment over the next century,” citing precedents that clearly demonstrate “coral communities have historically had a good capacity to track their re-distributed preferred physical niches.”

As Kinzie and Buddemeier (1996) recount, coral reefs have survived many periods of “massive environmental changes” throughout the geologic record. Reefs are survivors, they state, “because they

do not simply tolerate environmental changes” but “exhibit an impressive array of acclimations” that allow them to deal with a variety of challenges to their continued existence in any given area. It is highly unlikely anticipated increases in sea level would spell the doom of Earth's corals.

Rising sea levels may actually have a *positive* effect on coral reefs (Roberts, 1993). Over the past 6,000 years, relatively stable sea levels have limited upward reef growth, resulting in the development of extensive reef flats. As Buddemeier and Smith (1988) and Wilkinson (1996) have noted, the sea-level rises predicted to result from CO₂-induced global warming should be beneficial, permitting increased growth in these growth-restricted areas. As Chadwick-Furman (1996) noted, “many coral reefs have already reached their upward limit of growth at present sea level (Buddemeier, 1992), and may be released from this vertical constraint by a rise in sea level.” She also notes rising sea levels may allow more water to circulate between segregated lagoons and outer reef slopes, which could “increase the exchange of coral propagules between reef habitats and lead to higher coral diversity in inner reef areas.” She, too, concludes “coral reefs are likely to survive predicted rates of global change.”

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6.1.3 Crustaceans

The studies reviewed in this section examine the impact of rising temperatures on crustacean species. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- The larval form of the kelp crab is capable of adapting to both higher and lower temperatures than those at which it may have lived for long periods in the past.
- At higher temperatures, red king crab (*Paralithodes camtschaticus*) experienced “accelerated growth” and a “positive, indirect effect on survival,” as “larger size associated with high temperature could provide for earlier refuge in size from the typical fish and invertebrate predators.”
- A modest warming would prove advantageous to hymenosomatid crabs, increasing larval growth and survival rates, as well as fecundity.

- European green crabs (*Carcinus maenas*) on the west coast of North America have demonstrated phenotypic thermal tolerance and adaptation.
- *Palaemonetes varians*, a shallow-water brackish shrimp, “shows genuine acclimation capacities” due to the plasticity inherent in the organism’s critical thermal limit and heat shock response to temperature.
- Some Branchiopod crustaceans display “substantial physiological plasticity or important adaptive variation,” which enables them “to better cope with environmental change.”
- “Copepod diversity, especially in extra-tropical regions, is likely to increase with climate change as their large-scale distributions respond to climate warming,” because of a “strong positive correlation between diversity and temperature.”

Storch *et al.* (2009) note, “temperature is often invoked as the main determinant of distribution ranges and boundaries for marine and terrestrial species,” and the larval stages of many marine species “are more vulnerable to thermal and osmotic stresses than adults.” They explored the rigidity of this temperature determinant of livable range for the Chilean kelp crab (*Taliepus dentatus*) in its most temperature-sensitive larval state. They studied stage zoea I larvae of two populations of the crab—one from Southern Chile (SC, 43°54’S) and one from Central Chile (CC, 33°29’S)—measuring “temperature-dependent activity, oxygen consumption, cardiac performance, body mass and the carbon and nitrogen composition in order to (1) examine thermal effects from organismal to cellular levels, and (2) compare the thermal tolerance of larvae from two environmental temperature regimes.”

The six researchers report, “the thermal tolerance window of zoea from SC was found to be shifted to lower temperatures when compared with those from CC”; that is, the thermal tolerance window of zoea from CC was found to be shifted to higher temperatures when compared with those from SC. The Chilean and German scientists conclude “the small but clear shift between thermal tolerance windows between populations suggests an optimization of reaction norms and local adaptation in larvae of *T. dentatus*,” noting “this differentiation allows the species to cover a wider range of distribution than when restricted to one and the same thermal window for all populations,” which suggests the larval form of

the kelp crab is capable of adapting to both higher and lower temperatures than those at which it may have lived for long periods in the past.

Stoner *et al.* (2010) write, “temperature is a dominant environmental factor that mediates the behavior, physiology, growth, survival, distribution, and recruitment of ectothermic animals living in temperate and high latitudes.” They investigated how the growth and survival of the red king crab (RKC: *Paralithodes camtschaticus*) “may be affected by warming trends expected in Alaska,” since the RKC was once that state’s “most economically valuable crustacean fishery.” The authors reared RKC in “four temperature treatments ranging from 1.5 to 12°C for a period of 60 days, both individually and in low-density populations,” measuring various physiological processes and properties throughout this period.

The three researchers report “temperature had no significant effect on survival of RKC,” and “there was no consistent difference in survival between individually cultured crabs and those in populations.” Growth, they found, “was very slow at 1.5°C, and increased rapidly with temperature with both a contracted inter-molt period and small increase in growth increment.” In addition, “20% of the crabs held at 1.5°C never molted, while more than 90% of the crabs in 12°C reached juvenile state 4 or higher.” Overall, “growth increased as an exponential function of temperature, with slightly higher growth rates observed in populations than for isolated individuals.” They found “no evidence that culturing RKC juveniles at elevated temperatures led to a decrease in condition or nutritional status.”

Stoner *et al.* conclude the “accelerated growth” they observed in the RKC raised at the highest temperature might have a “positive, indirect effect on survival,” as “larger size associated with high temperature could provide for earlier refuge in size from the typical fish and invertebrate predators on RKC.”

Van den Brink *et al.* (2012) note “hymenosomatid crabs of the genus *Halicarcinus* have a reproductive strategy involving a terminal, pubertal moult where reproduction begins only when growth has ceased.” This strategy, they explain, “allows females to maximize their reproductive output during a comparatively short (approximately six month) adult life span by producing broods continuously and successively, without the need for the female to suspend reproduction for moulting,” citing Van den Brink and McLay (2009, 2010). Van den Brink *et al.* investigated the effect of temperature on brood development for “three intertidal hymenosomatid crabs: *Halicarcinus cookii*, *H. varius* and *H. innominatus*,” which

they collected from intertidal habitats around the Kaikoura Peninsula of New Zealand.

The results yielded three main findings. First, “if temperatures rise 2°C as predicted, each of the three species could produce one extra brood per female lifetime,” which the authors say “would result in the production of over 1000 extra larvae per female resulting in a 10–15% increase in fecundity” that could “result in a single female producing 10–50 extra surviving offspring per lifetime.” Second, “an increase in temperature is also likely to increase larval growth rates ... resulting in shorter development times,” which “may also increase survival rates to final instars and eventually adults, thus potentially increasing the size of the population.” Third, “the current six month peak breeding season in the three *Halicarcinus* species may increase as temperatures rise,” which “may allow the three *Halicarcinus* crabs more time to carry eggs and therefore produce even more offspring per lifetime.” These findings indicate a modest warming would prove extremely beneficial to hymenosomatid crabs.

Kelley *et al.* (2011) note, “measuring variation in physiological traits over broad spatial and temporal scales in an effort to investigate the ecological impacts of these traits (Chown *et al.*, 2004)” can “aid in predicting how species or communities will respond to climate change,” citing Baker *et al.* (2004), Harley *et al.* (2006), Hassol (2004), Helmuth *et al.* (2002, 2005), Kennedy *et al.* (2002), Parmesan (2006), Parmesan and Yohe (2003), Portner *et al.* (2001), and Stillman (2003). Employing this approach in their study of the European green crab (*Carcinus maenas*), Kelley *et al.* measured the upper lethal thermal thresholds of two populations of the invasive species living at the southern and northern limits of its current range on the west coast of North America—Sea Drift Lagoon, Stinson Beach California (CA; 37°54′27.82″N), and Pipestem Inlet, Vancouver Island, British Columbia (BC; 49°02.3′N). The two sites are separated by 1,200 km of coastline—where “ambient sea surface temperature in the northern part of the North American west coast range is 5 to 10°C lower, depending on the time of year, than near the southern range limit.” The species’ expansion from its initial introduction at the south end of its range to its current northern end occurred over a period of about 20 years.

The three U.S. scientists determined the warm-adapted southern CA group of crabs had the highest level of organismal thermotolerance and the greatest degree of heat shock protein 70 (Hsp70) production. They also found carapace widths of male and female

C. maenas individuals from CA were significantly smaller than those in BC. Kelley *et al.* say these findings “provide evidence that the northeastern Pacific population of *C. maenas* has incurred a shift in thermal tolerance compared to its southern counterpart,” and “thermal adaptation at the level of the phenotype is a likely cause due to the short timescale of the invasion and the genetic connectivity of the two populations.”

The authors state that over just two decades “it is possible that a large, northern cold-water phenotype may have already arisen,” which further suggests the reverse of this phenomenon also could have occurred over the same length of time if the driving force for phenotypic change had arisen due to the crabs migrating from a cooler to a warmer environment, or, by further inference, that it could have occurred during a period of equivalent climatic warming in the same physical setting without any relocation. This is yet another example of a species demonstrating a capacity to cope with projected global warming, without the need to migrate.

Ravaux *et al.* (2012) point out “all organisms possess some capacity to modify their behavioral, physiological or morphological characteristics in response to changes in environmental temperature” via a phenomenon they characterize as thermal acclimation, citing Angilletta (2009). This special case of phenotypic plasticity would be of great significance to all organisms in a warming world. Ravaux *et al.* studied *Palaemonetes varians*, a shallow-water brackish shrimp native to Western Europe, assessing both cold- and warm-acclimated specimens collected from the Bay of Mont Saint-Michel (France), the plasticity of a common index of thermal tolerance, the critical thermal maximum (CT_{max}), and the plasticity of a widespread and conserved molecular response to stress, known simply as heat shock response (HSR).

The seven scientists determined *P. varians* “shows genuine acclimation capacities” due to the plasticity inherent in the organism’s thermal limit (CT_{max}) and its heat shock response (*hsp70* induction temperature). Ravaux *et al.* conclude *P. varians* “is readily able to expand its thermal range since it can shift its thermal maximum to higher temperatures and also mobilize the HSR over a wide range of temperatures above those experienced in nature.” They state the shrimp “is potentially capable of expanding its upper thermal range,” which suggests it may not have to migrate toward cooler regions in a potentially warming world of the future.

Pinceel *et al.* (2013) studied the ability of large

branchiopod crustaceans to phenotypically adapt, constructing “a molecular phylogeny based on a data set which includes about 85% of the *Branchinella* species currently known to science, as well as a number of recently discovered lineages.” They discovered “substantial physiological plasticity or important adaptive variation present in some species, potentially enabling them to better cope with environmental change.”

Letessier *et al.* (2011) modeled the influence of a suite of physical, chemical, and biological variables on euphausiid species abundance. Euphausiids are small, pelagic, shrimplike crustaceans of the order Euphausiacea; the authors say they constitute “an important component of the pelagic realm,” where they “graze directly on phytoplankton and provide a food source for a range of predators including birds, seals, baleen whales and many commercially important fish species,” citing Verity *et al.* (2002). The authors used a generalized additive model running environmental changes based on IPCC A1B climate scenario to make predictions of future species abundance changes in the Pacific and Atlantic Oceans, which they sub-divided into cells having east-to-west lengths of 300 km and north-to-south lengths of 200 km.

Letessier *et al.* found “the main drivers of species abundance, in order of decreasing importance, were sea surface temperature (SST, explaining 29.53% of species variability), salinity (20.29%), longitude (-15.01%, species abundance decreased from West to East), distance to coast (10.99%) and dissolved silicate concentration (9.03%).” The three UK researchers say their results suggest “the present broad patterns apparent in species abundance (low in high latitudes, high in intermediate latitudes and intermediate in the tropics) will become less pronounced in a warming ocean,” and eventually, “species abundance will be enhanced within intermediate-to-high latitudes (30°N to 60°N and 30°S to 60°S) and diminished in the tropics (20°N to 20°S).” These changes, they write, are “consistent with changes already observed to be occurring in terrestrial systems in Europe and America,” citing Rosenzweig *et al.* (2008), and with “already-observed changes in zooplankton assemblages in the North Atlantic (i.e., communities shifting north),” as reported by Beaugrand *et al.* (2002), Beaugrand and Ibanez (2004), and Richardson and Schoeman (2004). Considered in their entirety, such shifts in euphausiid species abundance may be viewed as positive developments, especially in light of the three scientists’ finding that both the Atlantic and Pacific

Oceans “will on average see an increase in species abundance per cell.”

Rombouts *et al.* (2009) studied marine copepods—small ocean crustaceans that form a key trophic link between phytoplankton and fish. Some are planktonic and drift in sea water, but more are benthic and live on the ocean floor. Rombouts *et al.* developed the first global description of geographical variation in the diversity of marine copepods in relation to 10 environmental variables.

They found “ocean temperature was the most important explanatory factor among all environmental variables tested, accounting for 54 percent of the variation in diversity.” They report “diversity peaked at subtropical latitudes in the Northern Hemisphere and showed a plateau in the Southern Hemisphere where diversity remained high from the Equator to the beginning of the temperate regions.” This pattern, they write, “is consistent with latitudinal variations found for some other marine taxa, e.g. foraminifera (Rutherford *et al.*, 1999), tintinnids (Dolan *et al.*, 2006) and fish (Worm *et al.*, 2005; Boyce *et al.*, 2008), and also in the terrestrial environment, e.g. aphids, sawflies and birds (Gaston and Blackburn, 2000).”

“Given the strong positive correlation between diversity and temperature,” the six scientists conclude, “local copepod diversity, especially in extra-tropical regions, is likely to increase with climate change as their large-scale distributions respond to climate warming.” This state of affairs has typically been found on land for birds, butterflies, and several other terrestrial lifeforms, as their ranges expand and overlap in response to global warming. With more territory thus available to them, their foothold on the planet becomes increasingly strong, fortifying them against forces (many of them human-induced) that might otherwise lead to their extinction.

Tremblay *et al.* (2011) compared time series of ice cover, wind forcing, and satellite-based assessments of photosynthetic carbon production in the Canadian Beaufort Shelf for the years 2002–2008 with corresponding *in situ* measurements of salinity, nutrients, new production, biological stocks, and biogenic fluxes obtained during overwintering surveys of copepods in 2003–2004 and 2007–2008. The 15 researchers report that in 2007–2008, in areas where ice was no longer present, due to enhanced seasonal warming, there was significant wind-induced upwelling of growth-promoting nitrates, which were brought up from deep and dark waters into the euphotic zone, where photosynthesis occurs. As a result of this fertilization effect, the herbivorous

copepod *Calanus glacialis*—which they say is “the key link between diatom production and apex consumers on Arctic shelves,” citing Soreide *et al.* (2010)—experienced a total abundance “3 to 33 times higher than in 2003 during mid-fall and 1.6 to 13 fold higher than in 2004 during early summer.” On the region’s central shelf, the scientists observed “sedimentary chlorophyll *a* was over 20-fold higher than at any station not influenced by upwelling,” and “benthic carbon demand was among the highest ever observed in the Arctic ocean,” citing Clough *et al.* (2005). They report the “repeated instances of ice ablation and upwelling during fall 2007 and summer 2008 multiplied the production of ice algae, phytoplankton, zooplankton and benthos by 2 to 6 fold.”

Tremblay *et al.* conclude the phenomena they observed are “likely to prevail with the increasingly deep and frequent seaward retreat of the central ice pack and the greater incidence of upwelling-favorable winds,” as described in detail by Yang (2009), and “new production is also bound to rise as winds gain in intensity and upwelling draws deeper into the nutrient-rich, upper Pacific halocline.”

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Climate Change Reconsidered II: Biological Impacts

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6.1.4 Fish

The studies reviewed in this section examine the impact of rising temperatures on marine fish species. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Primary production increases expected to result from future greenhouse gas emissions and their IPCC-projected impacts on climate “will provide opportunities to recover overfished fisheries, increase profitability of fisheries and conserve threatened biodiversity” around Australia.
- The population of one-year-old chum salmon in the Okhotsk Sea “was less during the period from the 1940s to the mid–1970s compared to the period from the mid–1980s to the present.” This result “was directly affected by warmer sea

surface temperatures associated with global warming.”

- There has been a “rapid microevolution for earlier migration timing in” pink salmon in Alaska, which has allowed both the odd- and even-year groups of salmon “to remain resilient to environmental change.”
- Despite having low critical thermal maximum temperatures, a geographically diverse group of 11 species of Antarctic fishes “maintained the capacity to increase their heat tolerance through warm acclimation.”
- “Adult seahorses show great resilience to heat stress and are not expected to go through any physiological impairment and behavioral change with the projected near-future warming.”
- “Tropical marine fishes inhabiting fringing nursery environments may have the upper thermal tolerance necessary to endure substantial increases in sea temperatures.”
- Developmental plasticity in fish “may allow adaptation to changing environmental conditions to have delayed effects,” and “this may attenuate some of the more severe predictions about organisms’ responses to global warming and eutrophication.”

Brown *et al.* (2010) noted “effects of climate-driven production change on marine ecosystems and fisheries can be explored using food web models that incorporate ecological interactions such as predation and competition,” citing Cury *et al.* (2008). They used the output of an ocean general circulation model driven by a “plausible” greenhouse gas emissions scenario (IPCC 2007 scenario A2) to calculate changes in climate over a 50-year time horizon. They fed those results into a suite of models for calculating primary production of lower trophic levels (phytoplankton, macroalgae, seagrass, and benthic microalgae), and they used the results of those calculations as input to “twelve existing Ecopath with Ecosim (EwE) dynamic marine food web models to describe different Australian marine ecosystems.” This protocol ultimately predicted “changes in fishery catch, fishery value, biomass of animals of conservation interest, and indicators of community composition.”

The 17 scientists state under IPCC’s “plausible

climate change scenario, primary production will increase around Australia” with “overall positive linear responses of functional groups to primary production change,” and “generally this benefits fisheries catch and value and leads to increased biomass of threatened marine animals such as turtles and sharks.” They note the calculated responses “are robust to the ecosystem type and the complexity of the model used.” Brown *et al.* conclude the primary production increases suggested by their work to result from IPCC-envisioned greenhouse gas emissions and their calculated impacts on climate “will provide opportunities to recover overfished fisheries, increase profitability of fisheries and conserve threatened biodiversity.”

Drinkwater (2006) reviewed the status of marine ecosystems of the northern North Atlantic in the early twentieth century during a regime shift, which he defined as “a persistent radical shift in typical levels of abundance or productivity of multiple important components of the marine biological community structure, occurring at multiple trophic levels and on a geographical scale that is at least regional in extent.” Drinkwater reports, “in the 1920s and 1930s, there was a dramatic warming of the air and ocean temperatures in the northern North Atlantic and the high Arctic, with the largest changes occurring north of 60°N,” and this warming “led to reduced ice cover in the Arctic and subarctic regions and higher sea temperatures,” as well as northward shifts of multiple marine ecosystems.

The early twentieth century warming of North Atlantic waters “contributed to higher primary and secondary production,” Drinkwater notes, and “with the reduced extent of ice-covered waters, more open water allow[ed] for higher production than in the colder periods.” As a result, cod “spread approximately 1200 km northward along West Greenland,” and “migration of ‘warmer water’ species also changed with earlier arrivals and later departures.” Drinkwater notes, “new spawning sites were observed farther north for several species or stocks while for others the relative contribution from northern spawning sites increased.” Also, “some southern species of fish that were unknown in northern areas prior to the warming event became occasional, and in some cases, frequent visitors.”

Seo *et al.* (2011) note, “Pacific salmon (*Oncorhynchus* spp.) play an important role as both keystone species in North Pacific ecosystems and as an ecosystem service that provides human food resources for countries of the North Pacific rim,” citing Kaeriyama (2008), and they observe the

Hokkaido chum salmon (*O. keta*) experiences a period of critical mortality “characterized by size-dependent mortality and size-selective predation, immediately after seaward migration,” citing Healey (1982), Kaeriyama (1986), Kaeriyama and Ueda (1998), and Kaeriyama *et al.* (2007). To determine the effect of global warming on this critical mortality period in the life of Hokkaido chum salmon, Seo *et al.* used multiple regression and path analysis to examine the effects of regional and larger spatial scales of climatic/oceanic conditions on the growth, survival, and population dynamics of the species.

The three researchers from the Faculty of Fisheries Sciences at Japan’s Hokkaido University determined growth of one-year-old chum salmon in the Okhotsk Sea “was less during the period from the 1940s to the mid-1970s compared to the period from the mid-1980s to the present,” and this result “was directly affected by warmer sea surface temperatures associated with global warming.” They add, “the increased growth at age one led directly to higher survival rates and indirectly to larger population sizes.”

Bentley and Burgner (2011) studied juvenile sockeye salmon (*Oncorhynchus nerka*) in an Alaskan watershed that had experienced a 1.9°C increase in summer water temperature over the prior 46 years. They hypothesized the warming of the region “would have resulted in a corresponding increase in fish metabolism, and thus potential consumption rates, that would increase infestation rates of the tapeworm *Triaenophorus crassus*.” They tested their hypothesis by comparing infestation rate data for *T. crassus* collected between 1948 and 1960 with similar data obtained in 2008 and 2009 from the Wood River system of Bristol Bay, Alaska.

The two U.S. researchers from the University of Washington’s School of Aquatic and Fishery Sciences say in “comparing the average summer air temperature to the parasite prevalence of juvenile sockeye salmon, we found no significant relationship over the fifteen years of collected data.” They also report in “evaluating the influence of average summer air temperature on the parasite infestation rates of juvenile sockeye salmon, we again found no significant relationship for either parasite abundance or parasite intensity,” and “when we compared the 13 years of historic parasite prevalence to equivalent data collected in 2008 and 2009, we did not find a statistically significant positive long-term trend in the data.” Bentley and Burgner write, “the parasite abundance of examined sockeye salmon smolts also did not exhibit a statistically significant long-term

trend using the eight years of historic data and the two years of contemporary data.” They report, “evaluating the relationship between time and parasite intensity produced similar results as the other five comparisons, with there not being a statistically significant positive relationship.” Bentley and Burgner conclude their data demonstrate “the complex effects of warming have not summed to generate a measurable change in the infestation rates of juvenile sockeye salmon in the Wood River system.”

Kovach *et al.* (2012) studied salmon in Auke Creek, a small lake-outlet stream near Juneau, Alaska, where there have been complete daily counts of all adult pink salmon migrating into the creek since 1971. They used “phenotypic data on migration timing, archived genetic samples and data from a marker locus, the allele frequencies of which were experimentally altered more than 30 years ago, to determine whether change in migration timing in a population of pink salmon has a genetic basis (i.e., microevolution).” The three researchers determined both even- and odd-year adult pink salmon that spawn in the warming Alaskan stream are migrating into fresh water nearly two weeks earlier than their predecessors did 40 years ago. They also found experimental data “support the hypothesis that there has been directional selection for earlier migration timing, resulting in a substantial decrease in the late-migrating phenotype (from more than 30% to less than 10% of the total abundance).” They also report, “from 1983 to 2011, there was a significant decrease—over threefold—in the frequency of a genetic marker for late-migration timing, but there were minimal changes in allele frequencies at other natural loci.”

Kovach *et al.* say “these results demonstrate that there has been rapid microevolution for earlier migration timing in this population,” and this has allowed both the odd- and even-year groups of salmon “to remain resilient to environmental change,” as also was demonstrated by Kinnison and Hairston (2007). They note, “population abundance in 2011 was the second highest on record,” further indicating the salmon of Auke Creek are “persisting through rapid temperature warming.”

Aurelio *et al.* (2013) examined “the effect of environmental warming on the metabolic and behavioral ecology of a temperate seahorse, *Hippocampus guttulatus*.” They compared routine metabolic rates, thermal sensitivity, ventilation rates, food intake, and behavioral patterns at the average spring temperature (18°C), the average summer temperature (26°C), the temperature that seahorses

often experience during summer heat wave events (28°C), and the temperature of a near-future warming (+2°C) scenario (= 30°C) in Portugal’s Sado estuary.

The 10 scientists state “both newborn juveniles and adults showed significant increases in metabolic rates with rising temperatures,” with newborn juveniles being “more impacted by future warming via metabolic depression.” In addition, “in adult stages, ventilation rates also increased significantly with environmental warming, but food intake remained unchanged.” They report, “the frequency of swimming, foraging, swinging, and inactivity did not significantly change between the different thermal scenarios.” Aurelio *et al.* conclude “adult seahorses show great resilience to heat stress and are not expected to go through any physiological impairment and behavioral change with the projected near-future warming,” but juveniles in their early life stages “display greater thermal sensitivity and may face greater metabolic challenges.”

Bilyk and DeVries (2011) note “most animals do not have a static heat tolerance; rather it changes in response to their recent thermal history through acclimation.” They continue, “given the long residence of Antarctic fishes in constant freezing seawater, this plasticity had long been thought either lost or marginal (Brett, 1970).” They say “understanding the heat tolerance of Antarctic fishes and its plasticity is critical for understanding the threat to this cold adapted fauna,” especially “given the future predicted increases in water temperatures in the southern Ocean from global climate change.”

Bilyk and DeVries employed the critical thermal maximum (CTMax) methodology—the temperature at which an animal loses the ability to escape from constant rapid warming (Paladino *et al.* 1980)—“to survey heat tolerance in a geographically diverse group of eleven species of Antarctic fishes acclimatized to the cold water temperatures of their natural habitats.” They also used this methodology on eight of the species “following warm acclimation to 4°C, which when compared to their environmental CTMaxs provided a measure of the plasticity of their heat tolerance,” as these fish “had been caught or held at temperatures below -0.9°C.”

The researchers found “when acclimatized to their natural freezing water temperatures, environmental CTMaxs ranged from 11.95 to 16.17°C,” and when the eight further-studied species were warm-acclimated to 4°C, “all showed a significant increase over their environmental CTMaxs, with several showing plasticity comparable in magnitude to some far more eurythermal fishes.” Bilyk and DeVries write,

“despite their low CTMaxs, all the Antarctic species maintained the capacity to increase their heat tolerance through warm acclimation,” and when this capacity was quantified, it showed “a surprising level of thermal plasticity at low temperatures,” which they say was surprising “given the presumed loss of selection for thermal flexibility that has long been assumed in this fauna.”

Eme *et al.* (2011) write, “temperate fishes have been considered especially vulnerable to changing climate conditions,” and “increasing water temperatures may also threaten shallow-water marine fishes inhabiting nursery environments, like tropical mangroves and seagrass beds.” To evaluate these hypotheses, the authors “used critical thermal methodology to quantify critical thermal maxima (CTmaxima) of juvenile squaretail mullet (*Liza vaigiensis*) and juvenile crescent terapon (*Terapon jarbua*) captured from shallow seagrass nursery areas around Hoga Island, southeast Sulawesi, Indonesia.”

The three U.S. researchers report groups of mullet acclimated to a constant temperature of 37°C, as well as temperature cycles of 35–39°C or 37–41°C, all displayed statistically similar mean CTmaxima of 44.7, 44.4, and 44.8°C, respectively. They found terapon acclimated to a constant temperature of 37°C or a temperature cycle of 37–40°C both displayed mean CTmaxima of 43.8°C. Eme *et al.* conclude “terapon and mullet demonstrate exceptional tolerance to high temperatures,” and “it seems likely that shallow-water sea surface temperatures would have to be much higher to adversely affect these and other shallow water marine fishes (Eme and Bennett, 2009),” as these “exceptionally high CTmaxima afford mullet and terapon a significant measure of protection against changing habitat conditions.” The scientists write, “despite diverse independent origins across taxa, fishes may share a common suite of physiological adaptations allowing them to survive periodic exposure to high environmental temperature (Hochachka and Somero, 2002; Somero, 2010),” and “exceptional thermal tolerance may be common throughout the biodiverse shallow waters of the Indo-Pacific.” They conclude, “tropical marine fishes inhabiting fringing nursery environments may have the upper thermal tolerance necessary to endure substantial increases in sea temperatures.”

In a controlled laboratory experiment, Donelson *et al.* (2012) reared the offspring from eight wild-caught damselfish (*Acanthochromis polyacanthus*) for two generations, “in present day (+0.0°C) and predicted future increased water temperatures (+1.5°C and +3.0°C) to test their capacity for metabolic

acclimation to ocean warming.” After three months, the authors assessed the responses in resting metabolic rate (RMR) relative to maximum metabolic rate (MMR) for each individual. They used this “metabolic performance” measure to characterize changes in the ability of each fish to perform aerobic activities (which would include functions such as behavior, growth, and reproduction) at its summer average water temperature (+0.0°C) and above (+1.5°C and +3.0°C).

The experiment revealed second-generation offspring had superior metabolic performance at all temperatures when their parents had been reared to maturity at a temperature of +1.5°C or +3.0°C. In addition, one pair of damselfish (i.e., one particular genetic lineage) contributed many more second-generation offspring that did well at +3.0°C than did the other wild parents: 75% of all fish that reproduced at +3.0°C were the offspring of wild pair #41. In contrast, wild pair #41 contributed 57% of offspring reproducing at +1.5°C and only 44% of those reproducing at +0.0°C. Thus, in addition to acclimation occurring within two generations, there was rapid selection of genotypes (and associated phenotypes) tolerant of higher temperatures. Donelson *et al.* conclude “this study provides evidence that, contrary to some expectations, a tropical marine species has the capacity for acclimation and adaptation to temperature increases over timescales much shorter than the rate of anthropogenic climate change,” and “the discovery that advantageous offspring phenotypes are produced within two generations could indicate that some tropical marine species are more capable of coping with global warming than has been suggested.”

Grenchik *et al.* (2013) note “tropical ectotherms are predicted to be especially sensitive to global warming because they may possess a narrow thermal tolerance range as a result of having evolved in a relatively stable thermal environment.” They say having a narrow thermal tolerance range would mean “tropical species tend to live close to their thermal optimum,” so “even relatively small increases in temperature could lead to declines in individual performance,” because “as water temperature increases, so does the cost of maintaining basic cell function (resting metabolic rate, RMR; Bret, 1971).”

Grenchik *et al.* reared newly settled juveniles of the tropical damselfish *Pomacentrus moluccensis* for four months in four temperature treatments: current-day summer average (28.5°C) and up to 3°C above the average (29.5, 30.5, and 31.5°C). The three Australian researchers found the RMRs of fish reared

at 29.5 and 31.5°C were “significantly higher than the control group reared at 28.5°C,” and “fish that developed in 30.5 and 31.5°C exhibited an enhanced ability to deal with acute temperature increases.” They conclude, “this study shows that there is capacity for thermal acclimation during development, with individuals reared from an early age at some temperatures able to modify their physiology to maintain RMRs at near present-day levels,” and this developmental thermal acclimation “may assist coral reef fish to cope with increases in water temperature without a substantial loss to performance.”

Simpson *et al.* (2011) write, “marine ecosystems in the northeast Atlantic have warmed particularly rapidly, with mean sea temperatures in the North Sea and Celtic-Biscay Shelf regions increasing between 1982 and 2006 by 1.31°C and 0.72°C, respectively,” four times faster than the global average. They considered these regions and timeframe to be ideal for determining how real-world fish respond to real-world warming. The researchers “assessed the full impacts of warming on the commercially important European continental shelf fish assemblage using a data-driven Eulerian (grid-based) approach that accommodates spatial heterogeneity in ecological and environmental conditions.”

They analyzed “local associations of species abundance and community diversity with climatic variables, assessing trends in 172 cells from records of >100 million individuals sampled over 1.2 million km² from 1980–2008.” They contrasted this work with the climate envelope approach, which relies on macro-ecological analyses of the effects of climate change on marine fish assemblages that do not account for “constraints on distributional shifts due to population dependence on essential habitat, such as favored substrates, appropriate predator and prey fields, and close proximity to nursery grounds, all of which are often unknown and difficult to quantify.”

The seven scientists say they discovered “responses to warming in 72% of common species, with three times more species increasing in abundance than declining.” These trends were “reflected in international commercial landings,” where landings of nine species identified as declining in warm conditions fell by half during the period of their study, whereas landings of 27 species identified as increasing in warm conditions rose by 2.5 times. They write, this “profound reorganization of the relative abundance of species in local communities occurred despite decadal stability in the presence-absence of species,” such as would have been suggested by the climate envelope approach on a larger spatial scale.

Simpson *et al.* conclude their “finding of stability in presence-absence of species over decadal periods, but significant temperature-driven responses in local species abundance and assemblage composition, suggests that climate envelope models based on species presence-absence alone will not predict the most ecologically and economically significant effects of climate change.”

Lloyd *et al.* (2012) write, “at a broad geographical scale, species richness and diversity decrease as latitude increases both north and south of the equator,” and in marine systems this distribution pattern “has been linked most consistently to variation in sea temperature,” primarily via studies conducted in north-temperate seas, such as those of Fisher *et al.* (2008) and Hiddink and Hofstede (2008). Noting there is a paucity of such studies from the Southern Hemisphere, Lloyd *et al.* analyzed measurements of sea surface temperature and spear-fishing records pertaining to 84 species of marine fish personally harvested by one of their team. This analysis was performed for each day of diving over the years 1989–2007, during which time interval there was a 0.47°C increase in mean sea surface temperature, which rose from an average of 23.36°C for the period 1989–1996 to an average of 23.83°C for 2002–2007.

The five Australian researchers report over the specified time interval, “the proportion of the catch made up by temperate species, in terms of both the number and mass of fish, consistently decreased, whereas the proportion of the catch made up by tropical species consistently increased between the two time periods,” and “the contribution of broadly distributed species to the overall catch remained approximately the same.” In addition, “average species richness and diversity increased 33 and 15%, respectively, between the two time periods.” These findings, the authors write, “are broadly consistent with a predicted poleward shift in species ranges and a predicted increase in species richness and diversity with increasing sea temperature,” confirming “large-scale climate change causing a widening of the tropical belt and subsequent ocean warming is having a profound impact on marine species abundance patterns and community composition at a local scale in the sub-tropics.”

Capelin (*Mallotus villosus*) are small, short-lived forage fish that are the primary prey of many top predators in northern marine ecosystems. They typically spawn in one of two specific habitats with divergent temperature regimes: beach (warm, variable) and deep water (demersal: cool, stable). In recent years there has been some concern about how

capelin may respond to projected global warming.

In 2009 and 2010, Davoren (2012) investigated “the influence of temperature on spawning habitat selection in coastal Newfoundland by quantifying habitat-specific temperature, population-level habitat use, and individual-level movements of male capelin via acoustic telemetry.” The Canadian researcher reports “capelin spawned only at beaches in 2009, when temperatures were significantly colder and frequently fell below suitable ranges at demersal sites, whereas demersal sites were predominantly used under opposing conditions in 2010.” She remarks “males detected in both habitats primarily dispersed from the initial habitat when temperatures routinely fell outside of suitable ranges,” noting “this movement often involved traveling long distances (11.0–32.7 km) against currents, suggesting energetic costs.”

Davoren writes, “overall, temperature appeared to be an important environmental cue for habitat selection by capelin,” and she concludes, “the flexible use of spawning habitats under divergent temperature conditions suggests that capelin have a high capacity to respond to and possibly tolerate predicted ocean-climate change.”

Zambonino-Infante *et al.* (2013) note rising temperatures typically cause “a monotonic decrease in dissolved oxygen concentration in numerous coastal and estuarine ecosystems around the world, resulting in the increased frequency, intensity and length of hypoxia episodes in shallow areas,” with a primary consequence of these phenomena being the progressive widening of the gap between the availability of dissolved oxygen in the coastal water and the metabolic demand of various marine animals. Zambonino-Infante *et al.* studied the common sole (*Solea solea*), which inhabits shallow marine areas highly exposed to environmental changes, to see “whether temperature and trophic conditions experienced during the larval stage had delayed effects on life-history traits and resistance to hypoxia at the juvenile state,” thereby examining “the combined effect of global warming and hypoxia in coastal waters, which are potential stressors to many estuarine and coastal marine fishes.”

Their analysis showed “warmer larval temperature had a delayed positive effect on body mass and resistance to hypoxia at the juvenile stage,” which “suggests a lower oxygen demand of individuals that had experienced elevated temperatures during larval stages.” Zambonino-Infante *et al.* say “this study clearly demonstrates that environmental conditions experienced during early developmental

stages are important in controlling environmental adaptation performance at later life stages.” They state “sole that had experienced elevated temperatures during their early-life exhibited higher body masses and tolerance to hypoxia, probably through long-term programming of metabolic pathways,” noting “such a cohort effect on growth performance and hypoxia tolerance could have major implications for population dynamics.” They conclude, “developmental plasticity in animals may allow adaptation to changing environmental conditions to have delayed effects,” and “this may attenuate some of the more severe predictions about organisms’ responses to global warming and eutrophication.”

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6.1.5 Other Marine Species

In studying the impact of rising temperature on other marine species, researchers have made some important findings that challenge the projections of IPCC on this matter. As listed in the bullet points below and discussed further in the body of this section, such findings include:

Climate Change Reconsidered II: Biological Impacts

- Single environmental metrics, such as air temperature, are not sufficient for making projections of the impacts of climate change.
- Caution should be applied when interpreting results from laboratory-based studies, which are often incapable of mimicking conditions in the real world and often yield results quite different from those observed in nature.
- Warmer temperatures capable of reducing sea ice density and cover reduce the risk of narwhal mortality.
- Intertidal marine species along Australia's east coast have easily withstood a significant climatic warming of $\sim 1.5^{\circ}\text{C}$ over the past 60 years without having to migrate poleward.
- Thermal heterogeneity within marine habitats must be fully understood in order to properly interpret and ascribe patterns of biogeographic response to climate change.
- Offspring of female turtles grew larger and survived better at hotter incubation. The increased heat tolerance appears to be genetically based.

Helmuth *et al.* (2011) note “virtually every physiological process is affected by the temperature of an organism's body, and ... with the advent of new molecular and biochemical techniques for studying organismal responses to thermal stress ... there has been a renewed interest in the effects of temperature extremes on the ecology and physiology of organisms given the observed and forecasted impacts of global climate change.” Using a simple heat budget model that was ground-truthed with approximately five years of *in situ* temperature data obtained by biomimetic sensors, Helmuth *et al.* (2011) “explored the sensitivity of aerial (low tide) mussel body temperature at three tidal elevations to changes in air temperature, solar radiation, wind speed, wave height, and the timing of low tide at a site in central California USA (Bodega Bay).”

The six U.S. scientists found “while increases in air temperature and solar radiation can significantly alter the risk of exposure to stressful conditions, especially at upper intertidal elevations, patterns of risk can be substantially reduced by convective cooling such that even moderate increases in mean wind speed (~ 1 m/sec) can theoretically counteract the effects of substantial (2.5°C) increases in air

temperature.” They also found “shifts in the timing of low tide (+1 hour), such as occur [when] moving to different locations along the coast of California, can have very large impacts on sensitivity to increases in air temperature,” noting, “depending on the timing of low tide, at some sites increases in air temperature will primarily affect animals in the upper intertidal zone, while at other sites animals will be affected across all tidal elevations.” In addition, “body temperatures are not always elevated even when low tide air temperatures are extreme,” due to “the combined effects of convective cooling and wave splash.”

Helmuth *et al.* say their findings suggest the timing and magnitude of organismal warming “will be highly variable at coastal sites, and can be driven to a large extent by local oceanographic and meteorological processes.” They “strongly caution against the use of single environmental metrics such as air temperature” for “making projections of the impacts of climate change.” Moreover, caution should be applied in interpreting the findings of laboratory-based studies, which often do not mimic conditions in the real world and therefore can yield results and implications quite different from those observed in the real world.

Byrne *et al.* (2011) studied the thermotolerance of the planktonic life phase of sea urchin *Heliocidaris erythrogramma* along the southeast coast of Australia, where sea surface temperatures (SSTs) have risen by 2.3°C over the past 60 years. They employed experimental treatments ranging from 18 to 26°C , with the latter value representing a 3 to 4°C increase above recent ambient SSTs. They found “development success across all stages (gastrula, 24 h; larva, 72 h; juvenile, 120 h) decreased with increasing temperature,” and they acknowledge “significant deleterious effects were evident at $+3$ to 4°C .” They also report, “larvae that developed through the early bottleneck of normal development at 26°C metamorphosed successfully,” and there was a 25% decrease in planktonic larval duration (PLD) of the larvae in the highest of the temperature treatments. In parallel studies of progeny derived from the northern and southern parts of the coastline, they found “northern embryos had significantly higher thermotolerance.”

The five researchers say ocean warming may be advantageous to *H. erythrogramma* larvae “through early settlement and reduction of the vulnerable planktonic period.” They also state the higher thermotolerance of the species' northern embryos “provides the possibility that *H. erythrogramma* populations might keep up with a warming world through pole-

ward migration of thermotolerant propagules, facilitated by the strong southward flow of the East Australian Current.” They conclude “due to its extensive latitudinal distribution, its potential developmental thermotolerance and independence of its lecithotrophic larvae from exogenous food and the need to make a functional skeleton, *H. erythrogramma* may be particularly robust to ocean change.”

Laidre and Heide-Jorgensen (2005) used a combination of long-term satellite tracking data, climate data, and remotely sensed sea ice concentrations to detect localized habitat trends of the narwhal (*Monodon monoceros*) in Baffin Bay between Greenland and Canada—which is home to the largest numbers of the world’s narwhals—to study the species’ vulnerability to ongoing and projected climate change. The two researchers write, “since 1970, the climate in West Greenland has cooled, reflected in both oceanographic and biological conditions (Hanna and Cappelen, 2003),” with the result “Baffin Bay and Davis Strait display strong significant increasing trends in ice concentrations and extent, as high as 7.5% per decade between 1979 and 1996, with comparable increases detected back to 1953 (Parkinson *et al.*, 1999; Deser *et al.*, 2000; Parkinson, 2000a,b; Parkinson and Cavalieri, 2002; Stern and Heide-Jorgensen, 2003).”

Laidre and Heide-Jorgensen report, “cetacean occurrence is generally negatively correlated with dense or complete ice cover due to the need to breathe at the surface,” and “lacking the ability to break holes in the ice,” narwhals are vulnerable to reductions in open water availability, as has been demonstrated by ice entrapment events “where hundreds of narwhals died during rapid sea ice formation caused by sudden cold periods (Siegestad and Heide-Jorgensen, 1994; Heide-Jorgensen *et al.*, 2002).” These events are becoming more likely as temperatures continue to decline and sea ice cover and variability increase; the researchers found the latter two trends to be “highly significant at or above the 95% confidence level.” They conclude, “with the evidence of changes in sea ice conditions that could impact foraging, prey availability, and of utmost importance, access to the surface to breathe, it is unclear how narwhal subpopulations will fare in light of changes in the high Arctic.” Clearly, warmer temperatures capable of reducing sea ice cover would benefit narwhals, making them less vulnerable to death from the cold.

Poloczanska *et al.* (2011) resurveyed a historical census of rocky-shore marine fauna that had been conducted in the 1940s and 1950s, to ascertain whether there had been subsequent latitudinal

changes in the distribution and abundance of intertidal marine species consistent with global climate change along Australia’s east coast, which, as they demonstrate, “has undergone rapid warming, with increases in temperature of ~1.5°C over the past 60 years.” Their survey was conducted at 22 rocky-shore sites located between 23 and 35°S latitude, stretching across 1,500 km of coastline.

Of the 37 species the authors encountered that had distributional data available from both time periods, “only six species showed poleward shifts consistent with predictions of global climate change.” Four others moved in the opposite direction “inconsistent with expectations under climate change,” and the rest “showed no significant changes in range edges.” The seven scientists state a combination of wave exposure, local currents, and the presence of large sand islands—“not temperature”—“is the primary factor influencing biogeographic distributions along the subtropical east coast of Australia.”

The contemporaneous study of Seabra *et al.* (2011) supports this conclusion, describing how intertidal marine species can easily withstand significant climatic warming without having to migrate poleward. They examined the relative magnitudes of local-scale versus large-scale latitudinal patterns of the intertidal body temperatures of robolimpets (Lima and Wethey, 2009): autonomous temperature sensor/loggers mimicking the visual aspect and temperature trajectories of real limpets. These temperatures were measured at 30-minute intervals for recurring periods of 170 days at 13 exposed or moderately exposed rocky shores along 1,500 km of the Atlantic coast of the Iberian Peninsula, where they were attached to steep rocky surfaces—both north-facing (typically shaded) and south-facing (sun-exposed)—at three tidal heights covering the entire vertical range inhabited by real-life limpets.

The “most relevant finding” of the study, the four researchers write, was “sunny versus shaded differences were consistently larger than the variability associated with [a] the seasons, [b] shore-specific characteristics (topography, orientation, wave exposure, etc.) and [c] shore level.” Seabra *et al.* say these findings emphasize the importance of analyzing temperature variability at scales relevant to the organisms being studied, “since the usage of sea surface temperature (SST) derived from remotely sensed data to model the distribution of intertidal species may be missing key environmental features,” especially since their results “clearly show that other factors than SST play a much stronger role in

determining the body temperatures of these organisms.” They also suggest “the observed temperature variability may explain the weak correlations found in many studies modeling the distribution of intertidal species using SST data (e.g. Lima *et al.*, 2007b), which negatively impacts attempts of forecasting distributional changes in response to predicted climate warming.”

Seabra *et al.* further state “habitat heterogeneity as determined by surface orientation and, to a lesser extent, height on the shore may provide thermal refugia allowing species to occupy habitats apparently inhospitable when considering only average temperatures,” and “this may be important for understanding range shifts contrary to global warming predictions (e.g. Lima *et al.*, 2007a, 2009; Hilbish *et al.*, 2010).” Thus, they emphasize again “thermal heterogeneity within habitats must be fully understood in order to interpret patterns of biogeographic response to climate change.”

Webster *et al.* (2011) note sponges comprise a major component of coral reef macrofauna and play key ecological roles, including providing habitat for other invertebrates and complex microbial symbioses, citing Bell (2008). Concerned that projected increases in air and sea surface temperatures of up to 4°C by 2100, as suggested in IPCC (2007) report, will have a direct and significant impact on sponges and their holobionts, Webster *et al.* “assessed the effect of elevated seawater temperature on bacterial communities in larvae of the Great Barrier Reef sponge, *Rhopaloeides odorabile*,” in a series of laboratory experiments to “compare the thermal thresholds for the different life history phases of this model sponge species.”

Although *R. odorabile* adults were previously observed to experience significant negative repercussions above 32°C, the four researchers found their larvae exhibited “a markedly higher thermal tolerance,” with no adverse effects detected at temperatures up to 36°C, and their microbial communities “were conserved at temperatures up to 34°C.” The Australian scientists state, “we demonstrated that sponge larvae maintain highly stable symbioses at seawater temperatures exceeding those that are predicted under current climate change scenarios.” Given the likelihood both the sponge and its holobionts would experience considerable adaptive evolution between now and the end of the twenty-first century, it is safe to say predicted global warming would have little or no impact on their survival and normal functioning.

Weber *et al.* (2012) note, “temperature has a

profound effect on hatching success, embryonic development and sex in marine turtles,” and these effects have logically led to “growing concerns regarding the impacts of climate warming on their reproductive success.” Weber *et al.* tested for “local adaptation in an island-nesting population of green turtles (*Chelonia mydas*) where incubation temperatures vary dramatically among closely adjacent nesting beaches,” one with pale sand (Long Beach, LB) and one with dark sand (Northeast Bay, NEB) that was consistently 2–3°C warmer than the pale sand beach only 6 km away. They employed “a combination of *in situ* and common-garden approaches to compare survival (as a measure of fitness), developmental rates and size at hatching for offspring of LB and NEB females at different incubation temperatures, while simultaneously accounting for egg-mediated maternal effects.”

The six scientists report the offspring of female turtles nesting on the naturally hot (black sand) beach “survived better and grew larger at hot incubation temperatures” compared with the offspring of females nesting on the cooler (pale sand) beach. These differences, they write, were caused by “shallower thermal reaction norms in the hot beach population, rather than shifts in thermal optima, and could not be explained by egg-mediated maternal effects.” They conclude “the results of the common-garden experiment suggest that the increased heat-tolerance of NEB turtles has a genetic basis.”

Weber *et al.* also say their results suggest “marine turtle nesting behavior can drive adaptive differentiation at remarkably fine spatial scales,” and “previous studies may have underestimated the extent of adaptive structuring in marine turtle populations that may significantly affect their capacity to respond to environmental change.” They conclude, whereas “global warming is predicted to have multiple deleterious effects on the reproductive success of marine turtles, including the loss of nesting beaches to rising sea levels, increasingly feminized populations and reduced hatching success,” their results suggest “in at least one of these respects, marine turtles have the capacity to adapt to warmer temperatures.”

Doonan *et al.* (2012) write, “*Katharina tunicata*, commonly known as the Black Katy Chiton, is an abundant intertidal grazer with a limited pelagic larval stage of approximately six days (Paine, 1992),” which is distributed along the Pacific coast of North America from Alaska’s Aleutian Islands to southern California, where it is “an important regulator of intertidal ecosystems.” They say the species “has recently suffered declines in localized parts of its

range as a result of exploitation by humans and sea otters.” Noting it is also “under threat from the effects of climate change,” they sought to determine “whether local-scale barriers to gene flow could potentially compromise the dispersal capacity of the species in the face of climate change.” They “used nuclear single-nucleotide polymorphisms and mitochondrial DNA sequencing to elucidate fine-scale patterns of genetic variation between populations of the Black Katy Chiton separated by 15–150 km in southwest Vancouver Island.”

The four UK researchers from Queen’s University in Belfast report, “both the nuclear and mitochondrial data sets revealed no genetic differentiation between the populations studied,” and “an isolation-with-migration analysis indicated extensive local-scale gene flow, suggesting an absence of barriers to dispersal.” They write, “population demographic analysis also revealed long-term population stability through previous periods of climate change associated with the Pleistocene glaciations,” and at the Pleistocene-Holocene transition of approximately ten thousand years ago, as discussed by Fields *et al.* (1993). Doonan *et al.* conclude, “taken together, the current evidence of high dispersal and a lack of biogeographic barriers to gene flow, coupled with the signature of long-term population stability through previous periods of climate change, suggest that this dispersal potential may act as a lifeline for *K. tunicata* as their southerly habitats rapidly warm, and a poleward migration is required for survival,” citing Graham *et al.* (2010).

In an ecosystem-level study, Stuart-Smith *et al.* (2010) state, “despite increasing scientific and public concerns [about] the potential impacts of global ocean warming on marine biodiversity, very few empirical data on community-level responses to rising water temperatures are available.” They undertook “a study of sub-tidal reef communities over a decadal time scale, comparing data on fishes, macroinvertebrates and macroalgae collected at 136 sites, spanning hundreds of kilometers around the island of Tasmania (southeastern Australia) in the early to mid 1990s, with data from the same sites in 2006/2007.”

This region, they write, “has experienced relatively rapid warming during the last century as a consequence of a strengthening of the warm East Australian Current (Ridgway, 2007),” which manifested “an increase in sea surface temperature of $2.28 \pm 0.35^{\circ}\text{C}$ per century for the period 1944–2002 (Ridgway, 2007), which is considerably more rapid than the global mean of $0.6 \pm 0.2^{\circ}\text{C}$ per century estimated by Smith and Reynolds (2003), and a mean

increase in surface air temperature of $0.6\text{--}0.8^{\circ}\text{C}$ (Salinger, 2005; Hansen *et al.*, 2006).” The warming around this part of Tasmania has been more than three times greater than the global mean, making this region a prime location to examine the impacts of rising temperature on marine species in the real world.

Contrary to their expectations, the four researchers discovered “Tasmanian shallow rocky reef communities have been relative stable over the past decade,” despite the “substantial rise in sea surface temperature over this period” and the “continuation of a considerable warming trend in oceanographic conditions over the last 50 years.” They report, “the northeast and southeast bioregions, which are most influenced by the East Australian Current and hence have experienced the greatest warming over the last century, appeared to have actually changed very little,” adding, “not only were Tasmanian reef communities remarkably similar between 1994 and 2006 in a multivariate sense, but univariate community characteristics such as species richness and total fish abundance were also consistent.”

Poloczanska *et al.* (2013) “investigated the peer-reviewed literature that addresses the question of whether or not climate change impacts marine ecological phenomena, and found 208 studies of 857 species and assemblages.” From these reports they extracted “1,735 observations of the following types of response: distribution, phenology, abundance, community change, calcification and demography,” for which “either regional or global climate change was considered as a driver.”

The 20 researchers report, “from this database, 81–83% of all observations for distribution, phenology, community composition, abundance, demography and calcification across taxa and ocean basins were consistent with the expected impacts of climate change.” They add, “of the species responding to climate change, rates of distribution shifts were, on average, consistent with those required to track ocean surface temperature changes.” The findings of this massive review of the relevant scientific literature indicate Earth’s marine life is well-equipped to deal with predicted changes in the global ocean environment and are, in fact, already doing so.

Linares *et al.* (2013) note, “several studies have provided evidence that thermal stress affects the growth, survival and physiology of tropical and temperate macro-invertebrate species,” but “few studies have focused on sub-tidal temperate species and the potential differential thermal tolerances of

populations dwelling under contrasting temperature conditions.” Linares *et al.* assessed “the role that environmental history plays in the response of the temperate gorgonian *Eunicella singularis* to thermal stress,” comparing populations dwelling in the coldest and warmest areas of the NW Mediterranean Sea.

The four researchers report, “*E. singularis* populations from both areas exhibited a high resistance to thermal stress,” but “populations from warmer areas had an increased tolerance to thermal stress,” such that “the upper thermal limits found for cold and warm populations were 28 and 29°C, respectively.” Linares *et al.* conclude by noting their results “agree with results for other Mediterranean anthozoans (Rodolfo-Metalpa *et al.* 2006; Torrents *et al.*, 2008) and tropical corals (Middlebrook *et al.*, 2008), demonstrating thereby that shallow populations (acclimated to warm temperature conditions) have a higher tolerance to thermal stress than deep populations.”

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Aquatic Life

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6.2 Freshwater Warming

The vast majority of studies examining the potential effects of CO₂-induced global warming on aquatic life are focused on marine life, but some scientists have conducted research on the impacts of elevated temperature on freshwater species. The following bulleted key findings indicate the cautious optimism this research suggests, and the findings are discussed in greater detail thereafter.

- Increases in water temperature at Lake Zurich from 1977 to 2008 have resulted in an increase in the number of phytoplankton species and phytoplankton families.
- Annual bass growth is positively and significantly correlated with annual temperature metrics, revealing above-average growth during the warmest and driest years.
- Golden perch growth rates likely will increase in

southerly Australian populations due to warmer temperatures and a lengthening of the growing season.

- Over the past two decades, when IPCC claims Earth warmed at a rate and to a degree unprecedented over the past millennium, the majority of French fish—plus some newcomers to the country's streams and rivers—thrived under warmer water conditions, increasing in both species numbers (diversity) and population size.
- Many predictions of the impact of climate change on aquatic life assume a species-specific response to changing environments, yet substantial differences in thermal plasticity have been observed between populations within species, enabling some populations to cope effectively with changes in the environment that other populations cannot tolerate. The probability of climate-induced species extinctions is much lower than what is often projected.
- Three species of freshwater mussels can adjust their individual critical thermal maximum (the upper temperature at which the onset of behavioral incapacitation occurs) upwards in response to periodic heat waves or significantly warmer years.

In contrast to IPCC-based projections, modest warming has been shown to be highly beneficial to some freshwater species.

Pomati *et al.* (2012) explain that among human impacts on aquatic biodiversity, eutrophication has caused a number of undesirable environmental effects worldwide, including “a general reduction in species richness (Smith and Schindler, 2009) and a loss of ecosystem resilience against further degradation (Folke *et al.*, 2004).” They indicate “lake restoration programs in many regions started at the peak of the eutrophication period (late 1970s, early 1980s),” but the resulting reduction in nutrient loading “coincided with rising temperature from climate warming,” citing Van Donk *et al.* (2003) and Jeppesen *et al.* (2005), so we currently have “limited understanding of how combined climate change and reduction in nutrients affect species richness, ecosystem functioning or resilience.”

Pomati *et al.* analyzed physical and biological parameters in Lake Zurich on the Swiss Plateau just north of the Swiss Alps at depths of 0, 1, 2.5, 5, 7.5, 10, 12.5, 15, 20, 30, 40, 80, 120, and 135 meters that had been collected monthly over a number of decades

by the Zurich Water Supply Company, focusing on data from 1977 to 2008. The five scientists discovered increases in water temperature (0.24°C/decade at the lake surface; 0.13°C/decade near the lake bottom) and spatial (depth) heterogeneity were the best predictors of phytoplankton richness, as the number of phytoplankton species increased from about 40 to 100 and the number of phytoplankton families increased from approximately 25 to 45. They note phytoplankton richness and spatial heterogeneity had the strongest effects on zooplankton richness.

The researchers write, “our analysis highlights that climate warming and re-oligotrophication may favor an increase in spatial (depth) heterogeneity in the water column of deep lakes, enhancing the potential for phytoplankton species co-existence and an increase in plankton richness.” They conclude, “although our study focuses on a single lake, the responses we have documented may be common at least throughout lakes within the European peri-alpine climatic region,” citing Buergi and Stadelmann (2002), Buergi *et al.* (2003), and Anneville *et al.* (2005).

Morrongiello *et al.* (2011) analyzed the yearly growth increments laid down in the otoliths—aragonite (CaCO₃) structures in fish that are used for acoustic perception and balance, also known as earstones—of populations of a native fish species (the golden perch) living in two artificial impoundments (Lakes Mokoan and Eppalock) near their southerly distribution limits in central Victoria, Australia. Over a 15-year period that both predated and encompassed a significant supra-seasonal drought, the authors determined “fish growth declined as water levels in the lakes dropped during the drought,” but “this effect was offset by increased growth in warmer years.” It was in fact more than offset; based on the relationships they found in their data, future projections of mean annual growth of two-year-old golden perch in Lakes Mokoan and Eppalock in the year 2070, respectively, increase by 14.9% and 17.2% under low CO₂ emission and 56.5% and 58.6% under high CO₂ emission scenarios compared with 1990 CO₂ levels. The Australian scientists conclude, “despite climatic models predicting significant declines in future water availability, fish growth may increase due to a disproportionate lengthening of the growing season.” They forecast “golden perch growth rates in southerly [Australian] populations may increase as warmer conditions associated with climate change will lengthen the growing season and make these high [southern] latitude habitats more favorable.”

Rypel (2009) applied tree-ring techniques to the

otoliths of 397 largemouth bass (*Micropterus salmoides* Lacepede) to explore potential relationships between annual bass growth and various climate metrics in the southeastern USA, as manifest in six rivers and seven reservoirs in Georgia, Alabama, and Mississippi sampled during the summers and autumns of 2005–2008. Rypel reports, “results from multiple regressions suggested that on average roughly 50% of the annual variability in largemouth bass growth was attributable to climatic variations,” with annual growth indices typically being found to be “above-average during the warmest, driest years, and below-average during the coldest, wettest years,” because “annual bass growth was significantly negatively correlated with annual precipitation metrics, and significantly positively correlated with annual temperature metrics.”

These findings indicate the warming and drying that are predicted by models to occur in many places will benefit largemouth bass because an increase in temperature generally “stimulates metabolism, and enhances growth rates of fishes,” Rypel writes, citing Beitinger and Fitzpatrick (1979) and Brander (1995).

Poulet *et al.* (2011) write, “over the past 200 years, owing to the industrial and agricultural revolutions, various new and intense pressures have been applied to freshwater ecosystems resulting in the decline of many species both in range and number (Maitland, 1995).” Of these additional threats, they highlight five: overexploitation, water pollution, flow modification, destruction or degradation of habitat, and invasion by exotic species, citing Dudgeon *et al.* (2006). Poulet *et al.* used the extensive electrofishing database of the French National Agency for Water and Aquatic Environment to evaluate time trends of 48 freshwater fish taxa at 590 sites across France over the period 1990–2009, to assess the recent and ongoing net impact of these modern threats to the fish of France.

The three French researchers found “species richness increased steadily from the beginning of the monitoring period,” and “the number of species displaying a significant increase in spatial distribution or abundance was greater than those showing a significant decrease.” They write, “these results are in agreement with recent findings which describe an increase in the number of species and density of fish communities in large French rivers over the past 25 years,” citing Daufresne and Boet (2007). They add, “predictions about the future distribution of 30 common fish species in French streams in 2008, suggested increases in local species richness and in occurrences of the majority of species (Buisson *et al.*,

2008),” and they note “both studies described population growth of warm and cool water species in response to global warming.”

Over the past two decades, when IPCC claims Earth warmed at a rate and to a degree unprecedented over the past millennium or two, the majority of French fish, plus some newcomers to the country’s streams and rivers, thrived under warmer water conditions, increasing in both species numbers (diversity) and population size.

While not all aquatic species may respond in such a positive manner, there is little reason to accept IPCC’s model-based projections of widespread future species decline (and possible extinctions) in response to CO₂-induced global warming. A growing body of evidence demonstrates the ability of aquatic life to adapt and evolve to overcome challenges imposed by rising water temperatures.

Seebacher *et al.* (2012) note “within-individual plasticity (acclimation) counteracts potentially negative physiological effects resulting from environmental changes and thereby maintains fitness across a broad range of environments.” They write, “the capacity for the acclimation of individuals may therefore determine the persistence of populations in variable environments.”

They “determined phylogenetic relationships by Amplified Fragment Length Polymorphism (AFLP) analysis of six populations of mosquitofish (*Gambusia holbrooki*) from coastal and mountain environments and compared their capacity for thermal acclimation.” The six scientists demonstrated mosquitofish populations “are divided into distinct genetic lineages and that populations within lineages have distinct genetic identities.” They report, “there were significant differences in the capacity for acclimation between traits (swimming performance, citrate synthase and lactate dehydrogenase activities), between lineages, and between populations within lineages,” demonstrating “there can be substantial variation in thermal plasticity between populations within species.” They conclude “similar responses are likely to be found in other species that comprise structured populations.”

Noting “many predictions of the impact of climate change on biodiversity assume a species-specific response to changing environments,” Seebacher *et al.* argue, “this resolution can be too coarse and ... analysis of the impacts of climate change and other environmental variability should be resolved to a population level,” because their findings suggest some populations of a species may be able to cope with a change of climate with which others cannot,

thereby preventing the otherwise-inevitable climate-induced extinction of the species.

Gailbraith *et al.* (2012) studied thermal adaptation of three species of freshwater mussels (*Alasmidonta varicosa*, *Elliptio complanata*, and *Strophitus undulatus*) that had been acclimatized to a water temperature of either 15 or 25°C. The temperature of the water in which the mussels were immersed was gradually raised at a rate of 0.35°C per minute, until the researchers observed the onset of extreme gaping, a periodic valve movement resulting in the rapid opening and closing of the mussels' shells that indicates their impending demise. The authors thus studied the mussels' critical thermal maximum (CTM), defined as the upper (warm) temperature at which the onset of behavioral incapacitation (usually loss of equilibrium) occurs—in the words of Gailbraith *et al.* quoting Hutchison (1961)—“the animal loses its ability to escape from conditions that will promptly lead to its death.” Although it sounds like a fixed, immutable value for a given species, the CTM has been proven to be a function of temperature itself.

The three U.S. researchers report, “responses varied by species, but mussels acclimated to 25°C generally had a higher CTM than mussels acclimated to 15°C.” For one of the three species (*E. complanata*), they observed the effects of acclimation and another variable (aeration) were interactive, leading them to conclude “combinations of environmental stressors may influence thermal tolerance” and “such responses vary among species.” They note results similar to theirs “are well documented for other freshwater organisms, particularly for fish (Becker and Genoway, 1979; Elliott, 1981) but also for the zebra mussel, *Dreissena polymorpha* (McMahon and Ussery, 1995; Lutterschmidt and Hutchison, 1997).”

Although multiple factors may thus come into play in determining an animal's current CTM, it is evident from the results of Galbraith *et al.* that some degree of warming above that species-specific value can at times lead to a longer-term increase in the species' CTM. In the case of global warming, the evidence suggests species may adjust their individual CTMs upward in response to periodic heat waves or significantly warmer years.

Crozier *et al.* (2011) note “environmental change can shift the phenotype of an organism through either evolutionary or non-genetic processes,” but “despite abundant evidence of phenotypic change in response to recent climate change, we typically lack sufficient genetic data to identify the role of evolution.” They studied the potential role of rapid evolution by

investigating the drivers of a long-term trend toward earlier upstream migration date in adult sockeye salmon (*Oncorhynchus nerka* Walbaum) that currently migrate up the Columbia River 10.3 days earlier than they did in the 1940s. Noting water temperature records in the lower river showed a rise of 2.6°C in mean July temperature since 1949, the researchers “developed a functional model relating survival during upstream migration to temperature on the basis of the results of recent studies that tracked individual fish through the migration,” after which they “hindcast this function over the historical record to estimate the putative selection differential over the time series.” Thereafter, they “assembled a set of possible environmental drivers of interannual variation in migration timing from the literature” and used “a state-space modeling framework to combine selection and these environmental variables as covariates to explain mean population migration date in a formal time-series analysis,” employing “model-selection techniques to determine which factors best predicted annual migration timing.”

The three researchers from the Northwest Fisheries Science Center in Seattle, Washington (USA) determined “an evolutionary response to thermal selection was capable of explaining up to two-thirds of the phenotypic trend” they observed, and “adaptive plastic responses to June river flow explain most of the remainder.” Crozier *et al.* note the amount of evolutionary change they calculated to have taken place “is typical of numerous studies of contemporary evolution,” citing Hendry and Kinnison (1999) and Kingsolver *et al.* (2001). They suggest evolutionary change “will play an important role in protecting species from extinction during ongoing climate change, as demonstrated in recent simulations of evolution in Fraser River sockeye salmon,” citing Reed *et al.* (2011). They conclude, “directional environmental changes are very likely to induce more rapid evolution in the future.”

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6.3 Ocean “Acidification”

6.3.1 Introduction

As the air’s CO₂ content rises in response to increasing anthropogenic CO₂ emissions, more CO₂ dissolves in the surface waters of the world’s oceans. Theoretical reasoning, some of it reviewed in Section 6.3.1.2 below, suggests the pH values—a negative or inverse measure of the acidity of water—of the planet’s oceanic waters should be gradually decreasing.

By some estimates, the globe’s seawater has declined by about 0.1 pH unit relative to what it was in preindustrial times, and model calculations imply there could be an additional drop somewhere in the neighborhood of 0.3 to 0.7 pH by the year 2300. IPCC and others refer to this small potential change in oceanic pH and its presumed impacts on aquatic life as “ocean acidification.” That term, however, is misleading and deceptive. The world’s oceans are currently basic (or alkaline), with an average pH of around 8.1, and there is no chance future anthropogenic CO₂ emissions will ever cause the oceans to become acidic (pH less than 7). The general public, not scientifically trained, naturally interprets the phrase literally and assumes rising atmospheric CO₂ is turning the world’s oceans, lakes, and streams into a dangerous acid that is harming (or will harm) marine life.

IPCC characterizes the projected pH reduction as a cause for great concern, because it has been postulated to harm calcifying marine life such as corals, not only by reducing the calcifying rates of marine organisms but also by impeding the responses of other growth and developmental parameters of these organisms. The ocean chemistry aspect of this ocean acidification hypothesis is rather straightforward, but it is not as solid as model projections make it out to be. Some researchers, including Pieter

Tans, senior scientist at the National Oceanic and Atmospheric Administration (NOAA) Earth System Research Laboratory in Boulder, Colorado (USA), have published papers suggesting the drop in oceanic pH will not be nearly as great as IPCC and others predict. Figures 6.3.1.1 and 6.3.1.2 illustrate Tans’ analysis.

The first of the two figures depicts much of the past and projected history of fossil-fuel carbon utilization, together with historical and projected atmospheric CO₂ concentrations to the year 2500, as calculated by Tans (2009). As the figure shows, the air’s CO₂ concentration is expected to peak well before 2100 and at only 500 ppm, as compared to the 800 ppm predicted in one of IPCC’s scenarios. It is

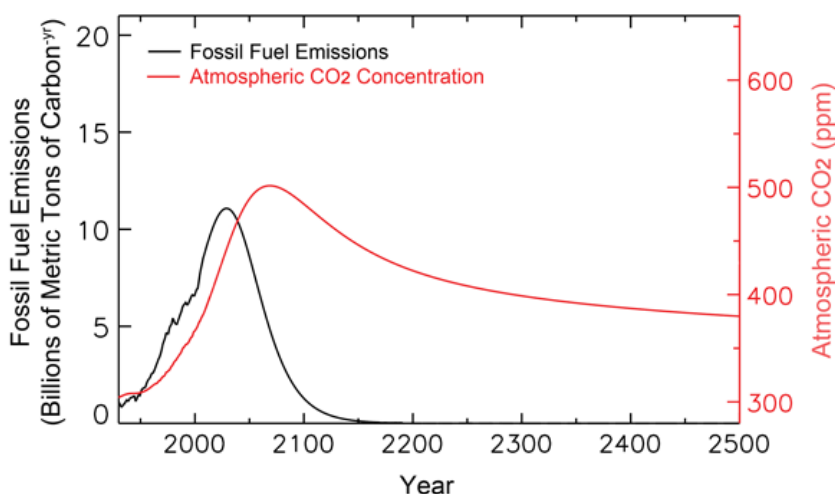


Figure 6.3.1.1. Past and projected trends of fossil-fuel carbon utilization and the atmosphere’s CO₂ concentration. Adapted from Tans (2009).

also worth noting that by the year 2500, the air’s CO₂ concentration should actually drop back to about what it is today.

When these emission estimates are calculated for their expected reductions of oceanic pH, as shown in Figure 6.3.1.2, the projected pH change at 2100 is far below what IPCC estimates. The pH projections from Tans’ data also suggest a recovery to values near those of today by the year 2500, a striking contradiction of IPCC’s estimates. (Tans’ research is described in more detail in the next section.)

The increase of CO₂ in the air should lead to additional weathering of terrestrial carbonates and dissolution of marine carbonates, which would increase delivery of Ca²⁺ and CO₃²⁻ to the oceans and largely compensate for the CO₂-induced decrease in

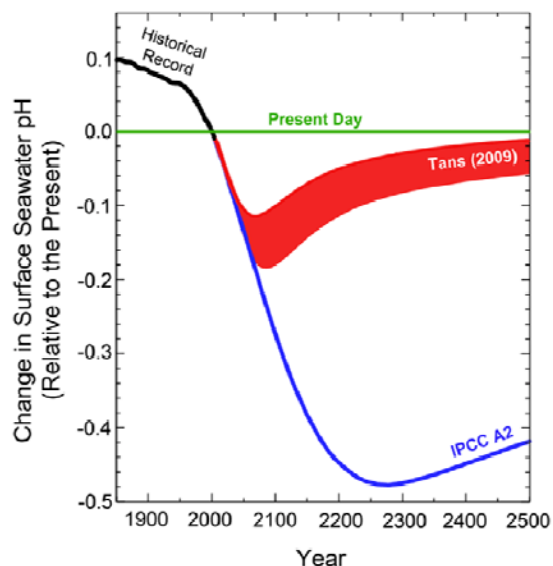


Figure 6.3.1.2. Past and projected trends of oceanic pH based on fossil-fuel carbon utilization estimates from Tans (2009) and IPCC's A2 scenario.

oceanic calcium carbonate saturation, further suggesting IPCC's projections of ocean acidification may be exaggerated. In addition, as with all phenomena involving living organisms, the introduction of life into the ocean acidification picture greatly complicates things, as several interrelated biological phenomena must be considered; when they are, it becomes much more difficult to draw such sweeping negative conclusions as IPCC does.

As the research reviewed in the subsections below demonstrates, the rising CO₂ content of Earth's atmosphere may be a beneficial phenomenon with many positive consequences for the oceans as well as other aspects of the environment (Idso, 2009).

Before proceeding into those specifics, however, we provide a brief discussion of changes in oceanic pH, followed by some additional considerations of ocean chemistry.

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6.3.1.1 Assessing and Projecting Changes in Oceanic pH

Based on four theoretical constructs—a geochemical model, an ocean general-circulation model, an IPCC CO₂ emissions scenario for the twenty-first century, and a projected logistic function for the burning of Earth's post-twenty-first century fossil-fuel reserves—Caldeira and Wickett (2003) calculated the atmospheric CO₂ concentration could approach 2,000 ppm around the year 2300, leading to a surface seawater pH reduction of 0.7 unit, a change they describe as being much more rapid and considerably greater “than any experienced in the past 300 million years.” This long time interval makes the phenomenon sound truly catastrophic, especially as IPCC claims this “ocean acidification” phenomenon will impede the process of calcification in corals and other marine life. In judging the plausibility of this scenario, it is important first to know whether the acidification phenomenon is really severe and unprecedented.

In a special issue of *Oceanography* published in December 2009, Feely *et al.* (2009) review what is known about the current pH status of the world's oceans and what can likely be expected by the end of the current century. The three researchers write, “estimates based on the Intergovernmental Panel on Climate Change business-as-usual emission scenarios suggest that atmospheric CO₂ levels could approach 800 ppm near the end of the century,” and “corresponding biogeochemical models for the ocean indicate that surface water pH will drop from a pre-industrial value of about 8.2 to about 7.8 in IPCC A2 scenario by the end of this century.” They warn, as a result, “the skeletal growth rates of calcium-secreting organisms will be reduced” and conclude, “if anthropogenic CO₂ emissions are not dramatically reduced in the coming decades, there is the potential for direct and profound impacts on our living marine ecosystems.”

In the same issue of *Oceanography*, Tans (2009) presents a much different take on the subject. He begins by noting the anthropogenic component of the air's CO₂ concentration “depends primarily on the total amount emitted, not on the rate of emissions,”

and “unfortunately, IPCC reports have not helped public understanding of this fact by choosing, somewhat arbitrarily, a rather short time horizon (100 years is most commonly used) for climate forcing by CO₂.”

“Instead of adopting the common economic point of view, which, through its emphasis on perpetual growth, implicitly assumes infinite Earth resources,” Tans notes the cumulative extraction of fossil-fuel carbon currently stands at about 345 gigatons of carbon (GtC), and there appears to be another 640 or so GtC of proven reserves, yielding a total original reserve of about 1,000 GtC, from which he proceeds with his analysis.

The past and projected history of fossil-fuel carbon utilization, together with historical and projected atmospheric CO₂ concentrations out to the year 2500, as calculated by Tans, is presented in Figure 6.3.1.1 above. According to the data presented there, Tans shows the air’s CO₂ concentration peaking well before 2100 at only 500 ppm, as compared to the 800 ppm Feely *et al.* take from IPCC. By the year 2500, the air’s CO₂ concentration drops back to about what it is today, according to Tans’ analysis.

Based on his more modest projections of future atmospheric CO₂ concentrations, Tans finds the projected pH reduction of ocean waters in the year 2100 to be only one-half of the 0.4 value calculated by Feely *et al.*, with a recovery to a reduction of slightly more than 0.1 pH unit by 2500, which is less than the range of pH values typical of today’s oceans (8.231 in the Arctic Ocean minus 8.068 in the North Indian Ocean equals 0.163, according to Feely *et al.*). Graphical data presented by Pelejero *et al.* (2010) depict interannual pH variations in the North Atlantic Ocean near Bermuda ranging from a high of approximately 8.18 to a low of about 8.03 at various times over the years 1984 to 2007 (Bates, 2007), further demonstrating large pH variations are occurring in some ocean basins as a result of seasonal seawater variability.

Even greater natural pH variability is evident on both shorter and longer time scales in still other of Pelejero *et al.*’s graphs. Over a mere two days in July 2001 on a Molokai (Hawaii) Reef flat, for example, seawater pH ranged from a high of 8.29 to a low of 7.79 (Yates and Halley, 2006). Over a period of about a decade in the mid-twentieth century, the pH at Arlington Reef in Australia’s Great Barrier Reef system ranged from a high of approximately 8.25 to a low of about 7.71 (Wei *et al.*, 2009). These natural and recurring pH declines (0.50 and 0.54) are greater than the 0.3 to 0.4 decline IPCC expects to occur between now and the end of the century, and much

greater than Tans’ estimate of about 0.2.

Hofmann *et al.* (2011) state “natural variability in pH is seldom considered when effects of ocean acidification are considered,” and they suggest this omission is disturbing because “natural variability may occur at rates much higher than the rate at which carbon dioxide is decreasing ocean pH,” which is about 0.0017 pH unit per year, according to Dore *et al.* (2009) and Byrne *et al.* (2010). They contend “ambient fluctuation in pH may have a large impact on the development of resilience in marine populations,” noting “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.”

Hofmann *et al.* recorded continuous high-resolution time series of upper-ocean patterns of pH variability with autonomous sensors deployed at 15 locations from 40.7303°N to 77.8000°S latitude and from 0 to 166.6712°E longitude and 0 to 162.1218°W longitude, over a variety of ecosystems ranging from polar to tropical, open ocean to coastal, and kelp forest to coral reef. The 18 researchers report their measurements revealed “a continuum of month-long pH variability with standard deviations from 0.004 to 0.277 and ranges spanning 0.024 to 1.430 pH units.” This variability was “highly site-dependent, with characteristic diel, semi-diurnal, and stochastic patterns of varying amplitudes.”

Hofmann *et al.* write, “these biome-specific pH signatures disclose current levels of exposure to both high and low dissolved CO₂, often demonstrating that resident organisms are already experiencing pH regimes that are not predicted until 2100.” These facts suggest the current real-world heterogeneity of the world’s oceans with regard to pH and pCO₂ exposure may already have “result[ed] in populations that are acclimatized to variable pH or extremes in pH,” such as those that have been predicted to be the new norm in 2100. Lower ocean pH levels may therefore not mature in the way projected by IPCC, a conclusion Loaiciga (2006) shares, having written years earlier, “on a global scale and over the time scales considered (hundreds of years), there would not be accentuated changes in either seawater salinity or acidity from the rising concentration of atmospheric CO₂.”

Marine photosynthesis may also reduce CO₂-induced lowering of ocean pH levels lower ocean pH levels, as it tends to increase surface seawater pH, countering the tendency for pH to decline as the air’s CO₂ content rises, as demonstrated by Lindholm and Nummelin (1999). This phenomenon has been found to dramatically increase the pH of marine bays,

lagoons, and tidal pools (Gnaiger *et al.*, 1978; Santhanam, 1994; Macedo *et al.*, 2001; Hansen, 2002) and significantly enhance the surface water pH of areas as large as the North Sea (Brussaard *et al.*, 1996).

Middelboe and Hansen (2007) studied a wave-exposed boulder reef in Aalsgaarde on the northern coast of Zealand, Denmark, plus a sheltered shallow-water area in Kildebakkerne in the Roskilde Fjord, Denmark. As one would expect if photosynthesis tends to increase surface-water pH, the two researchers found “daytime pH was significantly higher in spring, summer and autumn than in winter at both study sites,” often reaching values of 9 or more during peak summer growth periods vs. 8 or less in winter. They also found “diurnal measurements at the most exposed site showed significantly higher pH during the day than during the night,” sometimes reaching values greater than 9 during daylight hours but typically dipping below 8 at night, and “diurnal variations were largest in the shallow water and decreased with increasing water depth.”

In addition to their own findings, Middelboe and Hansen cite Pearson *et al.* (1998), who found pH averaged about 9 during the summer in populations of *Fucus vesiculosus* in the Baltic Sea; Menendez *et al.* (2001), who found maximum pH was 9 to 9.5 in dense floating macroalgae in a brackish coastal lagoon in the Ebro River Delta; and Bjork *et al.* (2004), who found pH values as high as 9.8 to 10.1 in isolated rock pools in Sweden. Noting “pH in the sea is usually considered to be stable at around 8 to 8.2,” the two Danish researchers conclude “pH is higher in natural shallow-water habitats than previously thought.”

Liu *et al.* (2009) note, “the history of ocean pH variation during the current interglacial (Holocene) remains largely unknown,” and it “would provide critical insights on the possible impact of acidification on marine ecosystems.” Working with 18 samples of fossil and modern *Porites* corals recovered from the South China Sea, the nine researchers employed ^{14}C dating using the liquid scintillation counting method, along with positive thermal ionization mass spectrometry to generate high-precision $\delta^{11}\text{B}$ (boron) data, from which they reconstructed the paleo-pH record of the past 7,000 years, as depicted in Figure 6.3.1.1.2.

As the figure illustrates, there is nothing unusual, unnatural, or unprecedented about the two most recent pH values. They are not the lowest of the record, nor is the rate of decline that led to them the greatest of the record. This strongly indicates these recent values have little to do with the nearly 40%

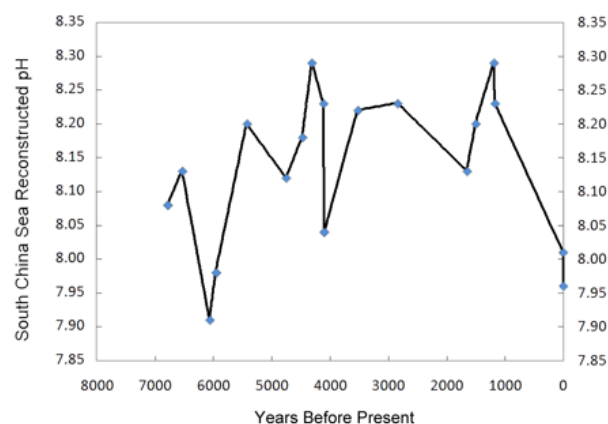


Figure 6.3.1.1.2. Reconstructed pH history of the South China Sea. Created from Table 1 of Liu *et al.* (2009).

increase in the air’s CO_2 concentration that occurred over the course of the Industrial Revolution. As for the prior portion of the record, Liu *et al.* note there is also “no correlation between the atmospheric CO_2 concentration record from Antarctica ice cores and $\delta^{11}\text{B}$ -reconstructed paleo-pH over the mid-late Holocene up to the Industrial Revolution.”

Further insight comes from the earlier work of Pelejero *et al.* (2005), who developed a more refined history of seawater pH spanning the period 1708–1988 (depicted in Figure 6.3.1.1.3), based on $\delta^{11}\text{B}$ data obtained from a massive *Porites* coral from Flinders Reef in the western Coral Sea of the southwestern Pacific. These researchers also found “no notable trend toward lower $\delta^{11}\text{B}$ values.” They discovered “the dominant feature of the coral $\delta^{11}\text{B}$ record is a clear interdecadal oscillation of pH, with $\delta^{11}\text{B}$ values ranging between 23 and 25 per mil (7.9 and 8.2 pH units),” which they say “is synchronous with the Interdecadal Pacific Oscillation.”

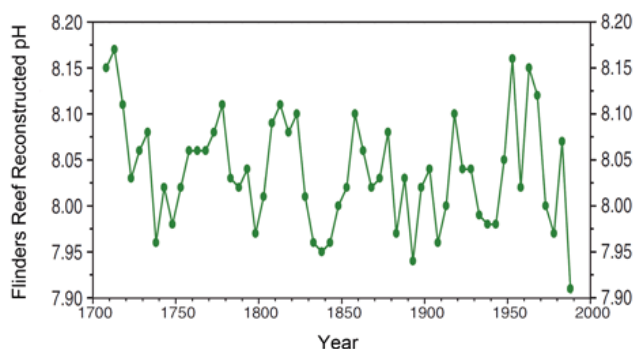


Figure 6.3.1.1.3. Reconstructed pH history of Flinders Reef of the Western Coral Sea of the Southwestern Pacific. Adapted from Pelejero *et al.* (2005).

Pelejero *et al.* also compared their results with coral extension and calcification rates obtained by Lough and Barnes (1997) over the same 1708–1988 time period. As best as can be determined from their graphical representations of these two coral growth parameters, extension rates over the last 50 years of this period were about 12% greater than they were over the first 50 years, and calcification rates were approximately 13% greater over the last 50 years.

Wei *et al.* (2009) derived the pH history of Arlington Reef (off the north-east coast of Australia). Their data show a 10-year pH minimum centered at about 1935 (which obviously was not CO₂-induced) and a shorter, more variable minimum at the end of the record (which also was not CO₂-induced). Apart from these two non-CO₂-related exceptions, the majority of the data once again fall within a band that exhibits no long-term trend.

Numerous scientific studies have demonstrated atmospheric CO₂ enrichment stimulates pH-boosting photosynthesis in marine micro- and macro-algae (see Sections 6.3.2 and 6.5.1). This phenomenon suggests anything else that enhances marine photosynthesis—such as nutrient delivery to the waters of the world’s coastal zones (i.e., eutrophication)—may do so as well, as Borges and Gypens (2010) have found.

Employing an idealized biogeochemical model of a river system (Billen *et al.*, 2001) and a complex biogeochemical model describing carbon and nutrient cycles in the marine domain (Gypens *et al.*, 2004), the two researchers investigated “the decadal changes of seawater carbonate chemistry variables related to the increase of atmospheric CO₂ and of nutrient delivery in the highly eutrophied Belgian coastal zone over the period 1951–1998.” They write, “the increase of primary production due to eutrophication could counter the effects of ocean acidification on surface water carbonate chemistry in coastal environments,” and “changes in river nutrient delivery due to management regulation policies can lead to stronger changes in carbonate chemistry than ocean acidification,” as well as changes “faster than those related solely to ocean acidification.” They add, “the response of carbonate chemistry to changes of nutrient delivery to the coastal zone is stronger than ocean acidification.”

Given its failure to account for the full spectrum of important phenomena that affect ocean acidification, IPCC’s current assessment of potential impacts on aquatic life should be considered far more uncertain and much less extreme than IPCC claims it to be.

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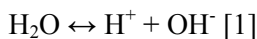
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6.3.1.2 Some Thoughts on Ocean Chemistry

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The “acidification” of the ocean—or rather its potential progression toward less alkaline conditions—is postulated to result in serious consequences to marine life, including the dissolution of lime shells of various marine organisms. However, the foundation of the ocean acidification scare is disputed and challenged in the scientific literature as indicated in the multiple peer-reviewed studies referenced throughout Sections 6.3–6.5. The present section approaches and critiques the hypothesis from a geochemical perspective.

Water (H₂O) in the ocean is about one pH unit alkaline. Water protolyses as:



The ordinary hydrogen atom (H) has one proton and one electron. When the hydrogen’s electron is lost to the hydroxyl (OH⁻), the remaining H⁺ is just a proton. This dissociation of water is called protolysis: the formation of a proton from water.

The concentration of such protons in water determines its acidity or alkalinity. A high concentration is typical of acids, while a dominance of hydroxyl is typical of alkalies. Water is considered neutral (neither alkaline or acidic) when concentrations of H⁺ and OH⁻ are equal. In thermodynamics the concentration is commonly expressed as activity—a thermodynamic concentration, denoted “a”.

pH (“power of hydrogen”) is a measure of the acidity of water, defined as the negative logarithm to the activity of H⁺ (a_{H+}):

$\text{pH} \equiv -\log a_{\text{H}^+}$ [2]

The protolysis constant for the chemical reaction for water protolysis, equation [1], has a value of $\sim 10^{-14}$ at 25°C. At this temperature, the pH has a range up to 14 units, with a value of 14 representing the most alkaline waters, a value of 7 indicating neutral water, and values below 7 for acidic waters. The protolysis constant varies with temperature (and somewhat by pressure), so the value for neutral water changes with changing temperatures. Dissolved gases and solids also can change the pH of water.

6.3.1.2.1 The Assertion of Ocean Acidification

Oceanic pH varies naturally with latitude and ocean depth across Earth. Hence, no single value exists to define oceanic pH. For instance, the pH of surface waters in the western Pacific Ocean varies from around 7.8 to 8.5 between 60°N and 60°S. Although significant pH variations can occur both above and below this range, ocean water is generally characterized as alkaline. And because pH units of measure fall on a logarithmic scale (each pH unit change requires an order of magnitude change in the activity of H^+), large additions of gases and/or dissolved solids into water are needed to induce significant changes in pH.

Some researchers assert ocean waters have become less alkaline (by about 0.1 pH unit) since preindustrial times (e.g., Caldeira and Wickett, 2003). Ocean waters are projected to experience a further pH decline of 0.1–0.2 unit during the next decennia, and a reduction of 0.5–0.7 by the year 2100, caused by anthropogenic CO_2 (NIVA, 2008).

In its first assessment report, published in 1990, IPCC claimed anthropogenic CO_2 has a long lifetime in the atmosphere, of between 50 and 200 years. This long lifetime, according to IPCC, accounts for the modern rise in atmospheric CO_2 , which they assert is caused by anthropogenic CO_2 emissions accumulating in the air year after year. Solomon *et al.* (2009) suggest an even longer residence time for anthropogenic CO_2 in the atmosphere, estimating it may be more than 1,000 years, where the CO_2 content flattens out asymptotically towards infinity in their model. Other researchers have provided contrasting findings. Many scientific papers, for example, contend the atmospheric CO_2 lifetime (half-life) is much shorter, at around five years (Bolin and Eriksson, 1959), that a similar lifetime is found for oceanic CO_2 , and that natural processes play a far more significant role

influencing the atmospheric content of CO_2 than previously thought (e.g., Segalstad, 1992; 1996; 1998; 2008; 2009; Starr, 1993; Rohde, 2000).

It is important to note the dissolution of CO_2 in water is governed by Henry's Law, evidenced by the fact there is approximately 50 times more CO_2 dissolved in the ocean than in the atmosphere at present. It is this vast mass of dissolved CO_2 in the ocean that holds the regulating power—not the relatively small amount of CO_2 contained in the air. Furthermore, the chemical reaction speeds involved in the dissolution of CO_2 are high, as is the ocean circulation speed in the upper parts of the ocean.

The ocean acidification hypothesis also ignores the presence of vast amounts of dissolved calcium in the ocean: the upper 200 m of ocean water contains enough dissolved calcium to bind all anthropogenic CO_2 as precipitated calcium carbonate (in the ocean) without affecting the ocean's pH (Jaworowski *et al.*, 1992a; Segalstad, 1996; 1998). The ocean acidification hypothesis also ignores or downplays other oceanic buffers (pH stabilizing reactions), the thermodynamic stability of solid calcium carbonate in ocean water, and photosynthesis by marine biological systems. Many assertions of ocean acidification are based on a methodology that has been called into serious question. For example, the Norwegian Institute for Water Research (NIVA, 2008) built its assertions of ocean acidification on a paper by Haugan and Drange (1996), who derived their claims from the work of Spivack *et al.* (1993). This latter group of authors presented a proxy history of the ocean's pH over the past 21 million years that used boron isotopes in foraminifera from only five dated boron isotope analyses. This methodology was challenged by Lemarchand *et al.* (2000), who found the boron isotopes in foraminifera represent changes in the marine boron isotope budget rather than changes in the ocean's pH. Claims that the oceans are presently “acidifying,” if based on boron isotope measurements, are highly questionable, if not altogether invalid.

6.3.1.2.2 The Geochemistry of CO_2

Depending on physical conditions, CO_2 can both rapidly dissolve and de-gas in water. This is succinctly demonstrated in the making of carbonated sodas canned by breweries and the degassing of the dissolved CO_2 to the air with time upon opening the soda container.

The dissolved CO_2 first hydrolyzes with the water

into carbonic acid, H_2CO_3 . Next, the carbonic acid protolyzes in two steps, first producing H^+ and dissolved bicarbonate HCO_3^- , and next producing H^+ and dissolved carbonate CO_3^{2-} . With the presence of vast amounts of dissolved calcium Ca^{2+} in the ocean, calcium combines with dissolved carbonate or bicarbonate (the dominating dissolved carbon species in the ocean) to form solid calcium carbonate. In simple terms, this process explains how and why some marine organisms form solid calcium carbonate shells. And it further explains how and why the chemical sedimentation of precipitated calcium carbonate can occur to make limestone (or dolomite) on the ocean floor.

Budyko *et al.* (1987) has pointed out periods of maximum carbonate precipitation (as limestone and dolomite) tend to occur at times of intense volcanism (releasing vast amounts of CO_2 from Earth's interior). These periods also tend to correspond with periods of higher atmospheric CO_2 , highlighting a geochemical path of CO_2 that initiates from Earth's interior, degasses from volcanoes to the atmosphere, dissolves into the oceans, and precipitates solid marine carbonate rocks on the ocean floor. The chemical reactions for these processes are illustrated below, where (g) = gas, (aq) = aqueous (dissolved in water), and (s) = solid. The protolysis of the water must be added to the system because the ocean water is alkaline, dominated by hydroxyl OH^- . By adding all the partial reactions in this system, the total net reaction for the marine precipitation of solid calcium carbonate from the air's CO_2 and dissolved calcium in ocean water can be obtained:

$\text{CO}_2 (\text{g}) \leftrightarrow \text{CO}_2 (\text{aq})$	dissolution [3]
$\text{CO}_2 (\text{aq}) + \text{H}_2\text{O} \leftrightarrow \text{H}_2\text{CO}_3 (\text{aq})$	hydrolysis [4]
$\text{H}_2\text{CO}_3 (\text{aq}) \leftrightarrow \text{H}^+ + \text{HCO}_3^- (\text{aq})$	1st protolysis [5]
$\text{HCO}_3^- (\text{aq}) \leftrightarrow \text{H}^+ + \text{CO}_3^{2-} (\text{aq})$	2nd protolysis [6]
$\text{Ca}^{2+} (\text{aq}) + \text{CO}_3^{2-} (\text{aq}) \leftrightarrow \text{CaCO}_3 (\text{s})$	precipitation [7]
$2 \text{H}^+ + 2 \text{OH}^- \leftrightarrow 2 \text{H}_2\text{O}$	protolysis [1]
$\text{CO}_2 (\text{g}) + \text{Ca}^{2+} (\text{aq}) + 2 \text{OH}^- \leftrightarrow \text{CaCO}_3 (\text{s}) + \text{H}_2\text{O}$	total net reaction [8]

The Law of Mass Action ensures when all these chemical reactions have been accounted for in the total net reaction (and when increasing the amount of a gas, CO_2 , in the air), calcium carbonate (solid) will be stabilized in the ocean, because the chemical reaction will be forced in the direction from left to right. This result is the opposite of what is commonly asserted (that solid calcium carbonate would be dissolved by the increasing amount of CO_2 in the air).

A simple example of this equation is seen in the

oft-demonstrated school chemistry experiment of blowing one's exhaled breath (CO_2 gas) through a straw into a reaction tube with dissolved calcium hydroxide $\text{Ca}(\text{OH})_2$ in water. Solid calcium carbonate precipitates out into the solution within seconds, providing a good visual of what happens in the ocean when gaseous CO_2 dissolves in the ocean, where there is an ample supply of dissolved calcium and hydroxyl.

6.3.1.2.3 pH Stabilizing Reactions in the Ocean

A "buffer" can be defined as a reaction system that modifies or controls the magnitude of an intensive (mass independent) thermodynamic variable, such as pressure, temperature, concentration, pH (acidity), etc. The ocean's carbonate system acts as a pH buffer through the presence of a weak acid (H_2CO_3 and its protolysis products) and a salt of the acid (CaCO_3). The pH of the water can be calculated as:

$$\text{pH} \approx [\log K + a(\text{CO}_2, \text{g}) + a(\text{Ca}^{2+}, \text{aq})] / -2 \quad [9]$$

where K is the chemical equilibrium constant, and a the activity (thermodynamic concentration). At the ocean surface the $a(\text{Ca}^{2+}, \text{aq})$ is much larger than the $a(\text{CO}_2, \text{g})$. Therefore the alkalinity is the determining factor for the pH, and not the activity (or the fugacity or the partial pressure) of atmospheric CO_2 (Charlson and Emerson, 2000).

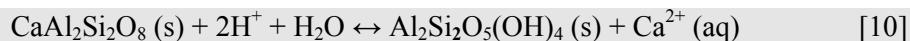
In his book on geochemical thermodynamic calculations, Bethke (1996) shows that in a system with only water and CO_2 , without mineral buffers present, more than a doubling of the amount of CO_2 in the air above the water surface will lead to a pH decrease of less than 0.4 pH unit. He further demonstrates this is within the natural variation, and thus nothing to worry about.

The ocean is not chemically uniform. Colder water will have a naturally lower pH, because the protolysis constant for water changes with temperature. An upwelling ocean current with colder water, or movement of water from higher latitudes, may lead to a somewhat lower pH within the natural variation—without an anthropogenic influence.

It is also important to note when solid calcium carbonate is brought into the system, a change in the amount of CO_2 gas alone cannot change the pH,

because of the buffer action of the calcium carbonate. Thermodynamic calculations on an ocean water composition in equilibrium with calcium carbonate at 25°C show the pH would have to be lowered by 2 units in order to dissolve the calcium carbonate at this temperature. This means the H^+ concentration would have to be increased by 2

acting in the ocean. The ocean has a set of other mineral-buffer-reactions, such as the buffer:



This anorthite feldspar $\leftrightarrow$ kaolinite buffer has a buffering capacity 1,000 times larger than the ocean's carbonate buffer (Stumm and Morgan, 1970). There are also clay mineral buffers, plus a calcium silicate $\leftrightarrow$ calcium carbonate CO_2 buffer (MacIntyre, 1970; Krauskopf, 1979) [for simplicity]:

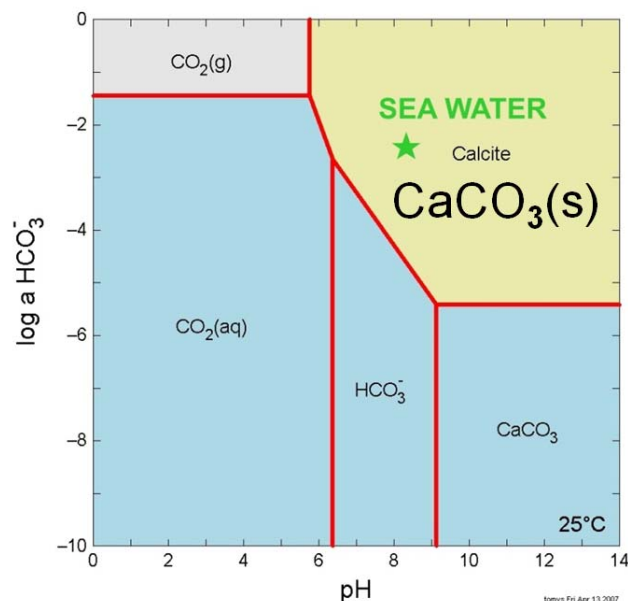


Figure 6.3.1.2.1. A phase diagram for the system CO_2 — H_2O — $CaCO_3$ at 25°C and water composition of average sea water. The blue stability fields show the stability of different aqueous species for given pH and log activity of bicarbonate. The green star indicates the sea water position, within the $CaCO_3$ stability field. The diagram was constructed using the program package “The Geochemist’s Workbench,” by Craig Bethke.

logarithm units, i.e. 100 times (see Figure 6.3.1.2.1).

When adding more CO_2 (g), more bicarbonate will be produced. Yet as the phase diagram illustrates (Figure 6.3.1.2.1), such a CO_2 addition will only stabilize $CaCO_3$ even more—the star in the figure (denoting the sea water composition) would move upward. Furthermore, the star would have to be moved out of the $CaCO_3$ (s) stability field in order for calcium carbonate (calcite) to be dissolved. This is impossible to do by adding CO_2 (g) when calcium carbonate is present (Segalstad, 2008). Hence, the pH of ocean water appears to be well buffered with respect to adding more CO_2 to the atmosphere. At 0°C the pH would have to be lowered 1.5 pH units for solid calcium carbonate (calcite) to be dissolved.

The carbonate buffer is not the only pH buffer

All these buffers act as a “security net” under the CO_2 (g) $\leftrightarrow$ $CaCO_3$ (s) buffer. Together they constitute an almost infinite buffer capacity (Stumm and Morgan, 1970; Segalstad and Jaworowski, 1991).

The last two buffers mentioned are slower than the CO_2 (g) $\leftrightarrow$ $CaCO_3$ (s) buffer at low temperatures. But their reactions are fast at the hot mid-ocean ridges, where temperatures can reach several hundred degrees C. There is no shortage of dissolved calcium in the ocean water, because this element is constantly being added from weathered surface rocks to the ocean by rivers, and by water-rock interactions at hot mid-ocean ridges.

Rainwater has a pH of about 5.7 (Krauskopf, 1979), because of the acidity caused by dissolution and protolysis of atmospheric CO_2 . All the acidic rain supplied to the ocean water through the millennia have not changed the ocean’s pH of near 8, which also supports the notion of strong pH buffering in ocean water (Pytkowicz, 1972).

6.3.1.2.4 Carbon Isotopes and Mass Balance Calculations

Stable $^{13}C/^{12}C$ isotope ratios, expressed as $\delta^{13}C$ vs. PDB, provide the only way to determine unequivocally the fraction of anthropogenic CO_2 in the atmosphere. The natural atmospheric CO_2 reservoir has $\delta^{13}C \approx -7\%$ when in isotopic equilibrium with marine HCO_3^- (aq) and $CaCO_3$ (s). CO_2 gas from burning of fossil-fuel and biogenic materials has $\delta^{13}C \approx -26\%$ (Ohmoto and Rye, 1979; Deines, 1980).

IPCC identifies 280 ppmv (ppm by volume) as the preindustrial CO_2 value, but that may be arbitrarily influenced by the selection of low-value

CO₂ data from ice cores (where measured values up to 7,400 ppmv were omitted), as well as from the mismatching of contemporary measurements with different ages (Jaworowski *et al.*, 1992a; 1992b). IPCC claims the rise in CO₂ to 353 ppmv in 1990, and 379 ppmv in 2005, is due only to anthropogenic CO₂ (IPCC, 1990; 2007).

The $\delta^{13}\text{C}$ value reported for atmospheric CO₂ was -7.489‰ in December 1978, decreasing 10 years later to -7.807‰ in December 1988 (Keeling *et al.*, 1989). If the resultant decrease were solely the product of mixing natural CO₂ with CO₂ produced from the burning of fossil fuels or plants (~79% / ~21% CO₂ mix; lifetime 50–200 years; IPCC, 1990), the current atmospheric CO₂ $\delta^{13}\text{C}$ value should be -11, much lower than reported (Segalstad, 1992; 2008).

The December 1988 atmospheric CO₂ composition has been computed for its 748 Gt C (Gt = 10¹⁵ g) total mass and $\delta^{13}\text{C}$ value of -7.807‰ for three components: (1) natural fraction remaining from the preindustrial atmosphere, (2) cumulative fraction remaining from all annual fossil-fuel CO₂ emissions, and (3) carbon isotope mass-balanced natural fraction. The masses of component (1) and (2) were computed for different atmospheric lifetimes of CO₂ (Segalstad, 1992).

The result fits a lifetime of about five years, in agreement with ¹⁴C studies (see Sundquist, 1985; Segalstad, 1998; 2009; for further references). The mass of all past fossil-fuel and biogenic emissions remaining in the current atmosphere was -30 Gt C or less; i.e. a maximum of around 4% of the total, corresponding to an atmospheric concentration of approximately 14 ppmv. The implication of the five-year lifetime is that approximately 135 Gt C (18%) of the atmospheric CO₂ is dynamically exchanged each year (Segalstad, 1992; 1996; 1998; 2008).

The above calculations also demonstrate that over this 10-year period (1978–1988), at least 96% of the atmospheric CO₂ is attributed to non-fossil-fuel sources, and this percentage has not likely varied much in the years since. Hence, it is clear marine degassing and juvenile degassing from sources such as volcanoes must be much more important for the atmospheric CO₂ budget than the burning of fossil-fuels and biogenic materials. IPCC has failed to recognize this conclusion.

6.3.1.2.5 Can Anthropogenic Carbon Double the Atmospheric CO₂ Content?

Many models suggest there is enough fossil carbon on

Earth that, if burned, would raise the atmospheric CO₂ concentration to two or more times its preindustrial value. There are reasons to conclude such an increase may never occur.

The equilibrium partition coefficient for the CO₂ distribution between the atmosphere and ocean is approximately 1:50 (Revelle and Suess, 1957; Skirrow, 1975), given by Henry's Law and the Henry's Law Constant. This partition coefficient can be used to set an upper limit for how much the CO₂ concentration will rise in the atmosphere if all available fossil carbon fuel (coal, petroleum, gas) were burned.

To permanently double the current level of CO₂ in the atmosphere under chemical equilibrium conditions, the atmosphere would have to be supplied with approximately 51 times the present amount of CO₂ if equilibrium should be attained, in order to keep the partition coefficient (air:sea = 1:50) constant according to Henry's Law. At the double amount of CO₂ in the air, the new ratio would have to be 2:100. In other words, an increase of one unit CO₂ in air leads to an increase of 50 units CO₂ in the sea; thus a total of 51 units has to be supplied. All available fossil fuel carbon amounts to 11 times the amount of carbon in today's atmospheric CO₂ (Jaworowski *et al.*, 1992a). Therefore, mankind does not have enough fossil fuel to double the current level of atmospheric CO₂ under equilibrium conditions, all other factors held constant.

If the total fossil fuel reservoir of 7,200 Gt C were burned during the next 300 years, only the dissolved organics (carbon pool of about 1,000 Gt C) would consume all manmade CO₂ by their photosynthesis, because this period covers 6 to 15 turnovers of the upper-ocean pool of dissolved organic carbon, based on radiocarbon (¹⁴C) studies. However, the vast oceanic dissolved inorganic carbon reservoir of 38,000 Gt C indicates the sea is a much more powerful sink for atmospheric CO₂. Hence, it is unlikely a permanent doubling of the amount of atmospheric CO₂ is attainable by human activities. See Jaworowski *et al.* (1992a) for further details and references.

6.3.1.2.6 Conclusion

Brian Mason (1966) wrote in his textbook, *Geochemistry* (3rd edition), "The ocean may thereby act as a self-balancing mechanism in which most of the elements have reached an equilibrium concentration."

That statement remains valid, as seen through a considerable constancy of sedimentation and pH over many past hundreds of millions of years. The circulation of CO₂ among the atmosphere, ocean, and biosphere is a fast exchange, with an average measured lifetime (half-life) for one atmospheric CO₂ molecule of about five years (Bolin and Eriksson, 1959; Segalstad, 1992; 1996; 1998; 2008; 2009; Starr, 1993; Rohde, 2000).

According to Mason, “it is apparent that the oceans, by controlling the amount of atmospheric CO₂, play a vital part in maintaining stable conditions suitable for organic life on the Earth.” As the material above demonstrates, physical chemistry and thermodynamics provide strong reasons for questioning the validity of the so-called ocean “acidification” hypothesis, especially when considering the vast buffering capacity of the ocean’s many buffering mechanisms.

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6.3.2 Effects on Marine Plants

6.3.2.1 Phytoplankton

6.3.2.1.1 Coccolithophores

Coccolithophores are single-celled algae and protists found throughout the surface euphotic zones of the world’s oceans. They contain chlorophyll, conduct photosynthesis, and possess special plates or scales known as coccoliths, which they create through calcification. This section reviews the results of studies that address how they may be affected by a possible decline in ocean pH levels in a CO₂-enriched world of the future. Several of the findings challenge the alarming negative projections of IPCC, as noted in the bullet points below and further discussed in the main portion of the section.

- Shifts in dominance among species of coccolithophores or clones within a species have been found to occur as the air’s CO₂ content rises, which may enable the species to function much as they do today—if not better—in a high-CO₂ world of the future.
- Contemporary evolution likely will help to maintain the functionality of microbial processes at the base of marine food webs in the face of projected lower pH levels.
- Various coccolithophore species appear able to track the environmental value of ocean pH in real time.
- There is evidence the coccolithophore *Calcidiscus leptoporus* has adjusted successfully to the 80 ppm CO₂ difference between preindustrial and the present, as well as the 180 ppm CO₂ difference between glacial times and the present.

Riebesell (2004) notes a doubling of present-day atmospheric CO₂ concentrations “is predicted to cause

a 20–40% reduction in biogenic calcification of the predominant calcifying organisms, the corals, coccolithophorids, and foraminifera.” But he also notes “a moderate increase in CO₂ facilitates photosynthetic carbon fixation of some phytoplankton groups,” including “the coccolithophorids *Emiliania huxleyi* and *Gephyrocapsa oceanica*.” In what constitutes a major challenge to the model-based claim atmospheric CO₂ enrichment will harm such marine organisms, Riebesell suggests “CO₂-sensitive taxa, such as the calcifying coccolithophorids, should therefore benefit more from the present increase in atmospheric CO₂ compared to the non-calcifying diatoms.”

Leonardos and Geider (2005) grew a non-calcifying strain (PML 92A) of the marine coccolithophorid *Emiliania huxleyi* (Lohmann) Hay & Mohler in chemostats-cyclostats aerated with air of either 360 or 2,000 ppm CO₂ under both high- and low-light conditions in seawater either replete with or deficient in nitrogen and/or phosphorus, while measuring a suite of physical and biochemical properties of the coccolithophorid populations and the media in which they lived. They found “increased atmospheric CO₂ concentration enhances CO₂ fixation into organic matter,” but “only under certain conditions, namely high light [HL] and nutrient limitation.” Under N-limited conditions, for example, they found particulate organic carbon (POC) “was greatest under HL and elevated CO₂ (by up to 46% relative to HL and ambient CO₂).” Their work also revealed “the increase in POC was a consequence of both an increase in cell density and an increase in the cell organic carbon content.”

The two UK researchers state “enhanced CO₂ uptake by phytoplankton such as *E. huxleyi*, in response to elevated atmospheric CO₂, could increase carbon storage in the nitrogen-limited regions of the oceans and thus act as a negative feedback on rising atmospheric CO₂ levels.” According to their calculations, if the results obtained for *E. huxleyi* are indicative of the effects of CO₂ on primary production in other N-limited phytoplankton, changes of the magnitude they measured in *E. huxleyi* due to increased CO₂ could increase export production of the oligotrophic ocean by an amount equivalent to the estimated postindustrial increase in the terrestrial carbon sink.

Leonardos and Geider state their findings are “consistent with the response of primary productivity to manipulation of aqueous phase CO₂ in the oligotrophic North Atlantic (Hein and Sand-Jensen, 1996),” where increases in primary productivity “of

up to 100% were observed, although the average increase was 15% to 19%.” They note “stimulation of carbon fixation by elevated CO₂ had already been documented for nutrient-limited lake phytoplankton (Urabe *et al.*, 2003).”

Working with two previously untested coccolithophores—*Calcidiscus leptoporus* and *Coccolithus pelagicus*—which they describe as two of the most productive marine calcifying species, Langer *et al.* (2006) conducted batch-culture experiments in which they observed a deterioration of coccolith production above as well as below present-day CO₂ concentrations in *C. leptoporus*, and a lack of a CO₂ sensitivity of calcification in *C. pelagicus* over an atmospheric CO₂ concentration range of 98–915 ppm. Both observations, they write, “refute the notion of a linear relationship of calcification with the carbonate ion concentration and carbonate saturation state,” as various scientists proposed early on.

With respect to *C. leptoporus*, Langer *et al.* observed that at both higher and lower CO₂ concentrations than those of today, the proportion of coccoliths showing incomplete growth and malformation notably increased. To determine whether this takes place in the real world, the seven scientists studied coccolith morphologies in six sediment cores extracted along a range of latitudes in the Atlantic Ocean. They report changes in coccolith morphology similar to those “occurring in response to the abrupt CO₂ perturbations applied in our experimental treatments are not mirrored in the sedimentary record.” This finding indicates, as they suggest, “in the natural environment *C. leptoporus* has adjusted to the 80 ppm CO₂ and 180 ppm CO₂ difference between present, preindustrial and glacial times, respectively.”

The team of researchers from Germany and the United Kingdom write, “it is reasonable to assume that *C. leptoporus* has adapted its calcification mechanism to the change in carbonate chemistry having occurred since the last glacial maximum,” suggesting as a possible explanation for this phenomenon “the population is genetically diverse, containing strains with diverse physiological and genetic traits, as already demonstrated for *E. huxleyi* (Brand, 1981, 1982, 1984; Conte *et al.*, 1998; Medlin *et al.*, 1996; Paasche, 2002; Stolte *et al.*, 2000).” They also state this adaptive ability “is not likely to be confined to *C. leptoporus* but can be assumed to play a role in other coccolithophore species as well.” Langer *et al.* conclude such populations “may be able to evolve so that the optimal CO₂ level for calcification of the species tracks the environmental

value.” The authors conclude “genetic diversity, both between and within species, may allow calcifying organisms to prevail in a high CO₂ ocean.”

Working with the same sediment core, Halloran *et al.* (2008) analyzed the size distribution of CaCO₃ particles in the less-than-10-μm sediment fraction over the past quarter-century. They found a history of “changing particle volume since the late 20th century consistent with an increase in the mass of coccoliths produced by the larger coccolithophore species,” leading them to conclude “in the real ocean the larger coccolithophore species increase their calcification in response to anthropogenic CO₂ release.” The four researchers state this positive calcification response “could be attributed to an alleviation of CO₂ limitation in species that partly rely on the diffusive supply of dissolved carbon dioxide for photosynthesis, as demonstrated by a rise in photosynthetic efficiency with increasing carbon dioxide in cultures of *E. huxleyi* (Rost *et al.*, 2003).”

Stoll (2009) addressed the speculative claims of scientists promoting the view “ocean acidification in response to excess carbon dioxide in the atmosphere could become a problem for marine organisms, especially those that make skeletons or shells out of calcium carbonate,” including the coccolithophorids that are, by volume, the most important shell producers. She had a much more optimistic view of the subject, thanks in large part to the research findings of Langer *et al.* (2009).

The latter scientists—from France, Germany, Spain, and the Netherlands—grew four strains of the coccolithophore *Emiliania huxleyi* in dilute batch cultures of seawater with carbonate chemistries characteristic of those expected to prevail beneath an atmosphere with CO₂ concentrations ranging from approximately 200 to 1,200 ppm, while they measured particulate organic carbon content, particulate inorganic carbon content, and organic and inorganic carbon production. They found the four strains “did not show a uniform response to carbonate chemistry changes in any of the analyzed parameters and none of the four strains displayed a response pattern previously described for this species.” In light of these findings, other aspects of their earlier studies (Langer *et al.* 2006, 2007), and the diverse findings of others who had used different strains of the species, the five scientists conclude “the sensitivity of different strains of *E. huxleyi* to acidification differs substantially” and “likely has a genetic basis.”

Stoll agrees with that assessment. She notes the work of those who foresaw disastrous consequences typically “precludes the kind of natural selection and

adaptation that might occur over decades and centuries in the ocean.” Langer *et al.* (2009) state “shifts in dominance between species and/or between clones within a species might therefore be expected,” as the air’s CO₂ content continues to rise; but they note far too often “the possibility of adaptation is not taken into account.”

Stoll notes the great genetic diversity that exists in the real world, both among and within species, “is good insurance in a changing ocean.” It can be interpreted as evidence coccolithophorids are well prepared for whatever the future may bring, for as Langer *et al.* (2006) state, “genetic diversity, both between and within species, may allow calcifying organisms to prevail in a high CO₂ ocean.” That appears to be the consensus of most studies that have moved on from theoretical speculation to the intermediate crucible of laboratory experimentation and the final test of real-world observation.

Beaufort *et al.* (2011) note “culture experiments investigating the physiological response of coccolithophore calcification to increased CO₂ have yielded contradictory results between and even within species,” citing Riebesell *et al.* (2000), Langer *et al.* (2006), Iglesias-Rodriguez *et al.* (2008), and Langer *et al.* (2009). They investigated 180 surface-water and 555 sediment-core samples encompassing a wide spectrum of present and past oceanic conditions, some stretching back in time as much as 40,000 years.

The 13 researchers report, “significant overall correlations of coccolith mass with pH and pCO₂ were recorded, but with notable regional variations, indicating that these parameters are not solely responsible for the observed trend.” They also report some cultured strains of coccolithophores “are capable of maintaining calcification (degree and/or rate) over certain carbonate-chemistry ranges, a phenomenon that could contribute to localized within-sample deviations from the broad trend linking coccolith mass to carbonate chemistry.” The results indicated changes in the relative abundance of taxa were “predominantly responsible for the decrease in coccolith mass with ocean acidification that was seen in modern samples.”

Beaufort *et al.* also note, “in Patagonian-shelf and Chilean upwelling waters with low CO₃²⁻, in which the overall trend would predict low coccolith mass,” they detected “an unexpectedly highly calcified *Emiliania huxleyi* morphotype,” and “the relative abundance of this morphotype increased with decreasing pH along the Pacific transect towards Chile.” Noting “coccolith morphotype is thought to be subject to genetic regulation (Langer *et al.*, 2009),”

they state “this highly calcified *E. huxleyi* morphotype may be a genetic entity with an adaptation enabling it to calcify heavily in the relatively acidic upwelling waters.”

The scientists conclude “the presence of highly calcified *E. huxleyi* in CO₂-rich modern waters demonstrates that prediction of future responses is unlikely to be straightforward,” and “such complexity could account for the lack of an obvious overall direction in the response of coccolithophore calcification over a potentially analogous ocean acidification event about 55 million years ago at the Palaeocene-Eocene Thermal Maximum,” citing Gibbs *et al.* (2006).

Fiorini *et al.* (2011) measured the growth rates of three coccolithophores (*Emiliana huxleyi*, *Calcidiscus leptoporus*, and *Syracosphaera pulchra*) in laboratory batch cultures in their haploid and diploid life stages, while they were growing in filtered seawater maintained in equilibrium with air containing either 400 or 760 ppm CO₂. For all three species, “the growth rate was consistently higher at elevated pCO₂,” but “the response of other processes varied among species.” Calcification rates of *C. leptoporus* and *S. pulchra*, for example, did not change at elevated pCO₂, whereas this important process was increased in the case of *E. huxleyi*. They also found these CO₂-induced impacts were most pronounced in the haploid stage.

Fiorini *et al.* state these effects “must be taken into account when predicting the fate of coccolithophores in the future ocean.” The European scientists write, “the phenotypic and physiological differences of the two life stages allow each species to use two different niches to exploit a wider range of ecological conditions (Cros *et al.*, 2000), to limit the competition in the utilization of resources (food, light) inside the species and to rapidly escape negative selection pressures exerted on one stage such as grazing, parasitic attack, viral infections (Frada *et al.*, 2008), or abrupt environmental changes (Noel *et al.*, 2004).” In this way, they continue, “the survival of a species is ensured by one life stage when the environmental conditions do not favor the development of the other life stage (Houdan *et al.*, 2005).”

Lohbeck *et al.* (2012) note the present understanding of the sensitivity of marine life to lower ocean pH levels has been based primarily on short-term experiments that often depict negative effects. Suggesting phytoplanktonic species with short generation times “may be able to respond to environmental alterations through adaptive evolution,” they studied “the ability of the world’s

single most important calcifying organism, the coccolithophore *Emiliana huxleyi*, to evolve in response to ocean acidification in two 500-generation selection experiments.”

The three German researchers grew freshly isolated coccolithophore genotypes from Bergen, Norway, in batch cultures for more than 500 asexual generations at three different atmospheric CO₂ concentrations—ambient (400 ppm), medium (1,100 ppm), and high (2,200 ppm)—where the medium CO₂ treatment was chosen to represent the atmospheric CO₂ level projected for the beginning of the next century. They conducted a multi-clone experiment designed to provide existing genetic variation that “would be readily available to genotypic selection,” plus a single-clone experiment initiated with one “haphazardly chosen genotype,” where evolutionary adaptation would require new mutations.

Compared with populations kept at ambient CO₂ partial pressure, Lohbeck *et al.* found those selected at increased CO₂ levels “exhibited higher growth rates, in both the single- and multi-clone experiment, when tested under ocean acidification conditions.” Calcification rates were somewhat lower under CO₂-enriched conditions in all cultures, but the research team state they were “up to 50% higher in adapted [medium and high CO₂] compared with non-adapted cultures.” They conclude “contemporary evolution could help to maintain the functionality of microbial processes at the base of marine food webs in the face of global change.”

The marine biologists say the swift adaptation processes they observed may “have the potential to affect food-web dynamics and biogeochemical cycles on timescales of a few years, thus surpassing predicted rates of ongoing global change including ocean acidification.” They also note “a recent study reports surprisingly high coccolith mass in an *E. huxleyi* population off Chile in high-CO₂ waters (Beaufort *et al.*, 2011).” This observation, they write, indicates “across-population variation in calcification, in line with findings of rapid microevolution identified here.”

Lohbeck *et al.* suggest “contemporary evolution could help to maintain the functionality of microbial processes at the base of marine food webs in the face of global change.” Writing about this development in a *News & Views* item in the same issue of *Nature Geoscience*, Collins (2012) notes, “marine microbes, with their large population sizes and fast division rates, are certainly going to evolve over a timeframe of decades,” and “we can expect that future

coccolithophore populations will be shaped by a combination of species succession and adaptive evolution.”

McCarthy *et al.* (2012) note diatoms are a type of algae, most of which are unicellular, that serve as primary producers in various marine food chains. They investigated how diatoms might respond to continued increases in the air's CO₂ content, since they are responsible for about 40% of current marine primary productivity (Field *et al.*, 1998). The team of four Canadian researchers grew the coccolithophore *Emiliania huxleyi* and two strains of the diatom *Thalassiosira pseudonana* under low light in turbidostat photobioreactors bubbled with air containing either 390 ppm or 750 ppm CO₂, finding “increased CO₂ led to increased growth rates in all three strains” and “CO₂ thus had a fertilization effect on all species, enhancing growth rates 20%–40%.” They observe, “total cellular protein did not change between ambient and 750 ppm CO₂ treatments,” but “cellular RUBISCO content showed a 2- to 3-fold increase with [elevated] CO₂ in both *E. huxleyi* and in the coastal diatom strain.”

McCarthy *et al.* note the CO₂ fertilization effect on the growth rates of *T. pseudonana* and *E. huxleyi* provides these species with increased competitive ability. They conclude their results suggest “there could be a net increase in capacity for primary productivity at 750 ppm CO₂, at least with regard to small diatoms and coccolithophores in coastal environments,” where the two types of phytoplankton provide the bulk of current marine primary productivity.

Smith *et al.* (2012) write, “laboratory studies are unrealistic in many respects and, because of their typically short timescales, preclude the possibility of evolutionary adaptation to the imposed change, a key uncertainty in OA [ocean acidification] research,” citing Gattuso and Buddemeier (2000), Langer *et al.* (2006), and Ridgwell *et al.* (2009). They decided “to complement laboratory experiments with observational studies of coccolithophores living in the natural habitats to which they are evolutionarily adapted.”

Focusing on two morphotypes (over-calcified and normal) of the world's most abundant coccolithophore species (*Emiliania huxleyi*), Smith *et al.* assessed their numbers, along with seawater carbonate chemistry and other environmental variables, at monthly intervals between September 2008 and August 2009 along a 1,000 km route, including over deep oceanic waters in the Bay of Biscay. They found a pronounced seasonality in the morphotypes of *E. huxleyi*. “Surprisingly,” they write, “the over-

calcified morphotype was found to dominate the *E. huxleyi* population in winter,” even though seawater pH and CaCO₃ saturation were lowest in winter. The heavily calcified form of *E. huxleyi* dominated dramatically, shifting from less than 10% of the total *E. huxleyi* population in summer to more than 90% of the population in winter.

Smith *et al.* acknowledge their findings “do not suggest that the changing carbonate chemistry was necessarily responsible for this shift in morphotypes.” But “if it was not, then the alternative is that carbonate chemistry is not the sole and overriding control over coccolithophore calcification.” This, they write, should “seriously call into question” the contention “ocean acidification will lead to a replacement of heavily-calcified coccolithophores by lightly-calcified ones.”

Jin *et al.* (2013) note, “as a key group of oceanic primary producers, coccolithophores play a crucial role in the global carbon cycle, not only in terms of photosynthesis but also by producing calcium carbonate in the form of extracellular plates.” They note coccolithophores are “important in the sulfur cycle in terms of dimethyl-sulphide (DMS) production (Malin and Erst, 1997),” which leads to enhanced cloud formation and the reflectance back to space of increased amounts of incoming solar radiation, which tends to cool the planet.

The three researchers also note the particulate inorganic carbon (PIC) produced by coccolithophores in the surface ocean sinks to deep in the sea; this phenomenon, known as the carbonate pump, “is a critical part of the global carbon cycle and has a major feedback effect on global climate (Hutchins, 2011).” Jin *et al.* grew in a laboratory environment the coccolithophore *Gephyrocapsa oceanica* for approximately 670 generations in water in equilibrium with both ambient and CO₂-enriched (1,000 ppm) air, with the latter treatment reducing the water's pH to a value of 7.8.

Jin *et al.* found “high CO₂-selected cells showed increases in photosynthetic carbon fixation, growth rate, cellular particulate organic carbon (POC) or nitrogen (PON) production, and a decrease in the C:N elemental ratio, indicating a greater up-regulation of PON than of POC production under ocean acidification.” They note these findings are “in good agreement with a recent study in which *E. huxleyi* positively adapted to increased CO₂ levels,” citing Lohbeck *et al.* (2012). Jin *et al.* conclude their data indicate “the coccolithophorid could adapt to ocean acidification with enhanced assimilations of carbon and nitrogen.”

Climate Change Reconsidered II: Biological Impacts

The experimental findings and real-world observations discussed above suggest coccolithophores are well-equipped to deal with whatever decline in ocean pH levels may be on the way.

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6.3.2.1.2 Cyanobacteria

Cyanobacteria—also known as blue-green algae, blue-green bacteria, or Cyanophyta (the smallest of which, less than two micrometers in diameter, are typically referred to as picocyanobacteria)—obtain their energy through photosynthesis and are thus important primary producers in many areas of the world's oceans, as well as significant components of the marine nitrogen cycle. This section briefly reviews studies that address how they may be affected by lower ocean pH levels in a CO₂-enriched world of the future, as noted in the bullet points below and further discussed in the main body of the section.

- Ocean acidification enhances the productivity of one of the world's most important diazotrophic (N-fixing) cyanobacteria (*Trichodesmium erythraeum*) in N-limited oligotrophic regions of the world's oceans, providing more essential nitrogen to support greater amounts of higher-order marine animal life.
- The same is true of the unicellular diazotrophic cyanobacterium *Crocospaera*, recognized as being perhaps equally as important as *Trichodesmium* to the global ocean's nitrogen cycle.
- Acidification-induced increases in photosynthesis and N₂ fixation by both types of cyanobacteria may stimulate productivity in N-limited oligotrophic regions and thus provide a negative feedback on rising atmospheric CO₂ levels.
- The potentially toxic cyanobacterium *Cylindrospermopsis raciborskii* becomes less profuse as atmospheric CO₂ concentrations rise.

Arguing cyanobacteria “should be one of the focus points regarding biological responses to the rise in atmospheric CO₂ concentration,” Lu *et al.* (2006) studied physiological changes in phycocyanin (PC)-rich and phycoerythrin (PE)-rich *Synechococcus* strains of picocyanobacteria under atmospheric CO₂ concentrations of 350, 600, and 800 ppm in batch cultures maintained in one-liter glass flasks under a

12-hour:12-hour light:dark regime for periods of 12 days, measuring physiological parameters related to the growth and well-being of the picocyanobacteria. They found the growth of the PE strain was unaffected by atmospheric CO₂ enrichment, but the PC strain grown at 800 ppm CO₂ experienced a 36.7% increase in growth compared to when it was grown at 350 ppm CO₂.

The PC strain showed no significant change in carbohydrate content over the CO₂ range investigated, but the PE strain exhibited a CO₂-induced increase of 37.4% at 800 ppm CO₂. The PC strain exhibited a 36.4% increase in its RNA/DNA ratio between 350 and 800 ppm CO₂, and this ratio, Lu *et al.* write, “provides a good estimate of metabolic activities and has been used extensively as a biochemical indicator of growth rate in a variety of marine organisms.” In both *Synechococcus* strains, cellular pigment contents were generally greater in the CO₂-enriched treatments than in the ambient-air controls. At day 12 in the PE strain, for example, they averaged more than 70% greater at 800 ppm CO₂ than at 350 ppm CO₂.

These results clearly indicate both strains of the *Synechococcus* picocyanobacteria benefited greatly from the extra CO₂, albeit in different ways. In comparing the different responses of the two strains, Lu *et al.* conclude, “the PC strain would probably benefit more than the PE strain from future increases in atmospheric CO₂ concentration,” but “differences in photosynthetic characteristics may allow the coexistence of the two picocyanobacterial strains through a subtle form of niche differentiation,” citing Ernst *et al.* (2003) and Stomp *et al.* (2004). Consequently, there is reason to believe the continuing rise in atmospheric CO₂ content will lead to a significant increase in primary production and nutrient cycling throughout the world’s oceans, driven by the positive impacts of “acidification” on these very tiny organisms.

Levitan *et al.* (2007) note, “among the principal players contributing to global aquatic primary production, the nitrogen (N)-fixing organisms (diazotrophs) are important providers of new N to the oligotrophic areas of the oceans.” They cite several studies demonstrating “cyanobacterial (phototrophic) diazotrophs in particular fuel primary production and phytoplankton blooms which sustain oceanic food-webs and major economies and impact global carbon (C) and N cycling.” They examined how the ongoing rise in the air’s CO₂ content might impact these relationships, exploring the response of the cyanobacterial diazotroph *Trichodesmium* to changes in the atmosphere’s CO₂ concentration. They studied

this particular diazotroph because it contributes more than 50% of total marine N fixation.

The eight Israeli and Czech researchers grew *Trichodesmium* IMS101 stock cultures in a YBCII medium (Chen *et al.*, 1996) at 25°C and a 12-hour:12-hour light/dark cycle (with the light portion of the cycle in the range of 80–100 μmol photons m⁻² s⁻¹) in equilibrium with air of three CO₂ concentrations (250, 400, and 900 ppm, representing low, ambient, and high concentrations, respectively). They continuously bubbled air of the three CO₂ concentrations through the appropriate culture vessels throughout various experimental runs, each lasting a little over three weeks, while they periodically monitored a number of diazotrophic physiological processes and properties. They found *Trichodesmium* in the high CO₂ treatment “displayed enhanced N fixation, longer trichomes, higher growth rates and biomass yields.” In the high CO₂ treatment there was “a three- to four-fold increase in N fixation and a doubling of growth rates and biomass,” and the cultures in the low CO₂ treatment reached a stationary growth phase after only five days, “while both ambient and high CO₂ cultures exhibited exponential growth until day 15 before declining.”

The researchers suggest “enhanced N fixation and growth in the high CO₂ cultures occurs due to reallocation of energy and resources from carbon concentrating mechanisms required under low and ambient CO₂.” They conclude, “in oceanic regions, where light and nutrients such as P and Fe are not limiting, we expect the projected concentrations of CO₂ to increase N fixation and growth of *Trichodesmium*,” and “other diazotrophs may be similarly affected, thereby enhancing inputs of new N and increasing primary productivity in the oceans.” They state in the final sentence of their paper, “*Trichodesmium*’s dramatic response to elevated CO₂ may consolidate its dominance in subtropical and tropical regions and its role in C and N cycling, fueling subsequent primary production, phytoplankton blooms, and sustaining oceanic food-webs.”

Fu *et al.* (2008) examined “the physiological responses of steady-state iron (Fe)-replete and Fe-limited cultures of the biogeochemically critical marine unicellular diazotrophic cyanobacterium *Crocospaera* [watsonii] at glacial (190 ppm), current (380 ppm), and projected year 2100 (750 ppm) CO₂ levels.” They employed semi-continuous culturing methods that used filtered, microwave-sterilized surface Sargasso seawater enriched with phosphate and trace nutrients. When the seawater was replete

with iron, daily primary production at 750 ppm CO₂ was 21% greater than it was at 380 ppm, whereas at 190 ppm CO₂ it was 38% lower than at 380 ppm. When the seawater was iron-limited, daily primary production at 750 ppm CO₂ was 150% greater than it was at 380 ppm, and at 190 ppm CO₂ it was 22% lower than at 380 ppm. N₂ fixation rates varied little among the three 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, and at 190 ppm CO₂ it was 33% lower than at 380 ppm.

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 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).” They conclude, “anthropogenic CO₂ enrichment could substantially increase global oceanic N₂ and CO₂ fixation.”

Kranz *et al.* (2009) write, “marine phytoplankton contribute up to 50% of global primary production (Falkowski *et al.*, 1998) and influence Earth’s climate by altering various biogeochemical cycles (Schlesinger, 2005).” They also note, among diazotrophic cyanobacteria (dinitrogen-fixers), *Trichodesmium* species contribute “about half of all marine N₂ fixation (Mahaffey *et al.*, 2005),” supporting “a large fraction of biological productivity in tropical and subtropical areas and exerting, over long timescales, a significant influence on global carbon cycles by providing a major source of reactive N to the water column (Falkowski and Raven, 1997).”

Kranz *et al.* grew *Trichodesmium erythraeum* IMS101 in semi-continuous batch cultures through which they bubbled air with CO₂ concentrations of either 370 or 1,000 ppm. After the cultures were acclimated to their respective CO₂ concentrations for at least 14 days (covering more than five generations), the scientists measured the rates of particulate organic carbon (POC) and particulate organic nitrogen (PON) fixation, discovering “a strong increase in photosynthesis and N₂ fixation under elevated CO₂ levels,” such that POC and PON production rates rose “by almost 40%.”

The German scientists note other scientists have worked with the same *Trichodesmium* species:

“Barcelos e Ramos *et al.* (2007) and Levitan *et al.* (2007) observed stimulation in N₂ fixation by approximately 40% and even up to 400%, while Hutchins *et al.* (2007) obtained stimulation by up to 35%.” Kranz *et al.* write, “the observed increase in photosynthesis and N₂ fixation could have potential biogeochemical implications, as it may stimulate productivity in N-limited oligotrophic regions and thus provide a negative feedback on rising atmospheric CO₂ levels.”

Kranz *et al.* (2011) wrote, “marine phytoplankton are responsible for almost half of all photosynthetic carbon fixation on Earth and play a vital role in altering the CO₂ exchange between ocean and atmosphere,” citing Maier-Reimer *et al.* (1996) and Gruber (2004). They point out a lack of nitrates often limits phytoplanktonic growth, and diazotrophic cyanobacteria that fix nitrogen, such as *Trichodesmium* species, thus play “a crucial role in many marine ecosystems by providing a new source of biologically available nitrogen.” The scientists describe how atmospheric CO₂ enrichment helps enhance both parts of this important phenomenon.

The three researchers from the Alfred Wegener Institute for Polar and Marine Research in Bremerhaven, Germany report, “four recent studies tested the effect of different CO₂ concentrations on the growth, biomass production and elemental composition of *Trichodesmium* (Barcelos e Ramos *et al.*, 2007; Hutchins *et al.*, 2007; Kranz *et al.*, 2009; Levitan *et al.*, 2007),” and these studies “concordantly demonstrated higher growth and/or production rates under elevated pCO₂, with a magnitude exceeding those CO₂ effects previously seen in other marine phytoplankton.”

Focusing on particulate organic nitrogen (PON) production, they note *Trichodesmium* species are particularly effective in this regard: “the stimulation in N₂ fixation and/or PON production between present-day pCO₂ values (370–400 ppm) and those predicted for the year 2100 (750–1000 ppm) ranged between 35 and 240%.” They state “data on CO₂ dependency of N₂ fixation rates from recent publications suggest that N₂ fixation by *Trichodesmium* species might increase by more than 20 Tg N per year to about 100 Tg N per year until the end of this century,” citing Hutchins *et al.* (2009).

These findings indicate the oceans are primed to do their part in preserving and protecting the biosphere, as they ramp up their productivity to sustain a greater population of aquatic organisms that may be tapped to supply additional food for the planet’s burgeoning human population, and remove

from the atmosphere and sequester in their sediments increasing amounts of carbon as anthropogenic CO₂ emissions continue to rise.

Garcia *et al.* (2011) emphasize N₂ fixation by marine diazotrophic cyanobacteria (such as various species of *Trichodesmium*) “contributes substantial new nitrogen to marine environments, including the North Atlantic, Pacific, and Indian Oceans (Carpenter *et al.*, 1993; Capone *et al.*, 1997, 2005; Karl *et al.*, 2002).” They further note phosphorus and iron have been identified as key factors that control N₂ fixation in those environments. They report other studies suggest the current low partial pressure of CO₂ in the atmosphere “may be another possible limiting factor for N₂ fixation and CO₂ fixation by *Trichodesmium*,” citing Barcelos e Ramos *et al.* (2007), Hutchins *et al.* (2007), Levitan *et al.* (2007, 2010), and Kranz *et al.* (2009).

In a laboratory study designed to explore the limiting potential of low partial pressure of CO₂, Garcia *et al.* examined the effects of near-present-day (~380 ppm) and elevated (~750 ppm) atmospheric CO₂ concentrations on CO₂ and N₂ fixation by *T. erythraeum* isolates from the Pacific and Atlantic Oceans under a range of irradiance conditions. According to the seven scientists, “the positive effect of elevated CO₂ on gross N₂ fixation was large (~50% increase) under mid and/or low irradiances compared with that at high light (~20% increase),” noting data from Kranz *et al.* (2010) and Levitan *et al.* (2010) corroborated their findings. In the Kranz *et al.* study, they report, “under low light, gross N₂-fixation rates were 200% higher in a high-CO₂ treatment (900 ppm) compared with a low-CO₂ treatment (150 ppm), whereas under high light, gross N₂-fixation rates were only 112% higher under elevated CO₂.” In the case of CO₂ fixation, they found CO₂-fixation rates increased significantly “in response to high CO₂ under mid- and high irradiances only.”

As the atmosphere’s CO₂ concentration continues to rise, therefore, this phenomenon should boost the growth rates of marine diazotrophic cyanobacteria and enable them to make more nitrogen available to themselves and co-occurring species, which should significantly increase both the quantity and quality of the worldwide phytoplanktonic food base that ultimately supports all marine animal life.

Holland *et al.* (2012) studied the potentially toxic cyanobacterium *Cylindrospermopsis raciborskii*, originally described as a tropical-subtropical species but increasingly found in temperate regions. Noting “climate change is hypothesized to be a factor in this expansion,” the five researchers state, “identifying

future risk from this, and other nuisance cyanobacteria, is paramount.” Working with a strain of the cyanobacterium that was originally isolated from a lake near Brisbane (Australia), Holland *et al.* “used continuous (turbidostats) and batch cultures grown under two different light regimes, and adjusted the alkalinity of the media (with an associated change in pH, HCO₃⁻ and CO₂) to assess the effect of these parameters on the specific growth rate, inorganic carbon acquisition and photosynthetic parameters of *C. raciborskii*.”

Although there were insufficient data to confirm results obtained from the low-light experiments, the Australian researchers discovered “there was a positive linear relationship in the ‘high’ light turbidostats between the growth rate and pH,” as the potentially toxic *C. raciborskii* grew more profusely when atmospheric CO₂ concentrations were low and water pH was high, leading Holland *et al.* to conclude high-CO₂/low-pH conditions may change the composition of marine communities “to favor species that are better adapted to these new growth conditions, such as Chrysophytes,” which are known to produce “more than half of the food consumed by aquatic animals,” citing Maberly *et al.* (2009).

Teira *et al.* (2012) “tested the direct effect of an elevated CO₂ concentration (1,000 ppm) on the biomass and metabolic rates (leucine incorporation, CO₂ fixation and respiration) of two isolates belonging to two relevant marine bacterial families, Rhodobacteraceae (strain MED165) and Flavobacteriaceae (strain MED217),” referring to the former as simply *Roseobacter* and the latter as *Cytophaga*. “Contrary to some expectations,” they found “lowering pH did not negatively affect bacterial growth.” Doing so in fact increased the growth efficiency of *Cytophaga*. The scientists note, “in both cases, the bacterial activity under high CO₂ would increase the buffering capacity of seawater,” concluding the responses of the two marine bacterial families “would tend to increase the pH of seawater, acting as a negative feedback between elevated atmospheric CO₂ concentrations and ocean acidification.”

Lomas *et al.* (2012) note, “marine cyanobacteria, both unicellular *Prochlorococcus* and *Synechococcus* and colonial *Trichodesmium* spp., play important roles in the ocean carbon cycle and the biological carbon pump, particularly in the subtropical and tropical gyres (e.g. Partensky *et al.*, 1999; Capone *et al.*, 2005),” adding, *Trichodesmium* “is thought to account for about half of the total N₂-fixation in the oceans,” citing Barcelos e Ramos *et al.* (2007),

Hutchins *et al.* (2007), Levitan *et al.* (2007), and Kranz *et al.* (2009, 2010).

Working on board the RV Atlantic Explorer between July 2009 and April 2010 at the Bermuda Atlantic Time-series Study (BATS) site in the subtropical North Atlantic Ocean about 86 km southeast of Bermuda, Lomas *et al.* examined the C-fixation responses of natural assemblages of cyanobacteria dominated by *Synechococcus* and *Prochlorococcus* and the N₂- and C-fixation responses of isolated *Trichodesmium* colonies to changes in pH/pCO₂ conditions between the time of the last glacial minimum (8.4/150 ppm) and projected year 2100 values (7.8/800 ppm). They found “whole community assemblages dominated by *Prochlorococcus* and *Synechococcus*, whether nutrient-replete or P-limited, did not show a clear response of C-fixation rates to changes in pH/pCO₂.” They observed “Fe- and P-replete colonies of *Trichodesmium* increased N₂-fixation rates at pH 7.8 by 54% over ambient pH/pCO₂ conditions, while N₂-fixation at pH 8.4 was 21% lower than at ambient pH/pCO₂.” They found C-fixation rates of *Trichodesmium* “were on average 13% greater at low pH than at ambient pH and 37% greater than at high pH.” They note “these results for natural populations of all three cyanobacteria concur with previous research and suggest that one important response to changes in ocean pH and pCO₂ might be an increase in N₂ and C fixation by *Trichodesmium* under nutrient-replete conditions.”

Lomas *et al.* say their results for *Trichodesmium*, along with similar findings by several other marine scientists, suggest “ocean acidification would likely result in a positive feedback on the growth and physiology of natural populations, resulting in a positive change in their role in ocean carbon and nitrogen cycles.”

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6.3.2.1.3 Diatoms

Diatoms are a type of algae, most of which are unicellular, although they also form colonies that take the shape of filaments or ribbons. A unique feature of diatom cells is that they are encased within a special cell wall made of silica that is called a frustule, which can assume a wide variety of forms but usually consists of two asymmetrical sides with a split between them. Functionally, diatoms serve as primary producers in various marine food chains, and thus it is important to know how they may respond to continued increases in the air's CO₂ content. This section reviews much of what scientists have learned about the subject over the past several years, as summarized in the following bullet points.

- The light-saturated photosynthetic rate of the widely distributed *Skeletonema costatum* diatom is increased by elevated CO₂'s stimulating of cell numbers, chlorophyll *a* content, the photosynthetic chemistry of photosystem II, and the efficiency of its light reaction.
- The growth-promoting effect of elevated atmospheric CO₂ on diatoms and coccolithophores

probably has been responsible for limiting the rise in atmospheric CO₂ since the dawn of the Industrial Revolution to approximately 90% of what it otherwise would have been.

- Because diatoms are responsible for about half of the world's primary marine production, their enhanced growth due to atmospheric CO₂ enrichment should provide a significant brake on the rate of rise of the air's CO₂ content and reduce its ability to cause global warming.
- As diatoms serve as primary producers in numerous marine food chains, the several trophic levels above them should benefit from lower ocean pH levels as the atmosphere's CO₂ content continues to rise.

Chen and Gao (2004) grew a strain (2042) of *Skeletonema costatum*—a unicellular marine diatom, widely distributed in coastal waters throughout the world, that constitutes a major component of natural assemblages of most marine phytoplankton—in filtered nutrient-enriched seawater maintained at 20°C under a 12-hour/12-hour light/dark cycle at a light intensity of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, while continuously aerating both cultures with air of either 350 or 1,000 ppm CO₂ as they measured physiological parameters of the diatom's photosynthetic activity.

The scientists report cell numbers of the diatom “increased steadily throughout the light period, and they were 1.6 and 2.1 times higher after the 12-hour light period for the alga grown at 350 and 1000 ppm CO₂, respectively.” They also found chlorophyll *a* concentrations in the bulk of the two CO₂ cultures “increased 4.4- and 5.4-fold during the middle 8 hours of the light period for the alga grown at 350 and 1000 ppm CO₂, respectively,” and “the contents of cellular chlorophyll *a* were higher for the alga grown at 1000 ppm CO₂ than that at 350 ppm CO₂.” The initial slope of the light saturation curve of photosynthesis and the photochemical efficiency of photosystem II “increased with increasing CO₂, indicating that the efficiency of light-harvesting and energy conversion in photosynthesis were increased.” The two scientists report “the light-saturated photosynthesis rate based on cell number, the chlorophyll *a* content, the photosynthetic chemistry of photosystem II and the efficiency of the light reaction all increased to various degrees with elevated CO₂.”

Three years later, in a study conducted between 15 May and 9 June of 2005 at the Espesrend Marine Biological Station of the University of Bergen, on a

fjord in southern Norway, Riebesell *et al.* (2007) maintained nine cylindrical mesocosms—which extended from the water surface to a depth of 9–10 meters—in equilibrium with air of either ambient CO₂ concentration (350 ppm), doubled CO₂ (700 ppm) or tripled CO₂ (1,050 ppm), while measuring several phytoplanktonic physiological parameters. They found “net community carbon consumption under increased CO₂ exceeded present rates by 27% (2 x CO₂) and 39% (3 x CO₂),” and continuous oxygen measurements in the mesocosms identified “enhanced net photosynthesis to be the source of the observed CO₂ effect.”

Noting “the phytoplankton groups dominating in the mesocosm studies—diatoms and coccolithophores—are also the main primary producers in high productivity areas and are the principal drivers of biologically induced carbon export to the deep sea,” the 11 scientists say their findings “underscore the importance of biologically driven feedbacks in the ocean to global change.” Noting “increased CO₂ has been shown to enhance fixation of free nitrogen, thereby relaxing nutrient limitation by nitrogen availability and increasing CO₂ uptake (Barcelos e Ramos *et al.*, 2007),” Arrigo (2007) states in a *News & Views* discussion of Riebesell *et al.*'s paper “neither these, nor other possible non-steady-state biological feedbacks, are currently accounted for in models of global climate—a potentially serious omission, given that the biological pump is responsible for much of the vertical CO₂ gradient in the ocean.” Arrigo reports the diatom and coccolithophore growth-promoting effect of CO₂ measured and described by Riebesell *et al.* probably has been responsible for limiting the rise in atmospheric CO₂ since the dawn of the Industrial Revolution to approximately 90% of what it otherwise would have been.

Sobrinho *et al.* (2008) grew cultures of *Thalassiosira pseudonana*, “a widely distributed diatom,” exposing them to either photosynthetically active radiation (PAR: 400–700 nm) or PAR plus ultraviolet radiation (UVR: 280–400 nm) in 500-mL Teflon bottles maintained at 20°C, using a semi-continuous approach that employed daily dilutions with fresh growth medium (filtered seawater from the Gulf Stream that was enriched with f/2 nutrients) through which air of one of two atmospheric CO₂ concentrations (380 or 1,000 ppm) was continuously bubbled. They discovered exposure of the seawater medium to CO₂-enriched air increased the photosynthetic rate of the marine diatoms by approximately 45% in the presence of PAR and by about 60% in the

presence of both PAR and UVR, and it increased their growth rate by approximately 20% in both of the radiation environments. They note, “among the phytoplankton species inhabiting the [ocean’s] surface layer, diatoms are responsible for almost 40% of the ocean primary productivity (Nelson *et al.*, 1995).”

Tortell *et al.* (2008) measured CO₂ uptake of *in situ* phytoplankton assemblages collected at 35 stations in the Ross Sea polynya during austral spring and summer, together with ¹⁴C uptake for a subset of 11 station samples, while they conducted CO₂ manipulation experiments with phytoplankton collected at three Ross Sea locations in the Southern Ocean via shipboard incubations using a semi-continuous batch-culture technique. The researchers report, “for the *Phaeocystis*-dominated springtime phytoplankton assemblages, there was a statistically significant increase in ¹⁴C fixation between 100 and 380 ppm CO₂, but no further effects observed at 800 ppm CO₂.” In the case of the diatom-dominated summertime phytoplankton assemblages, the CO₂-induced increase in both relative growth rate and primary productivity continued through 800 ppm, and it promoted “a shift towards larger chain-forming species.” Noting the larger chain-forming species of diatoms “are prolific bloom formers with a very high capacity for organic carbon export to the sediments (Stickley *et al.*, 2005),” Tortell *et al.* conclude “potential CO₂-dependent productivity increases and algal species shifts could thus act to increase the efficiency of the biological pump, enhancing Southern Ocean CO₂ uptake and contributing to a negative feedback on increased atmospheric CO₂.”

Wu *et al.* (2010) suggest increased CO₂ availability may benefit marine phytoplankton, because “the low affinity of their carboxylating enzyme (Rubisco) for CO₂ (Badger *et al.*, 1998) ... could lead to enhanced phytoplankton growth and photosynthetic carbon fixation” in a high-CO₂ world of the future, as had been suggested by the work of Riebesell *et al.* (1993) and Hein and Sand-Jensen (1997).

Wu *et al.* cultured the diatom *Phaeodactylum tricornutum*, which had been isolated from the South China Sea, for at least 20 generations in artificial seawater equilibrated with air of either 388 or 1,000 ppm CO₂, which resulted in water pH values of either 8.15 or 7.80, respectively, while they measured the diatom’s photosynthetic carbon fixation, dark respiration, and growth rates. The three researchers found photosynthetic carbon fixation was enhanced by 12% under the high CO₂ and low pH conditions. Since dark respiration also was enhanced, the daily

net photosynthetic production was stimulated by a lesser 5.8%, and this value “closely agreed with the observed increase in growth,” which they had independently determined to have been enhanced by 5.2% under the high CO₂ and low pH conditions.

Wu *et al.* write, if “the roughly 5% increase in the growth of diatoms were taken into account based on the values obtained in this study, this would allow diatoms to rapidly accumulate more biomass (by about 34% in 6 days) and draw down available nitrogen and other nutrients, leading to a greater biological carbon flux to the deep sea.” And because diatoms contribute “about half of the marine primary production,” this phenomenon would provide a significant brake on the rate of rise of the atmosphere’s CO₂ concentration and its ability to cause global warming.

Boelen *et al.* (2011) assessed the photophysiology of the Antarctic diatom *Chaetoceros brevis* in seawater equilibrated with ambient CO₂ air (380 ppm) and air of approximately twice-ambient CO₂ (750 ppm) and half-ambient CO₂ (190 ppm), under four irradiance regimes: two simulating deep and shallow vertical mixing, and two that mimicked limiting and saturating stable water column conditions.

The six scientists found no significant differences between the enhanced and reduced CO₂ levels with respect to “growth, pigment content and composition, photosynthesis, photoprotection and Rubisco activity.” They conclude, “within the range tested, CO₂ does not significantly affect the photo-physiological performance of *C. brevis*.” Their results “agree with other studies on marine diatoms showing little or no effect of elevated CO₂ on growth (Burkhardt *et al.*, 1999) or maximum rates of photosynthesis (Rost *et al.*, 2003; Trimborn *et al.*, 2009),” although they note in other studies “elevated CO₂ concentrations enhanced growth rates (e.g., Riebesell *et al.*, 1993; Clark and Flynn, 2000),” and “a recent field study in the Southern Ocean (Tortell *et al.*, 2008) showed an increase in phytoplankton productivity and the promotion of large chain-forming *Chaetoceros* species under elevated CO₂.”

Boelen *et al.* state, “under saturating and limiting, as well as under dynamic and constant irradiance conditions, the marine Antarctic diatom *C. brevis* has the ability to adjust its cellular physiology in response to changing CO₂ levels with minimal effects on growth and photosynthesis.” Although this maintenance of the status quo could be considered a neutral response to elevated CO₂, it also could be regarded as a positive finding, given that many people

contend atmospheric CO₂ enrichment will be bad for almost all forms of oceanic life.

Crawford *et al.* (2011) note diatoms are very important for the productivity of the world's oceans, as they contribute about 45% of global marine primary production, citing Mann (1999); therefore it is essential to understand how diatoms and other marine phytoplankton will respond to the higher aqueous CO₂ and lower pH conditions that will prevail in ocean surface waters in the near future, as a result of the dissolution of anthropogenic CO₂ in them. They grew more than 100 generations of the diatom *Thalassiosira pseudonana* in seawater maintained in equilibrium with air of either current (ambient) CO₂ concentration or expected end-of-the-century (twice-ambient) CO₂ concentration (380 or 760 ppm)—which produced pH values of 8.1 and 7.8, respectively—for three months, after which they evaluated a number of the species' physical and physiological characteristics. The five UK researchers found “very few effects on *T. pseudonana* of long-term culture at different pCO₂ and pH.” They report, “growth rates were identical in cultures supplied with 780 or 360 ppm CO₂,” and “similar results have been reported for other diatom species,” citing Tortell *et al.* (1997), Tortell (2000), Kim *et al.* (2006), and Shi *et al.* (2009). Crawford *et al.* conclude, “if all diatoms respond in a similar fashion to *T. pseudonana*, acidification of this magnitude in the future ocean may have little effect on diatom productivity.”

McCarthy *et al.* (2012) grew two strains of the diatom *Thalassiosira pseudonana* under low light in turbidostat photobioreactors bubbled with air containing either 390 or 750 ppm CO₂. They found the increased concentration of CO₂ led to increased growth rates in both strains of 20%–40%. They also report total cellular protein did not change between the ambient and 750 ppm CO₂ treatments, but cellular rubisco content showed a two- to three-fold increase with elevated CO₂. McCarthy *et al.* state the CO₂ fertilization effect on the growth rate of *T. pseudonana* observed at low light and nutrient repletion imparts this species with increased competitive ability, concluding “there could be a net increase in capacity for primary productivity at 750 ppm CO₂, at least with regard to small diatoms in coastal environments.”

Li *et al.* (2012) investigated the diatom *Phaeodactylum tricornutum* as a model organism, culturing its cells in both low CO₂ (390 ppm) and high CO₂ (1,000 ppm), as well as at low nitrogen (10 μmol/L) and high nitrogen (110 μmol/L) concentrations. They report, “no direct effects on growth

rate were found between the CO₂ treatments” and “no direct effects on pigmentation were found between the CO₂ treatments.” They also note “no significant change in the [quantum] yield was found between the low and high CO₂ levels” and “increased dissolved CO₂ concentration did not affect the mean cell size and cell volume of *Phaeodactylum tricornutum*.” Moreover, “under the nitrogen replete treatment the CO₂ concentration did not affect the C:N ratio, even though the cells at the high CO₂ level significantly increased their nitrogen content by 13%.”

Real-world data suggest diatoms will continue to operate much as they have over prior millennia as the air's CO₂ content continues to rise, or they will be significantly stimulated to do everything they did before, only much better and on a larger scale. Given that diatoms serve as the primary producers in numerous marine food chains, the several trophic levels above them also should be at worst unharmed, and probably benefited by, lower ocean pH levels.

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6.3.2.1.4 Foraminifera

Foraminifera are amoeboid protists with reticulating pseudopods—fine strands of cytoplasm that subdivide into branches that merge to form a dynamic network. They are typically less than one mm in size (but can be much larger), and they produce an elaborate calcium carbonate shell called a test, which may have one or more chambers. According to Schiebel (2002), these widespread calcifying protozoa are responsible for 32–80% of the global deep-ocean flux of calcite. Therefore, it is important to determine how various forams, as they are often called, may be affected by likely future declines in ocean pH levels. This section describes some of what scientists have learned about this subject over the past several years, briefly summarized in the following bullet points.

- Some foraminiferal species will tolerate CO₂ values one to two orders of magnitude higher than those predicted for the next few centuries.
- Other forams will tolerate CO₂ values one to two orders of magnitude greater than those predicted to occur for the extreme case of burning all the fossil fuels in Earth's crust.

- Some forams not only survive but successfully reproduce in seawater maintained in equilibrium with air containing as much as 200,000 ppm of CO₂.

Lombard *et al.* (2010) cultured specimens of *Orbulina universa* collected by scuba divers off the coast of Catalina Island, California (USA) and *Globigerinoides sacculifer* obtained near Puerto Rico (USA) under high and low irradiances (335 and 35 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, respectively) in filtered seawater that had its pH and carbonate ion concentration (CO₃²⁻) manipulated by adding NaOH or HCl to it. They measured the forams' initial and final size, survival time (days from collection to gametogenesis), and final shell weight for individuals that underwent gametogenesis and grew at least one chamber. They determined under the IS92a "business as usual" scenario as defined by IPCC and projected for the year 2100, the calcification rates of *G. sacculifer* and *O. universa* "could decline by 6–13% compared to recent rates." That is not a large decline, and the four researchers note, "the future increase in temperature [predicted by IPCC] could increase the production of calcite by foraminifera, counter-acting the negative impact of ocean acidification."

Kuroyanagi *et al.* (2009) cultured asexually produced individuals of *Marginopora kudakajimensis*—a large calcifying microorganism that contributes to organic and inorganic carbon production in coral reefs—under laboratory conditions for 71 days in glass jars containing approximately 110 ml of filtered natural seawater (control pH of about 8.2) and two less-basic pH conditions of about 7.9 and 7.7, with the lower values being created by addition of 0.1 N HCl. In declining from the control pH of 8.2 to a pH of 7.9, the mean maximum shell diameter of the large foraminifer rose by 8.6%; its mean shell weight rose by a much smaller and insignificant 0.7%. As the seawater's pH declined to 7.7, the organism's mean maximum shell diameter fell by 12.1% and its mean shell weight fell by 49.3%. Kuroyanagi *et al.* conclude if oceanic pH remains within the range of 8.2 to 7.9, "large foraminifers should be able to maintain present calcification rates."

Bernhard *et al.* (2009) grew the marine foraminiferal protist *Allogromia laticollaris*—which they described as "a ubiquitous protistan constituent of marine microbial systems" and "an important link in the marine food web"—in a mixture of 32% seawater and Alga-Gro seawater medium in 20-ml glass culture tubes, examining its response to several

super-high atmospheric CO₂ concentrations to which the tubes were exposed: 15,000, 30,000, 60,000, 90,000 and 200,000 ppm, values compared to the study's atmospheric control concentration of 375 ppm CO₂. The protist was "able to survive 10–14-day exposure to elevated CO₂ as high as 200,000 ppm." They write, "both ATP [adenosine triphosphate, an indicator of cellular energy] data and microscopic examination demonstrated that considerable populations of *A. laticollaris* survived exposure to all experimental treatments of elevated CO₂, even both replicates of the 200,000-ppm CO₂ experiments." They also found "at least three specimens reproduced during exposure to either 90,000 ppm or 200,000 ppm CO₂," whereas "such reproduction was observed only once in an atmospheric [375-ppm CO₂] treatment."

The four researchers state "*A. laticollaris* is an appropriate species to predict the response of shallow-water thecate foraminifera to predicted increases in atmospheric CO₂, given its isolation [i.e., acquisition] from a shallow-water semi-tropical setting." They say their results indicate "at least some foraminiferal species will tolerate CO₂ values that are one to two orders of magnitude higher than those predicted for the next few centuries." Indeed, their results indicate *A. laticollaris* will tolerate CO₂ values one to two orders of magnitude greater than those predicted to occur for the "extreme case" of burning all fossil fuels in Earth's crust.

But aren't *all* forams amazingly resilient creatures? In a study broaching this question, Cannariato *et al.* (1999) investigated the character, magnitude, and speed of biotic responses of benthic foraminifera to millennial-scale climatic oscillations, using data from an ocean sediment core in the Northeast Pacific that extended back in time some 60,000 years. A number of rapid climatic switches over the 60,000-year record were noted, representing periods of what the three researchers call "extreme environmental variability." They found no evidence of extinctions, and the benthic ecosystems appeared to be "both resilient and robust in response to rapid and often extreme environmental conditions." The scientists note faunal turnovers occurred within decades throughout the record "without extinction or speciation." They conclude, "broad segments of the biosphere are well adapted to rapid climate change," which suggests broad segments of the biosphere may be equally well adapted to lower ocean pH levels.

Hikami *et al.* (2011) measured foram net calcification rates of two algal symbiont-bearing, reef-dwelling forams (*Amphisorus kudakajimensis* and *Calcarina gaudichaudii*) in seawater maintained

at five $p\text{CO}_2$ concentrations (245, 375, 588, 763, and 907 ppm). They also conducted a second culture experiment in seawater in which bicarbonate ion concentrations were varied, while keeping carbonate ion concentration constant.

In the first experiment, Hikami *et al.* found “net calcification of *A. kudakajimensis* was reduced under higher $p\text{CO}_2$, whereas calcification of *C. gaudichaudii* generally increased with increased $p\text{CO}_2$.” In the second experiment, they found “calcification was not significantly different between treatments in *Amphisorus hemprichii*, a species closely related to *A. kudakajimensis*, or in *C. gaudichaudii*.”

Explaining the results of their first experiment, the nine researchers note the upward calcification trend of *Calcarina* with rising $p\text{CO}_2$ “can probably be attributed to the increase in CO_2 , possibly through enhancement of symbiont photosynthesis, a phenomenon known as the CO_2 -fertilizing effect (e.g., Ries *et al.*, 2009).” They note *Calcarina* harbor diatoms, and “both a single-species culture experiment (Wu *et al.*, 2010) and a mesocosm bloom experiment (Engel *et al.*, 2008) have shown that high- CO_2 seawater is favorable to diatom growth,” which in turn stimulates calcification. They also note Rost *et al.* (2006) report dinoflagellates, which are harbored by *Amphisorus*, “use HCO_3^- as their carbon source, so their rate of carbon fixation may remain unaffected by fluctuating CO_2 levels.”

As for the second experiment, the seawater pH varied but little between the different bicarbonate ion concentration treatments, resulting in little variation in the calcification rates of both species. Hikami *et al.* conclude the different influences of sea-water chemistry they observed in the two forams may have been attributable to the different types of symbiotic algae they hosted.

Vogel and Uthicke (2012) note, “several studies highlight the importance of large benthic foraminifera (LBF) as biological indicators for water quality and ecosystem health,” citing Hallock *et al.* (2003), Uthicke and Nobes (2008), and Uthicke *et al.* (2010), but “impacts of ocean acidification on LBF physiology are not well studied.” They investigated “the influence of increased CO_2 on calcification and photobiology of LBF hosting different types of photosynthetic endosymbionts.” The two researchers collected samples of the foraminifers *Amphistegina radiata*, *Heterostegina depressa*, and *Marginopora vertebralis* from two locations on Australia’s Great Barrier Reef on several field trips between October 2010 and April 2011. They exposed the samples in a laboratory over a period of six weeks to four seawater

conditions (467, 784, 1,169, and 1,662 ppm CO_2), periodically measuring a number of physiological parameters and processes.

The researchers found no negative effects of elevated CO_2 on the calcification of any of the LBF species investigated compared to control conditions. The growth rate of *M. vertebralis* increased with elevated CO_2 , with mean calcification rates at the two highest CO_2 treatments (1,169 and 1,662 ppm) being 63% greater than those at the two lowest treatments (467 and 784 ppm). Increased CO_2 had no effect on chlorophyll *a* content in either *A. radiata* or *H. depressa*, but “chlorophyll *a* content approximately doubled in *M. vertebralis* from initial to final measurements.” In addition, “the maximum quantum yield of *A. radiata*, *H. depressa* and *M. vertebralis* did not vary significantly between different CO_2 treatments.” Nor did they find significant negative impacts on photosynthetic production and respiration in the three LBF species.

Vogel and Uthicke say their study “illustrated that the species investigated were still able to build up their calcite skeletons in CO_2 conditions predicted for the year 2100 and beyond,” and “contrary to expectations, *M. vertebralis* showed significantly increased growth rates in elevated CO_2 .”

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6.3.2.1.5 Other Individual Types

Scientists also have studied phytoplankton other than coccolithophores, cyanobacteria, diatoms, and foraminifera, and this brief section reviews the findings of studies where the responses of these species to lower ocean pH levels have been either experimentally or observationally determined, as described in the bullet points below and in the text that follows them.

- Atmospheric CO₂ enrichment induced “a protective effect against the oxidative damage of UV-B-induced stress” in *Platymonas subcordiformis*, suggesting elevated CO₂ should be able to

“enhance the capacity of [UV-B] stress resistance.”

- A study of *Stichococcus cylindricus* and *Stichococcus minor* revealed the two marine microalgae “were able to tolerate a broad range of pH from pH 5.0 to 9.5,” as well as a broad range of salinities.
- A 2.63-fold increase in the air’s CO₂ content led to increases in photosynthetic rates among the 16 ecotypes of a unicellular species of marine green alga (*Ostreococcus tauri*) that ranged from 1.02- to 2.18-fold greater than the current mean, while CO₂-induced size differences among ecotypes were found to range from 1.3- to 1.9-fold greater than the current mean. Differences in plastic responses for C/N ratios, which partly determine the food quality of phytoplankton, were found to range from 1.06- to 1.56-fold greater than the current mean.

Gordillo *et al.* (2003) studied the CO₂-induced growth response of the microalgal chlorophyte *Dunaliella viridis*, which possesses a carbon-concentrating mechanism and has been used as a model species for the study of inorganic carbon uptake. They batch-cultured the chlorophyte, one of the most ubiquitous eukaryotic organisms found in hypersaline environments, in 250-ml Perspex cylinders under laboratory conditions at high (5 mM) and low (0.5 mM) nitrate concentrations, while continuously aerating the cultures with air of either 350 or 10,000 ppm CO₂.

They found atmospheric CO₂ enrichment had little effect on dark respiration in both N treatments, and it had little effect on photosynthesis in the low-N treatment. In the high-N treatment, the extra CO₂ increased photosynthesis by 114%. In the case of biomass production, the results were even more divergent: in the low-N treatment elevated CO₂ had no effect, but in the high-N treatment it nearly tripled the cell density of the culture solution. Gordillo *et al.* note “it has long been debated whether phytoplankton species are growth-limited by current levels of CO₂ in aquatic systems, i.e. whether an increase in atmospheric CO₂ could stimulate growth (Riebesell *et al.*, 1993).” Their results clearly indicate it can, if sufficient nitrogen is available.

Gordillo *et al.* also learned that in the high-N treatment, where elevated CO₂ greatly stimulated photosynthesis and biomass production, once the logarithmic growth phase had run its course and

equilibrium growth was attained, approximately 70% of the carbon assimilated by the chlorophyte was released to the water, whereas in the low- CO₂ treatment only 35% was released. Gordillo *et al.* write, “the release of organic carbon to the external medium has been proposed as a mechanism for maintaining the metabolic integrity of the cell (Ormerod, 1983),” and “according to Wood and Van Valen (1990), organic carbon release would be a sink mechanism protecting the photosynthetic apparatus from an overload of products that cannot be invested in growth or stored.” They also note stores of photosynthetic products “are reduced to avoid overload and produce a high demand for photosynthates.” Under these conditions, they conclude the process would “divert assimilated C to either the production of new biomass, or the release to the external medium once the culture conditions do not allow further exponential growth.”

A second consequence of CO₂-enhanced organic carbon release is that the internal C:N balance of the phytoplankton is maintained within a rather tight range. This phenomenon has been observed in the green seaweed *Ulva rigida* (Gordillo *et al.*, 2001) and the cyanobacterium *Spirulina platensis* (Gordillo *et al.*, 1999). What the study of Gordillo *et al.* (2003) reveals about the response of *Dunaliella viridis* to atmospheric CO₂ enrichment may be applicable to many, if not most, aquatic plants.

Yu *et al.* (2004) grew the marine microalgae *Platymonas subcordiformis* (Wille) Hazen 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 UV-B radiation characteristic of that anticipated to result from a 25% stratospheric ozone depletion under clear sky conditions in summer. By itself, they report, the elevated UV-B treatment “significantly decreased [microalgal] dry weight, photosynthetic rate, chlorophyll *a* and carotenoid contents,” and the elevated CO₂ treatment by itself “enhanced dry weight and photosynthetic rate, but chlorophyll *a* content and carotenoid content had no major difference compared with those of ambient UV-B and ambient CO₂.” They also report elevated UV-B by itself significantly increased the production of the toxic superoxide anion and hydrogen peroxide, as well as malonyldialdehyde, which is an end-product of lipid peroxidation, whereas elevated CO₂ by itself did just the opposite. In the treatment consisting of both elevated UV-B and elevated CO₂, the concentrations of these three malevolent substances were lower than those observed in the elevated UV-B and ambient CO₂

treatment. Finally, they note elevated CO₂ decreased the levels of several antioxidant enzymes found in the microalgae, reflecting their reduced need for detoxification of reactive oxygen species in the elevated CO₂ treatment.

Yu *et al.* conclude atmospheric CO₂ enrichment “could reduce the oxidative stress of reactive oxygen species to *P. subcordiformis*, and reduce the lipid peroxidation damage of UV-B to *P. subcordiformis*.” They also state, “CO₂ enrichment showed a protective effect against the oxidative damage of UV-B-induced stress,” and, therefore, elevated CO₂ should be able to “enhance the capacity of stress resistance.” They conclude microalgae grown under high CO₂ “would better overcome the adverse impact of environmental stress factor[s] that act via generation of activated oxygen species.”

Moazami-Goudarzi and Colman (2012) measured the growth rates of two marine microalgae (*Stichococcus cylindricus* and *Stichococcus minor*) in artificial seawater, as per Berges *et al.* (2001), within 125-ml Erlenmeyer flasks at pH values of 5.0, 6.0, 7.0, 8.2, 9.0, and 9.5, as well as at a variety of salinity levels (25, 50, 100, 200, and 470 mM). The two Canadian researchers discovered both species had similar growth rates and grew over the range of pH 5.0 to 9.5, with “cells grown at pH 5.0, 6.0 and 7.0 showing no significant difference in growth rates.” They also report “both species were found to have similar growth rates and to grow over a range of salinities at sodium chloride concentrations of 25, 50, 100, 200 and 470 mM.” Moazami-Goudarzi and Colman found *S. minor* and *S. cylindricus* “were able to tolerate a broad range of pH from pH 5.0 to 9.5,” as well as the broad range of salinities they investigated.

Schaum *et al.* (2013) write, “marine phytoplankton are the foundation of ocean ecosystems,” noting “these small but mighty microbes are responsible for roughly half of global carbon fixation” and they “form a fundamental part of the biological carbon pump that exports fixed carbon to the deep ocean.” They state “empirical studies so far predict changes [in response to rising atmospheric CO₂ concentrations] in phytoplankton communities using single or a few genotypes to represent functional groups,” whereas the real-world variation in responses within functional groups “has not been quantified.” The four researchers used “16 ecotypes of *Ostreococcus tauri* [a unicellular species of marine green alga] from nine habitat types,” which “were obtained from the Roscoff Culture Collection and the Plymouth Marine Laboratory, grown in Keller medium and made clonal by dilution, so that each

culture originated from single cells.” Those samples were “acclimated for 5–7 asexual generations to 380 ppm CO₂ or 1,000 ppm CO₂ in a closed-system and grown in semi-continuous batch cultures at low densities,” allowing the researchers to “quantify variations in plastic responses to elevated CO₂ for ecologically relevant traits such as photosynthesis” while also characterizing “changes in traits affecting food quality for five of these ecotypes.”

Schaum *et al.* note they were able to “link plasticity in photosynthesis rates to changes in the relative fitness of ecotypes during asexual growth,” and they were further able to “use this link to predict which ecotypes are likely to rise in frequency in a high-CO₂ environment.” They found the 2.63-fold increase in the air’s CO₂ content of their experiment led to increases in photosynthetic rates among the 16 ecotypes they studied, ranging from 1.02- to 2.18-fold greater than the current mean, and CO₂-induced size differences among ecotypes were found to range from 1.3- to 1.9-fold greater than the current mean. Differences in plastic responses for C/N ratios, which partly determine the food quality of phytoplankton, were found to range from 1.06- to 1.56-fold greater than the current mean. The four scientists conclude, “as CO₂ levels increase, *O. tauri* will grow and photosynthesize faster, and have larger cells with a higher C/N ratio than contemporary cells,” with the result “*Ostreococcus*, along with other green algae and cyanobacteria, are likely to increase in abundance in high-CO₂ conditions” with concomitant benefits for the biosphere.

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6.3.2.1.6 Mixtures of All Types

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on mixtures of various types of marine phytoplankton. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Ultra-high CO₂ enrichment (5,000 ppm) promoted the growth of six species of marine microalgae.
- The effects of atmospheric CO₂ enrichment on various marine phytoplankton in a fjord adjacent to the Large-Scale Facilities of the Biological Station of the University of Bergen in Espesrend, Norway revealed no significant species shifts between treatments, and “the ecosystem composition, bacterial and phytoplankton abundances and productivity, grazing rates and total grazer

abundance and reproduction were not significantly affected by CO₂ induced effects.”

- “Changes in iron speciation and the resulting potential negative feedback mechanism of phytoplankton productivity on atmospheric CO₂”—i.e., the drawdown of atmospheric CO₂ due to enhanced phytoplanktonic growth and transferral of the carbon thus removed from the atmosphere to the ocean depths—“need to be considered when assessing the ecological effects of ocean acidification.”
- The “broad level of pH-tolerance” observed in coastal environments likely results from the adaptation of organisms living there to the large pH fluctuations that routinely occur “as a result of respiratory and photosynthetic processes,” as well as “hydrographical events,” that alter the “seasonal, and even diurnal, fluctuations in coastal seawater pH” over a large range.
- “Nitrifying organisms in coastal systems tolerate a wide range of pH values,” suggesting “the current hypothesis of the negative impacts of ocean acidification on nitrification, at least for the coastal ocean, might need reevaluation.”
- Atmospheric CO₂ enrichment is not likely to lead to a degradation of planktonic food quality in Arctic waters.

Wolf-Gladrow *et al.* (1999) examined the direct effects of atmospheric CO₂ enrichment on marine phytoplankton, including the consequences of these phenomena for the world’s oceanic carbon pump, finding the ongoing rise in the air’s CO₂ content may also benefit the planet’s marine biota, producing significant increases in phytoplanktonic growth rates that may “serve as negative feedbacks to anthropogenic CO₂ increase.”

More than a decade later, Joint *et al.* (2011) note “the pH of the surface ocean is changing as a result of increases in atmospheric carbon dioxide,” and “there are concerns about potential impacts of lower pH and associated alterations in seawater carbonate chemistry on the biogeochemical processes in the ocean.” They note “it is important to place these changes within the context of pH in the present-day ocean.”

According to the three researchers, “marine and freshwater assemblages have always experienced variable pH conditions.” For example, “phytoplankton blooms can rapidly reduce pCO₂, with a

concomitant increase in pH,” which subsequently declines as the blooms die out, demonstrating “pH is naturally variable and that marine organisms—particularly microbes—must already be capable of adapting to rapid and sometimes large changes in pH.” They also note, “oceanic pH can change by up to 0.06 pH unit during the year even in the oligotrophic Central Pacific, which does not experience the dramatic phytoplankton blooms of temperate oceans.” Regarding freshwater ecosystems, Joint *et al.* report, “Maberly (1996) showed that diel variations in a lake can be as much as 2–3 pH units,” and “Talling (2006) showed that in some English lakes, pH could change by >2.5 pH units over a depth of only 14 m,” noting “phytoplankton, bacteria, archaea and metazoans are all present in lakes, and appear to be able to accommodate large daily and seasonal changes in pH.”

The three researchers conclude, “perhaps the most appropriate null hypothesis to test is that marine microbes possess the flexibility to accommodate pH change and there will be no catastrophic changes in marine biogeochemical processes that are driven by phytoplankton, bacteria and archaea.” Many researchers have done just that.

Yu *et al.* (2006) grew monocultures of six species of marine microalgae (*Chlorella* sp., *Dunaliella salina*, *Isochrysis galbana* Parke 8701, *Nitzschia closterium*, *Platymanas subcordiformis*, and *Platymanas* sp.) in Erlenmeyer flasks under 14:10 dark:light 24-hour cycles through which air of either 360 or 5,000 ppm CO₂ was continuously bubbled for five days. They measured algal cell densities at one-day intervals in order to calculate and compare algal specific growth rates. All six species responded positively to the ultra-high CO₂ enrichment of the air, with the ratios of their specific growth rates in the CO₂-enriched compared to ambient-air treatments being 1.15 for *Chlorella* sp., 1.35 for *Dunaliella salina*, 1.35 for *Isochrysis galbana*, 1.40 for *Nitzschia closterium*, 1.47 for *Platymanas subcordiformis*, and 1.60 for *Platymanas* sp.

Yu *et al.* conclude, a “high concentration of CO₂ promotes the growth of microalgae,” citing not only their results but also the findings of other researchers, including Lin (1991), Nobutaka *et al.* (1992), Riebesell *et al.* (1993), Hein and Sand-Jensen (1997), Liang and Yonemoto (1999), Hu and Gao (2001), and Xia and Gao (2001, 2002). They note, “possibly, the CO₂ enrichment made the chloroplast[s] more developed,” so “both the photosynthesis and cell division rate were increased,” and, therefore, “the algal cell density was enhanced.”

Vogt *et al.* (2008) studied the effects of atmospheric CO₂ enrichment on various marine microorganisms in nine marine mesocosms maintained within two-meter-diameter polyethylene bags submerged to a depth of 10 meters in a fjord adjacent to the Large-Scale Facilities of the Biological Station of the University of Bergen in Espesgrend, Norway. They maintained three of the mesocosms at ambient levels of CO₂ (~375 ppm), three at levels expected to prevail at the end of the current century (760 ppm or 2x CO₂), and three at levels predicted for the middle of the next century (1,150 ppm or 3x CO₂), taking measurements of numerous ecosystem parameters over a period of 24 days.

Vogt *et al.* detected no significant phytoplankton species shifts between treatments, and “the ecosystem composition, bacterial and phytoplankton abundances and productivity, grazing rates and total grazer abundance and reproduction were not significantly affected by CO₂ induced effects,” citing the work of Riebesell *et al.* (2007), Riebesell *et al.* (2008), Egge *et al.* (2007), Paulino *et al.* (2007), Larsen *et al.* (2007), Suffrian *et al.* (2008), and Carotenuto *et al.* (2007). The eight researchers say their observations suggest “the system under study was surprisingly resilient to abrupt and large pH changes.”

Three oceanic CO₂-enrichment experiments (I, II, and III) were carried out in 2001, 2003, and 2005 at the Marine Biological Station of the University of Bergen at Espesgrend, Norway, where researchers maintained nine marine ecosystems in two-meter-diameter polyethylene bags submerged to a depth of 10 meters in an adjacent fjord, keeping three of the mesocosms at ambient levels of CO₂ (1xCO₂), three others at 2xCO₂ and three more at 3xCO₂ (via aeration of the water column and the overlying atmosphere with CO₂-enriched air). They performed this work in the context of the Pelagic Ecosystem CO₂ Enrichment (PeECE) program, enabling the PeECE I, PeECE II, and PeECE III

experiments.

After a one-time addition of nutrients intended to initiate a phytoplankton bloom on the day before the start of their 24-day study, Egge *et al.* (2009) measured primary production in the nine mesocosms at two-day intervals during the PeECE III experiment, along with oxygen production and consumption, the presence of transparent exopolymer particles, and the composition of the phytoplanktonic community. The seven scientists report, “in the second half of the experiment there was a tendency of higher production at elevated CO₂ levels,” which was “visible from ca. day 10 in the cumulative production, with a significant difference between 3x and 1x CO₂ from day 20 onward,” as shown in Figure 6.3.2.1.6.1.

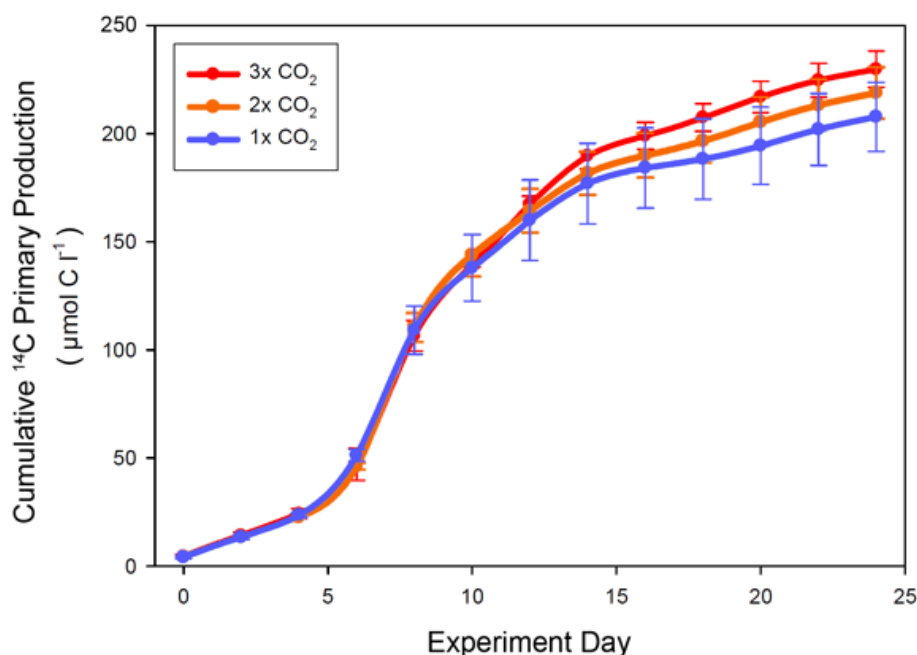


Figure 6.3.2.1.6.1. Cumulative primary production from the start of the PeECE III experiment of Egge *et al.* (2009), adapted from the authors' paper.

Egge *et al.* state their results “demonstrate a small, but statistically significant effect of elevated CO₂ on daily primary production” that is “consistent with the over-consumption of dissolved inorganic carbon at elevated CO₂ reported by Riebesell *et al.* (2007) and Bellerby *et al.* (2008).” These observations once again suggest the planet’s rising atmospheric CO₂ concentration may stimulate oceanic primary production and thereby enable the sustaining of a greater population of higher-trophic-level marine organisms.

Breitbarth *et al.* (2010) write, “studies of artificial and natural iron input have demonstrated iron control of phytoplankton productivity and CO₂ drawdown over vast oceanic regions (Boyd *et al.*, 2007; Blain *et al.*, 2007; Pollard *et al.*, 2009) and in coastal upwelling regions (Bruland *et al.*, 2001; Hutchins and Bruland, 1998),” and “temporal control of iron on phytoplankton productivity was also observed in a Norwegian fjord system (Ozturk *et al.*, 2002).” Breitbarth *et al.* measured dissolved iron (dFe) concentrations as well as levels and oxidation rates of Fe(II)—a necessary trace element (the ferrous species of iron) used by almost all living organisms—over the course of natural phytoplanktonic blooms to determine whether lower ocean pH levels may affect iron speciation in seawater. The researchers made measurements in mesocosms consisting of two-meter-diameter polyethylene bags submerged to a depth of 10 meters and maintained in equilibrium with air possessing CO₂ concentrations of either 350, 700, or 1,050 ppm via aeration of the water column and the overlying atmosphere with air of the three CO₂ concentrations (Schulz *et al.*, 2008).

The eight researchers report CO₂ perturbation and phytoplanktonic bloom development resulted in pH value ranges of 8.13–8.26, 7.82–8.08, and 7.67–7.97 at 3570, 700, and 1050ppm CO₂, respectively. They say their measurements revealed significantly higher dFe concentrations in the high CO₂ treatment compared to the mid and low CO₂ treatments, and the high-CO₂ mesocosms showed higher values of Fe(II) compared to the lower CO₂ treatments.

Breitbarth *et al.* conclude “ocean acidification may lead to enhanced Fe-bioavailability due to an increased fraction of dFe and elevated Fe(II) concentrations in coastal systems ... due to pH induced changes in organic iron complexation and Fe(II) oxidation rates,” noting these phenomena “will result in increased turnover of Fe in surface seawater, potentially maintaining iron bioavailability given a sufficient supply of total Fe, since equilibrium partitioning eventually restores the bioavailable Fe pools that have been depleted by biological uptake.” They write, “these processes may further fuel increased phytoplankton carbon acquisition and export at future atmospheric CO₂ levels,” citing Riebesell *et al.* (2007). They conclude, “changes in iron speciation and the resulting potential negative feedback mechanism of phytoplankton productivity on atmospheric CO₂—the drawdown of atmospheric CO₂ due to enhanced phytoplanktonic growth and transferral of the carbon thus removed from the atmosphere to the ocean depths—“need to be considered when

assessing the ecological effects of ocean acidification.”

According to Wyatt *et al.* (2010), “the assimilation of inorganic nutrients fuels phytoplankton growth,” and therefore, “any alteration in the bioavailability of these nutrients is likely to impact productivity and, by extension, climate regulation through the uptake of CO₂ by marine algae.” The authors note, “the reduction of surface ocean pH anticipated for the next century will alter the equilibrium coefficient between dissolved ammonia (NH₃(aq)) and ammonium (NH₄⁺) shifting the equilibrium towards NH₄⁺ (Zeebe and Wolf-Gladrow, 2001; Bell *et al.*, 2007, 2008).” As a result, the future decrease in ocean pH due to the ongoing rise in the air’s CO₂ content could result in the transfer of more gaseous NH₃ from the overlying atmosphere to the ocean, as has been noted by Jacobson (2005).

Wyatt *et al.* collected surface seawater samples from a coastal monitoring site in the Western English Channel (WEC) from 17 March to 21 July 2008, a period of time that included two distinct phases of the annual spring phytoplankton bloom (a pre-bloom period of five weeks and the bloom proper of 11 weeks). They measured ambient pH for carbonate system estimates and dissolved inorganic nutrients, and they equilibrated the samples with CO₂-in-air mixtures that resulted in CO₂ concentrations of 380, 500, 760, and 1,000 ppm that led to pH values of 8.05, 8.01, 7.87, and 7.76, respectively, to be compared with the mean ambient value of 8.18.

The six scientists report the phytoplankton community “was predominantly limited by the availability of inorganic nitrogen,” and “during early and mid-summer, NH_x became the primary source of inorganic nitrogen.” They also found “an overall increase in NH_x concentrations by 20% was observed between the present day CO₂ treatment (380 ppm) and 1000 ppm.” Wyatt *et al.* write, “as excess CO₂ dissociates in the oceans, the increased hydrogen ion concentration ionizes NH₃(aq) and decreases the ratio of NH₃(aq):NH₄⁺,” and this reduction in NH₃(aq) “would lead to an imbalance in the equilibrium between NH₃(aq) in the surface water and gaseous NH₃ in the overlying atmosphere resulting in the drawdown of atmospheric NH₃ to the surface ocean.” Whereas the surface waters of the WEC “are a net source of 150 μmol/m²/year of NH₃ to the atmosphere at present (2009),” they say it is likely “the WEC will become a net sink of 300 μmol/m²/year for atmospheric NH₃ as atmospheric CO₂ rises to 717 ppm and the surface pH decreases to 7.83,” due to the increase in phytoplanktonic productivity driven

by the increased transfer of gaseous NH_3 from the air to the surface waters of the WEC. This phenomenon would boost the productivity of higher oceanic trophic levels, help sequester more carbon at the bottom of the sea, and thereby reduce the rate of increase in radiative forcing that is speculated to fuel global warming.

Nielsen *et al.* (2012) set out to test “whether reduced pH would affect plankton communities over an incubation period of 14 days.” They conducted their experiment “in a laboratory microcosm setup using a natural plankton community from the Derwent River estuary, Australia,” in which “two treatments with reduced pH (8.0 and 7.7) were compared to an unaltered control of pH 8.3,” and “measured parameters included community photosynthesis, nutrient uptake and biomass build-up, as well as enumeration of 25 protist taxa and quantitative HPLC of phytoplankton pigments.” They found nutrient uptake and photosynthetic parameters “were all unaffected by pH treatments 8.3–7.7,” treatments they say “match the predicted 21st century changes in CO_2 and pH.” They note “cellular carbon and total particulate organic carbon were both completely unaffected by pH treatment within this range,” and “the same was true for the succession of all 25 enumerated protist species.” They report “phytoplankton pigment analysis did not show effects of pH either,” and “the investigated plankton community was thus, in all ways, resilient to pH changes between 8.3 and 7.7,” noting once again these changes are equivalent to the changes predicted for the next century.

Nielsen *et al.* write, “others have also found no or very limited changes in phytoplankton communities in response to 21st century predicted changes in pH and CO_2 ,” citing Kim *et al.* (2006), Riebesell *et al.* (2007), and Suffrian *et al.* (2008). They also note, “many coastal plankton communities are impervious to such changes,” citing Nielson *et al.* (2010). One potential reason for this “broad level of pH-tolerance,” as they describe it, is “pH in coastal waters often fluctuates as a result of respiratory and photosynthetic processes” and “hydrographical events,” with the result “seasonal, and even diurnal, fluctuations in coastal seawater pH have been shown to encompass 7.5 to 9.6 (Macedo *et al.*, 2001; Hansen, 2002).” They conclude “it is unlikely that the investigated plankton community would be significantly affected by a pH and CO_2 change as predicted for the 21st century.”

Regarding the effects of lower ocean pH levels on the marine nitrogen cycle, Fulweiler *et al.* (2011)

write, “the current hypothesis, based on the manipulation of water column pH in laboratory studies, states decreasing pH will impact the nitrogen cycle by decreasing nitrification,” and this decrease in the microbial conversion of ammonium to nitrate would likely negatively impact both marine phytoplankton composition and production.

Fulweiler *et al.* “compiled an existing unique data set of concurrent water column nitrification rates and water column pH values from a temperate New England estuary (Narragansett Bay, Rhode Island, USA),” which had been obtained and reported previously by Berounsky (1990) and Berounsky and Nixon (1985a,b, 1990, 1993). Fulweiler *et al.* say they “found the exact opposite trend to the current hypothesis: water column nitrification rates were highest at low pH and decreased significantly as pH increased,” and “these results are in direct contradiction to some of the more recently published studies examining the impact of ocean acidification on marine nitrification (Huesemann *et al.*, 2002; Beman *et al.*, 2011).” They note their findings “are consistent with previous studies from three decades ago,” citing Anthonisen *et al.* (1976) and Focht and Verstraete (1977).

Fulweiler *et al.* emphasize their results “highlight that nitrifying organisms in coastal systems tolerate a wide range of pH values,” and “the degree of negative correlation with pH may depend on site-specific environmental conditions.” They conclude their findings indicate “the current hypothesis of the negative impacts of ocean acidification on nitrification, at least for the coastal ocean, might need reevaluation.”

Leu *et al.* (2013) write, “ocean acidification occurs as a consequence of increasing atmospheric CO_2 concentrations, and is thought to represent a major threat for some groups of marine organisms” because polyunsaturated fatty acids or PUFAs—essential metabolites that are synthesized only by algae and therefore have to be acquired via their ingestion by all other organisms—may not be as prominent in Arctic plankton in a high- CO_2 world as they are today, leading to a degradation of planktonic food quality. The five researchers studied the effect of lower ocean pH levels on a natural plankton community in the Arctic in a large-scale mesocosm experiment carried out in Kongsfjorden (Svalbard, Norway at 79°N), where nine mesocosms of $\sim 50 \text{ m}^3$ each were exposed to eight CO_2 levels (from natural background conditions to $\sim 1,420 \text{ ppm}$, yielding pH values ranging from ~ 8.3 to 7.5).

Leu *et al.* report, “no indications were found for a

generally detrimental effect of ocean acidification on the planktonic food quality in terms of essential fatty acids.” They write, “it is remarkable that the overall community response with respect to the relative amount of PUFAs to increased CO₂ concentrations was rather positive.” They conclude “findings about detrimental effects of ocean acidification on single species in laboratory studies (as, for instance, Riebesell *et al.* (2000) or Tsuzuki *et al.* (1990)), and even their consequences for grazers (Rossoll *et al.*, 2012) are probably less relevant in a natural situation where other, more CO₂-tolerant species take over.”

Leu *et al.* write, “the overall availability of essential PUFAs for higher trophic levels seems not to be affected negatively, although the specific fatty acid composition may change.” They note “the overall amount of essential PUFAs available to the entire community (or at least within a certain size class) is the important measure for the algal food quality,” which “also holds true for the implications for trophic transfer efficiency and consequences for phytoplankton-zooplankton ratios,” as discussed by Brett and Muller-Navarra (1997).

Aberle *et al.* (2013) also set out to “test whether Arctic coastal plankton communities will be in any way affected by high pCO₂/low pH and thus susceptible to ocean acidification [(OA)].” They conducted a mesocosm experiment on a natural Arctic plankton community in Kongsfjorden, Svalbard. Over a period of about one month, they deployed and moored nine polyethylene mesocosms and injected CO₂-enriched seawater into them to achieve three degrees of CO₂ equilibrium concentrations—low (175–250 ppm), intermediate (340–600 ppm), and high (675–1,085 ppm). They added nutrients to all three mesocosm treatments 13 days later “to ensure a sufficient nutrient supply for bloom development.”

Aberle *et al.* report they “found almost no direct effects of OA on microzooplankton composition and diversity,” and “both the relative shares of ciliates and heterotrophic dinoflagellates as well as the taxonomic composition of microzooplankton remained unaffected by changes in pCO₂/pH.” Aberle *et al.* conclude they must reject their hypothesis that a high CO₂ concentration would alter microzooplankton community structure, carrying capacity, or phenology, on the basis of their mesocosm experiment, noting the findings of their study point to “a relatively high robustness of microzooplankton towards elevated CO₂ in coastal waters.”

Johnson *et al.* (2013) write, “in response to low ambient CO₂ concentrations, most marine microalgae have evolved a carbon concentrating mechanism

(CCM) to elevate concentrations at the site of carbon fixation (Beardall and Giordano, 2002; Raven and Beardall, 2003; Raven *et al.*, 2011).” They note, since “increases in dissolved CO₂ are predicted to cause down-regulation of microalgal CCM capacity (Giordano *et al.*, 2005; Hopkinson *et al.*, 2011),” which should reduce the energetic costs of CCMs (Raven, 1991), this phenomenon “will potentially allow more energy for other growth processes.” They write, “as the carbon acquisition mechanisms and efficiencies of CCMs differ between algae, it is thought that rising CO₂ will benefit different species to varying degrees (Hein and Sand-Jensen, 1997; Tortell *et al.*, 2000; Rost *et al.*, 2003; Beardall and Raven, 2004; Riebesell, 2004; Fu *et al.*, 2008) and may result in dramatic community shifts with profound consequences for marine biogeochemistry (Hutchins *et al.*, 2009).”

Johnson *et al.* compared periphyton assemblages on artificial substrata installed along a coastal CO₂ gradient, ranging from a median value of 419 to 592 to 1,611 ppm, at a shallow-water cold-vent system off the island of Vulcano, NE Sicily, with the aim of testing the hypothesis that periphyton assemblages respond to CO₂ gradients and characterizing any changes in diatom and cyanobacteria populations to better understand the ecological effects of real-world lower ocean pH levels.

The six scientists report periphyton communities were indeed “altered significantly as CO₂ concentrations increased,” and “CO₂ enrichment caused significant increases in chlorophyll *a* concentrations and in diatom abundance.” Furthermore, “by using chl *a* as an index of the photosynthetic standing crop (Underwood, 1984),” they say “periphyton biomass was found to increase substantially (fivefold) at the CO₂-enriched stations,” indicating “elevations in CO₂ stimulate primary productivity in these benthic assemblages.” Johnson *et al.* conclude lower ocean pH levels are “likely to have wide-ranging consequences from local-scale influences on the structure of overlying benthic communities to effects on food web structure and larger-scale biogeochemical cycles.”

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6.3.2.2 Macroalgae

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on macroalgae. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in

the bullet points are included in the main body of the section.)

- Cultures of two red macroalgae grown in seawater treatments of + 650-ppm and +1,250-ppm CO₂ were enhanced by 20% and 60%, respectively, for *Gracilaria chilensis*, and by 130% and 190%, respectively, for *Gracilaria sp.*
- The ongoing rise in the air's CO₂ content likely will not "hasten the transformation of reef community structure from coral to algal dominance."
- "Elevated levels of CO₂ in seawater increase the growth rate of many seaweed species despite the variety of ways in which carbon is utilized in these algae."
- At twice the current ambient CO₂ concentration, daily net carbon gain and total wet biomass production rates of a red seaweed common to the Northeast Atlantic intertidal zone were 52 and 314% greater than under ambient CO₂ conditions.
- Slightly less than a doubling of the air's CO₂ concentration increased the mean relative growth rate of a brown seaweed from along the coast of Nanao Island, Shantou, China by about 50%, as well as its mean rate of nitrate uptake during the study's 12-hour light periods by some 200%, and its nitrate reductase activity by approximately 20% over a wide range of substrate nitrate concentrations.
- Elevated CO₂ experiments on eelgrass "led to significantly higher reproductive output, below-ground biomass and vegetative proliferation of new shoots in light-replete treatments."
- "Ocean acidification will stimulate seagrass biomass and productivity, leading to more favorable habitat and conditions for associated invertebrate and fish species."
- The global increase of CO₂ "may enhance seagrass survival in eutrophic coastal waters, where populations have been devastated by algal proliferation and reduced column light transparency."
- High pH values created by seagrass photosynthesis can help increase calcification rates of nearby marine organisms.

Gao *et al.* (1993) grew cultures of the red alga *Gracilaria sp.* and *G. chilensis* in vessels enriched with nitrogen and phosphorus continuously aerated with normal air of 350 ppm CO₂, air enriched with an extra 650 ppm CO₂, or air enriched with an extra 1,250 ppm CO₂ for 19 days. Compared to the control treatment, the relative growth enhancements in the +650-ppm and +1,250-ppm CO₂ treatments were 20% and 60%, respectively, for *G. chilensis*, and 130% and 190%, respectively, for *Gracilaria sp.* Gao *et al.* say these results suggest, "in their natural habitats or cultivation sites, photosynthesis and growth of *Gracilaria* species are likely to be CO₂-limited, especially when the population density is high and water movement is slow." As the air's CO₂ content continues to rise, these marine macroalgae should be able to grow increasingly well. That also may be true of many other macroalgae, for Gao *et al.* note "photosynthesis by most macroalgae is probably limited by inorganic carbon sources in natural seawater," citing Surif and Raven (1989), Maberly (1990), Gao *et al.* (1991), and Levavasseur *et al.* (1991).

This finding might be construed to imply corals in a CO₂-enriched world may be out-competed by marine macroalgae, which, to quote Langdon *et al.* (2003), "are not conspicuous on healthy reefs, but due to various anthropogenic pressures ... are becoming increasingly abundant." In an experiment they conducted at the Biosphere-2 facility near Oracle, Arizona (USA), where they studied gross primary production and calcification in a macrophyte-dominated ecosystem that had a coral cover of 3%, Langdon *et al.* found the ongoing rise in the air's CO₂ content will not "hasten the transformation of reef community structure from coral to algal dominance."

Xu *et al.* (2010) write, "*Gracilaria lemaneiformis* (Bory) Weber-van Bosse is an economically important red seaweed that is cultivated on a large scale in China due to the quantity and quality of agar in its cell walls." They note, "much attention has been paid to the biofiltration capacity of the species (Yang *et al.*, 2005, 2006; Zhou *et al.*, 2006)," and some researchers have suggested it to be "an excellent species for alleviating coastal eutrophication in China (Fei, 2004)." Xu *et al.* examined how this seaweed might respond to elevated CO₂. They grew plants from thalli collected at 0.5 m depth from a farm located in Shen'ao Bay, Nanao Island, Shantou (China) for 16 days in 3-L flasks of natural seawater maintained at either natural (0.5 µM) or high (30 µM) dissolved inorganic phosphorus (Pi) concentrations in contact with air of either 370 or 720 ppm CO₂,

measuring their photosynthetic rates, biomass production, and uptake of nitrate and phosphate.

As best as can be determined from Xu *et al.*'s graphical representations of their results, the 95% increase in the air's CO₂ concentration increased algal photosynthetic rates by only 5% in the natural Pi treatment but approximately 41% in the high Pi treatment. With respect to biomass production, the elevated CO₂ elicited a 48% increase in the natural Pi treatment but no increase in biomass in the high Pi treatment. The extra 29.5 µM Pi in the high Pi treatment itself had boosted biomass production of the low-CO₂ natural-Pi treatment by approximately 83%, and additional CO₂ did not increase growth rates beyond that point.

The three Chinese researchers write, "elevated levels of CO₂ in seawater increase the growth rate of many seaweed species despite the variety of ways in which carbon is utilized in these algae." They note "some species, such as *Porphyra yezoensis* Ueda (Gao *et al.*, 1991) and *Hizikia fusiforme* (Harv.) Okamura (Zou, 2005) are capable of using HCO₃⁻, but are limited by the current ambient carbon concentration in seawater," and "enrichment of CO₂ relieves this limitation and enhances growth." Regarding the results they obtained with *Gracilaria lemaneiformis*—which they say "efficiently uses HCO₃⁻ and whose photosynthesis is saturated at the current inorganic carbon concentration of natural seawater (Zou *et al.*, 2004)"—they write, "the enhancement of growth could be due to the increased nitrogen uptake rates at elevated CO₂ levels," which in their experiment were 40% in the natural Pi treatment, because "high CO₂ may enhance the activity of nitrate reductase (Mercado *et al.*, 1999; Gordillo *et al.*, 2001; Zou, 2005) and stimulate the accumulation of nitrogen, which could contribute to growth."

Kubler *et al.* (1999) grew a red seaweed common to the Northeast Atlantic intertidal zone, *Lomentaria articulata*, for three weeks in hydroponic cultures subjected to various atmospheric CO₂ and O₂ concentrations to determine the effects of these gases on growth. They report oxygen concentrations ranging between 10 and 200% of ambient had no significant effects on daily net carbon gain or total wet biomass production rates in this seaweed. In contrast, CO₂ concentrations ranging between 67 and 500% of ambient had highly significant effects. At twice the current ambient CO₂ concentration, for example, daily net carbon gain and total wet biomass production rates were 52 and 314% greater than under ambient CO₂ conditions. Although this seaweed was likely

carbon-saturated, when grown at five times the ambient CO₂ concentration it still exhibited daily net carbon gain and wet biomass production rates 23 and 50%, respectively, greater than those of control plants.

Zou (2005) collected specimens of a brown seaweed (*Hizikia fusiforme* (Harv.) Okamura) from intertidal rocks along the coast of Nanao Island, Shantou, China, and maintained them in glass aquariums in filtered natural seawater enriched with 60 µM NaNO₃ and 6.0 µM NaH₂PO₄, where they were continuously aerated with ambient air of 360 ppm CO₂ or enriched air of 700 ppm CO₂. He measured the specimens' relative growth and nitrogen assimilation rates and their nitrate reductase activities. The CO₂ enrichment increased the seaweed's mean relative growth rate by about 50%, its mean rate of nitrate uptake during the study's 12-hour light periods by 200%, and its nitrate reductase activity by approximately 20% over a wide range of substrate nitrate concentrations.

Zou notes "the extract of *H. fusiforme* has an immunomodulating activity on humans and this ability might be used for clinical application to treat several diseases such as tumors (Suetsuna, 1998; Shan *et al.*, 1999)." He also reports the alga "has been used as a food delicacy and an herbal ingredient in China, Japan and Korea." He says it "is now becoming one of the most important species for seaweed mariculture in China, owing to its high commercial value and increasing market demand." In addition, Zou notes "the intensive cultivation of *H. fusiforme* would remove nutrients more efficiently with the future elevation of CO₂ levels in seawater, which could be a possible solution to the problem of ongoing coastal eutrophication."

Palacios and Zimmerman (2007) conducted an experiment on eelgrass (*Zostera marina*) at the Duke Energy-North America Power Plant at Moss Landing, California (USA), where flue gas generated by the power plant furnace was piped approximately 1 km to a site where it was bubbled through outdoor flow-through seawater aquaria at rates that produced four aqueous CO₂ treatments characteristic of: "(1) the present day atmosphere, with approximately 16 µM CO₂(aq), (2) CO₂ projected for 2100 that increases the CO₂(aq) concentration of seawater to approximately 36 µM CO₂(aq), (3) CO₂ projected for 2200 that increases the CO₂(aq) concentration of seawater to 85 µM CO₂(aq), and (4) a dissolved aqueous CO₂ concentration of 1123 µM CO₂(aq), which triples the light-saturated photosynthesis rate of eelgrass (Zimmerman *et al.*, 1997)."

The researchers found elevated CO₂ “led to significantly higher reproductive output, below-ground biomass and vegetative proliferation of new shoots in light-replete treatments,” those receiving light at 33% of the surface irradiance level. They write, “shoots growing at 36 μM CO₂(aq) were 25% larger than those in the unenriched treatment [16 μM CO₂(aq)],” and “at 85 μM CO₂(aq) shoots were 50% larger than those in the unenriched treatment and at 1123 μM CO₂(aq) shoots were almost twice as large as those in the unenriched treatment.” They found at 1123 μM CO₂(aq) “22% of the shoots differentiated into flowers, more than twice the flowering output of the other treatments at this light level.”

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 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 “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.”

According to Suarez-Alvarez *et al.* (2012), “the increase of coastal activities which produce important amounts of wastes, including inorganic nutrients (Troell *et al.*, 2003), makes micro- and macroalgae interesting organisms to predict possible impacts, responses, and remediation processes by considering biomass production through cultivation techniques,”

citing Gao *et al.* (1991, 1993), Gao and McKinley (1994), Keffer and Kleinheinz (2002), Doucha *et al.* (2005), and Israel *et al.* (2005). They note, “macroalgae, in particular, have been the object of additional interest for CO₂ remediation (Gao and McKinley, 1994) because of their solar energy conversion capacity, high productivity values (higher than most productive terrestrial crops) and the possibility of being, in many cases, intensively cultivated.”

Suarez-Alvarez *et al.* cultivated 8-gram fragments of the macroalga *Hypnea spinella* in 1-L flasks containing filtered seawater enriched with 140 μM NH₄Cl and 14 μM KH₂PO₄ for seven days of acclimation. They then culled the plants to their initial density and grew them for nine more days at ambient (360 ppm), 750, or 1,600 ppm atmospheric CO₂, measuring various plant physiological properties and processes. The authors report light-saturated net photosynthesis rates in the 750 ppm and 1,600 ppm CO₂ treatments were 41.5% and 50.5% greater, respectively, than in the 360 ppm treatment. Relative growth enhancements were 85.6% and 63.2% greater, respectively, and maximum ammonium uptake rates were enhanced by 24.2% and 19.9%, respectively. “From a practical point of view,” Suarez-Alvarez *et al.* write, “these results suggest that intensive culture of *H. spinella* operated in biofilters might be enhanced by CO₂ supply to generate higher biomass productivities and better nitrogen biofiltration efficiencies,” and “the use of flue gases for this purpose would also improve the ability of bioremediation of these biofilters, as has already been tested for *Gracilaria cornea*,” citing Israel *et al.* (2005).

Jiang *et al.* (2010) note “seagrasses are flowering plants that thrive in shallow oceanic and estuarine waters around the world, and are ranked as one of the most ecologically and economically valuable biological systems on Earth,” citing Beer *et al.* (2006). They also observe *Thalassia hemprichii* “is among the most widely-distributed seagrass species in an Indo-Pacific flora, dominating in many mixed meadows,” citing Short *et al.* (2007). They collected intact vegetative plants of *T. hemprichii* from Xincun Bay of Hainan Island, Southern China, which they transported to the laboratory and cultured in flow-through seawater aquaria bubbled with four concentrations of CO₂ representative of the present global ocean, with a pH of 8.10; the projected ocean for 2100, with a pH of 7.75; the projected ocean for 2200, with a pH of 7.50; and the ocean characteristic of “an extreme beyond the current predictions” (a 100-fold

increase in free CO₂, with a pH of 6.2).

The three researchers found the “leaf growth rate of CO₂-enriched plants was significantly higher than that in the unenriched treatment,” “nonstructural carbohydrates (NSC) of *T. hemprichii*, especially in belowground tissues, increased strongly with elevated CO₂,” and “belowground tissues showed a similar response with NSC.” The Chinese scientists list several implications of their finding that “CO₂ enrichment enhances photosynthetic rate, growth rate and NSC concentrations of *T. hemprichii*.” With higher atmospheric CO₂ concentrations, they write, “colonization beyond current seagrass depth limits is possible,” the extra stored NSC “can be used to meet the carbon demands of plants during periods of low photosynthetic carbon fixation caused by severe environmental disturbance such as underwater light reduction,” it can enhance “rhizome growth, flowering shoot production and vegetative proliferation,” and it “may buffer the negative effects of transplant shock by increasing rhizome reserve capacity.” They also write, “the globally increasing CO₂ may enhance seagrass survival in eutrophic coastal waters, where populations have been devastated by algal proliferation and reduced column light transparency.” They conclude “ocean acidification will stimulate seagrass biomass and productivity, leading to more favorable habitat and conditions for associated invertebrate and fish species.”

Wu *et al.* (2008) listed several known effects of a CO₂-enriched atmosphere on micro- and macro-algae living in the world’s oceans. According to the authors, “enriched CO₂ up to several times the present atmospheric level has been shown to enhance photosynthesis and growth of both phytoplanktonic and macro-species that have less capacity of CCMs [CO₂-concentrating mechanisms],” and “even for species that operate active CCMs and those whose photosynthesis is not limited by CO₂ in seawater, increased CO₂ levels can down-regulate their CCMs and therefore enhance their growth under light-limiting conditions,” because “at higher CO₂ levels, less light energy is required to drive CCM.” They report enhanced CO₂ levels have been found to enhance the activity of nitrogen reductase in several marine plants, and this phenomenon “would support enhanced growth rate by providing adequate nitrogen required for the metabolism under the high CO₂ level.” They write, “altered physiological performances under high-CO₂ conditions may cause genetic alteration in view of adaptation over long time scales,” and “marine algae may adapt to a high CO₂ oceanic environment so that evolved communities in

[the] future are likely to be genetically different from contemporary communities.”

Semesi *et al.* (2009) investigated whether diel variations in seawater pH caused by the photosynthetic activity of seagrass meadows within Chwaka Bay (Zanzibar, Tanzania) could affect the calcification and photosynthesis rates of calcareous red algae (*Hydrolithon* sp. and *Mesophyllum* sp.) and green algae (*Halimeda renschii*) growing within the marine meadows. They measured rates of calcification and relative photosynthetic electron transport (rETR) of the algae *in situ* in open-bottom incubation cylinders either in the natural presence of the rooted seagrasses or after their leaves had been removed.

Semesi *et al.* report “seagrass photosynthesis increased the seawater pH within the cylinders from 8.3–8.4 to 8.6–8.9 after 2.5 hours (largely in conformity with that of the surrounding seawater), which, in turn, enhanced the rates of calcification 5.8-fold for *Hydrolithon* sp. and 1.6-fold for the other 2 species.” They also found “the rETRs of all algae largely followed the irradiance throughout the day and were (in *Mesophyllum* sp.) significantly higher in the presence of seagrasses.” The three researchers conclude “algal calcification within seagrass meadows such as those of Chwaka Bay is considerably enhanced by the photosynthetic activity of the seagrasses, which in turn increases the seawater pH.”

They state the high pH values created by seagrass photosynthesis are what caused the elevated calcification rates of the macroalgae, and this observation has further implications. It suggests, for example, the lowering of seawater pH caused by higher atmospheric CO₂ concentrations—which results in a lowering of the calcium carbonate saturation state of seawater, and which has been predicted to lead to reductions in coral calcification rates—may be counteracted by CO₂-induced increases in the photosynthetic activity of the symbiotic zooxanthellae of Earth’s corals, which may boost the pH of seawater in intimate contact with the coral host, allowing the host to *increase* its calcification rate in CO₂-enriched seawater, or at least not suffer a major reduction in calcification.

Smith *et al.* (2013) provide additional support for this thesis. They state, “benthic marine primary producers affect the chemistry of their surrounding environment through metabolic processes.” They note, “photosynthesis and respiration will elevate or depress the concentration of oxygen in the diffusive boundary layer,” and “acid-base regulation and

biomineralization/dissolution for calcifying species can alter the relative concentration of inorganic carbon species and thus pH.”

To compare species-specific rates of change in pH and oxygen concentrations over a diel cycle for several species of common benthic coral reef organisms—including corals, turf algae, and fleshy and calcifying macroalgae—Smith *et al.* assessed the generality of results across divergent types of reefs in the Caribbean and Pacific. They found “more productive fleshy taxa have the potential to raise both oxygen and pH during the day to a greater extent than calcified species.” This discovery, as well as similar observations reported by Anthony *et al.* (2011) and Kleypas *et al.* (2011), suggest “non-calcifying primary producers, especially those driving large amplitudes in diurnal pH fluctuations, may be important ‘buffer organisms’ against potential ocean acidification on coral reefs.” They write, “while particular species of macroalgae can negatively affect corals in a variety of ways,” some fleshy algae “may provide a buffering capacity to future ocean acidification scenarios.”

Johnson *et al.* (2012) note, “CO₂ gradients in natural settings, where whole ecosystems have been exposed to elevated levels of CO₂, allow us to investigate changes in the interactions, competition, predation and/or herbivory that involve long-lived metazoan species in benthic marine ecosystems.” They observe, “volcanic CO₂ gradients are beginning to reveal the ecological shifts that can be expected to occur with globally increasing atmospheric CO₂ in both temperate (Hall-Spencer *et al.*, 2008) and tropical ecosystems (Fabricius *et al.*, 2011).” Johnson *et al.* assessed the abundance of herbivores (sea urchins) and the response of brown macroalgae (*Padina* spp.) to increasing levels of CO₂ in two natural settings. One of the sites was a set of shallow, volcanic CO₂ seeps on the island of Vulcano, NE Sicily, where *P. pavonica* was studied. The other site, where they studied *P. australis*, was a comparable set of seeps in the D’Entrecasteaux Island group, Papua New Guinea.

The five scientists found “a reduction in sea urchin abundances alongside a proliferation of *Padina* spp., as CO₂ levels increased” along both temperate and tropical rocky shores. The predator sea urchins were absent from locations that had the highest CO₂ levels (lowest pH), while “even in the lowest pH conditions, *P. pavonica* and *P. australis* were still able to calcify, seemingly from the enhancement of photosynthesis under high levels of CO₂.”

Johnson *et al.* suggest the absence of sea urchins

in the CO₂-enriched areas “may be one explanation for the proliferation of *Padina* spp., as it becomes released from the top-down control by these keystone grazers,” noting “this effect of sea urchin removal has been observed in other *Padina* sp. populations (Sammarco *et al.*, 1974) and across other Phaeophyte assemblages (Leinaas and Christie, 1996; Ling *et al.*, 2010).” They note “increased photosynthetic activity at high CO₂ has also been observed in other calcified macroalgae (Reiskind *et al.*, 1988; Semesi *et al.*, 2009),” and in “non-calcified macroalgae (Kubler *et al.*, 1999; Connell and Russell, 2010; Russell *et al.*, 2011).”

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Climate Change Reconsidered II: Biological Impacts

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6.3.3 Effects on Marine Animals

6.3.3.1 Bivalves

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on marine bivalves. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Juvenile king scallops display a tolerance to lower ocean pH levels at *p*CO₂ levels below 1,600 ppm.
- Mussel larvae (*Mytilus edulis*) reared in a laboratory setting mimicking a cold-water environment revealed “no marked effect on fertilization success, development time, or abnormality to the D-shell stage, or on feeding of mussel larvae” from lower ocean pH levels, and under such conditions (pH 7.6) the larvae “were still able to develop a shell in seawater undersaturated with respect to aragonite.”
- A laboratory experiment examining “the combined effects of elevated *p*CO₂ and food availability on juvenile *M. edulis* growth and calcification” showed “only minor impacts of *p*CO₂ up to 3350 μ atm.”
- At a naturally CO₂-enriched ocean site, growth and calcification rates of *M. edulis* were “seven times higher” at an “inner fjord field station (mean *p*CO₂ ca. 1000 μ atm) in comparison to a low *p*CO₂ outer fjord station (ca. 600 μ atm),” demonstrating “a high inherent resilience of calcifying benthic communities in an estuarine, eutrophic habitat to elevated seawater *p*CO₂,” where “food supply, and not *p*CO₂, appears to be the primary factor driving biomass and biogenic CaCO₃ production, as well as community structure.”
- “Selective breeding may be a solution to ‘climate-proof’ [the Sydney rock oyster] from the impacts of ocean acidification.”

- Larvae spawned from adult Sydney rock oysters (*Saccostrea glomerata*) growing in elevated CO₂ (reduced pH) seawater “were larger and developed faster” than those spawned from adults growing under ambient conditions, suggesting “previous studies that have investigated the effects of elevated CO₂ on the larvae of molluscs and other marine organisms [whose predecessors had not been exposed to elevated CO₂] may overestimate the severity of their responses” to lower ocean pH levels.
- Sperm swimming speeds and fertilization success of the Pacific oyster (*Crassostrea gigas*) are slightly increased under lower ocean pH levels.
- Effects of lower ocean pH levels on *Crassostrea gigas* larvae “during the first three days of development are not significant as long as CO₃²⁻ concentrations remain above aragonite saturated conditions.”
- The “pre-adapted ability to resist a wide range of decreased pH may provide *C. gigas* with the necessary tolerance to withstand rapid pH changes over the coming century.”
- The discovery of four-decades-old mussels living “in natural conditions of pH values between 5.36 and 7.29” attest to “the extent to which long-term adaptation can develop tolerance to extreme conditions.”

Sanders *et al.* (2013) “investigated the effects on oxygen consumption, clearance rates and cellular turnover in juvenile [king scallop] *Pecten maximus* following three months’ laboratory exposure to four pCO₂ treatments (290, 380, 750, and 1140 ppm).” The four researchers state “none of the exposure levels were found to have significant effects on the clearance rates, respiration rates, condition index or cellular turnover (RNA:DNA) of individuals.” These findings are compatible with those of Anderson *et al.* (2013), who also studied the growth, development, and survival of the initial larval stages of *P. maximus* and found them to be susceptible to the deleterious effects of lower ocean pH levels only at pCO₂ levels of 1,600 ppm and above. Sanders *et al.* conclude their results suggest “where food is in abundance, bivalves like juvenile *P. maximus* may display a tolerance to limited changes in seawater chemistry.”

Berge *et al.* (2006) collected blue mussels (*Mytilus edulis* L.) from the outer part of the

Oslofjord outside the Marine Research Station Solbergstrand in Norway and placed them in five 5-L aquariums continuously supplied with low-food-supply seawater extracted from the top meter of the Oslofjord outside the Marine Research Station Solbergstrand in Norway, continuously adding CO₂ to the waters of the aquaria so as to maintain them at five pH values (means of 8.1, 7.6, 7.4, 7.1, and 6.7) for 44 days. Shell lengths at either the time of death or at the end of the study were determined and compared to lengths measured at the start of the study.

According to the authors, “the increased concentration of CO₂ in the water and the correspondingly reduced pH had no acute effects on the mussels.” The Norwegian researchers report, “mean increments of shell length were much lower for the two largest CO₂ additions compared to the values in the controls, while for the two smallest doses the growth [was] about the same as in the control, or in one case even higher,” such that there were “no significant differences between the three aquaria within the pH range 7.4–8.1.”

Berge *et al.* conclude their results “indicate that future reductions in pH caused by increased concentrations of anthropogenic CO₂ in the sea may have an impact on blue mussels,” but “comparison of estimates of future pH reduction in the sea (Caldeira and Wickett, 2003) and the observed threshold for negative effects on growth of blue mussels [which they determined to lie somewhere between a pH of 7.4 and 7.1] do however indicate that this will probably not happen in this century.” Caldeira and Wickett’s calculation of the maximum level to which the air’s CO₂ concentration might rise yields a value that approaches 2,000 ppm around the year 2300, representing a surface oceanic pH reduction of 0.7 units, which drops the pH only to 7.4, the upper limit of the “threshold for negative effects on growth of blue mussels” found by Berge *et al.*

Noting “there is a particular need to study effects of OA [lower ocean pH levels] on organisms living in cold-water environments due to the higher solubility of CO₂ at lower temperatures,” Bechmann *et al.* (2011) maintained mussel (*Mytilus edulis*) larvae in a laboratory setting under the OA scenario predicted for the year 2100 (pH 7.6) and compared them against batches of larvae held under the current oceanic pH of 8.1 (the control treatment), keeping water temperature at a constant 10°C. They found “no marked effect on fertilization success, development time, or abnormality to the D-shell stage, or on feeding of mussel larvae in the low-pH treatment,”

and the *M. edulis* larvae “were still able to develop a shell in seawater under-saturated with respect to aragonite (a mineral form of CaCO_3).” They also found after two months of exposure the mussels were 28% smaller in the pH 7.6 treatment than in the control treatment. They write, “if only the larger larvae settle and survive in the field, the effects of OA on the mussel population may not be dramatic.”

Thomsen *et al.* (2010) note, “as most laboratory experiments cannot account for species genetic adaptation potential, they are limited in their predictive power.” Thus studies investigating “naturally CO_2 -enriched habitats” have “recently gained attention, as they could more accurately serve as analogues for future, more acidic ecosystems.” Thomsen *et al.* studied the macrobenthic community in Kiel Fjord, a naturally CO_2 -enriched site in the Western Baltic Sea dominated by calcifying marine invertebrates. They determined in 34%, 23%, and 9% of the 42 weeks they were there, the partial pressure (p) of CO_2 in the water exceeded preindustrial $p\text{CO}_2$ (280 ppm) by a factor of three (>840 ppm), four ($>1,120$ ppm), and five ($>1,400$ ppm), respectively.

The German scientists report juvenile blue mussel (*Mytilus edulis*) recruitment “peaks during the summer months, when high water $p\text{CO}_2$ values of ~ 1000 ppm prevail.” Their short-term laboratory research indicates “blue mussels from Kiel Fjord can maintain control rates of somatic and shell growth at a $p\text{CO}_2$ of 1400 ppm.” At 4,000 ppm $p\text{CO}_2$, however, both shell mass and extension rates were significantly reduced; but “regardless of the decreased rates of shell growth at higher [1,400] $p\text{CO}_2$, all mussels increased their shell mass at least by 150% during the 8-week trial, even at Ω_{arg} (Ω_{calc}) as low as 0.17 (0.28),” where Ω is the calcium carbonate saturation state of either aragonite (arg) or calcite (calc).

Thomsen *et al.* conclude it is likely “long-term acclimation to elevated $p\text{CO}_2$ increases the ability to calcify in *Mytilus* spp.,” citing Michaelidis *et al.* (2005) and Ries *et al.* (2009) in addition to their own study. They say they could find “no causal relationship between the acid-base status and metabolic depression in this species at levels of ocean acidification that can be expected in the next few hundred years (IPCC, 2007),” after discovering in the waters of Kiel Fjord (and demonstrating in the laboratory) “communities dominated by calcifying invertebrates can thrive in CO_2 -enriched coastal areas.”

Working at the same location three years later with a different set of coauthors in a similarly coupled laboratory and field study, Thomsen *et al.* (2013)

examined “the annual $p\text{CO}_2$ variability in [the Kiel Fjord] habitat and the combined effects of elevated $p\text{CO}_2$ and food availability on juvenile *M. edulis* growth and calcification.” In the laboratory experiment, “mussel growth and calcification were found to chiefly depend on food supply, with only minor impacts of $p\text{CO}_2$ up to 3,350 μatm .” In the field location (Kiel Fjord), where maximum $p\text{CO}_2$ values experienced during the summer were about 2,500 μatm at the surface of the fjord and more than 3,000 μatm at its bottom, they observed “seven times higher growth and calcification rates of *M. edulis* at a high $p\text{CO}_2$ inner fjord field station (mean $p\text{CO}_2$ ca. 1,000 μatm) in comparison to a low $p\text{CO}_2$ outer fjord station (ca. 600 μatm).” They note this high inner fjord productivity “was enabled by higher particulate organic carbon concentrations,” as a result of the fjord’s “being ‘highly impacted by eutrophication, which causes bottom water hypoxia and consequently high seawater $p\text{CO}_2$.’” Thomsen *et al.* conclude their study demonstrates “a high inherent resilience of calcifying benthic communities in an estuarine, eutrophic habitat to elevated seawater $p\text{CO}_2$,” where “food supply, and not $p\text{CO}_2$, appears to be the primary factor driving biomass and biogenic CaCO_3 production, as well as community structure.”

Range *et al.* (2011) conducted a 75-day controlled CO_2 perturbation experiment designed to test the effects of increased $p\text{CO}_2$ and reduced pH of seawater on the calcification, growth, and mortality of juvenile *Ruditapes decussatus* clams. They manipulated the carbonate chemistry of seawater by diffusing pure CO_2 into natural seawater to attain two reduced pH levels (by -0.4 and -0.7 pH unit compared to unmanipulated seawater). The authors hypothesized the juvenile clams would exhibit reduced net calcification, reduced growth of the shell and soft tissue, and increased mortality in the lower-pH conditions. At the conclusion of their experiment, however, the eight researchers found “no differences among pH treatments in terms of net calcification, size or weight of the clams,” disproving the first two of their three hypotheses. Their third hypothesis also proved to be wrong—doubly wrong, in fact—for not only was juvenile clam mortality not increased in the low-pH seawater, mortality was significantly reduced in the acidified treatments, which they describe as an “unexpected result.”

The Portuguese scientists conclude by noting life is intriguingly complex and “the generalized and intuitively attractive perception that calcification will be the critical process impacted by ocean acidification is being increasingly challenged,” citing Widdicombe

and Spicer (2008) and Findlay *et al.* (2009).

To provide a better understanding of the potential for the Sydney rock oyster (*Saccostrea glomerata*) to adapt to the threat of lower ocean pH levels, Parker *et al.* (2011) measured the within- and between-population variability in the species' growth response to elevated $p\text{CO}_2$, working with oysters (denoted as *wild*) they collected from intertidal and shallow subtidal habitats along the southeast coast of Australia, as well as two lines (QB and LKB) of the same species that had been selectively bred to support the country's oyster aquaculture industry. The authors report the wild oysters experienced a 64% reduction in growth after four days in an elevated $p\text{CO}_2$ environment of 1,000 ppm (with a water pH of 7.84) compared to wild oysters reared in the ambient $p\text{CO}_2$ environment of 375 ppm (with a water pH of 8.20). The growth reduction experienced by QB oysters growing in the same two environments was 45%, and that experienced by LKB oysters was 25%. They report the LKB oysters reared at elevated $p\text{CO}_2$ "grew slightly better than the wild oysters reared at ambient $p\text{CO}_2$." Such observations, Parker *et al.* write, provide "preliminary evidence that selective breeding may be a solution to 'climate-proof' important aquaculture industries from the impacts of ocean acidification."

Parker *et al.* (2012) introduce their follow-up study by noting analyses of the impact of lower ocean pH levels on marine organisms conducted to date "have only considered the impacts on 'adults' or 'larvae,' ignoring the potential link between the two life-history stages and the possible carry-over effects that may be passed from adult to offspring," citing Dupont *et al.* (2010), Hendriks *et al.* (2010), and Kroeker *et al.* (2010). Parker *et al.* placed adults of wild-collected and selectively bred populations of the Sydney rock oyster (*Saccostrea glomerata*), obtained at the beginning of reproductive conditioning, in seawater equilibrated with air of either 380 ppm CO_2 or 856 ppm CO_2 which produced seawater pH values of 8.2 and 7.9, respectively, after which they measured the development, growth, and survival responses of the two sets of larvae.

The six scientists found "larvae spawned from adults exposed to elevated PCO_2 were larger and developed faster." In addition, "selectively bred larvae of *S. glomerata* were more resilient to elevated CO_2 than wild larvae," as "measurement of the standard metabolic rate (SMR) of adult *S. glomerata* showed that at ambient CO_2 , SMR is increased in selectively bred compared with wild oysters," and it is further increased "during exposure to elevated CO_2 ." These findings suggest "previous studies that have

investigated the effects of elevated CO_2 on the larvae of molluscs and other marine organisms [whose predecessors had not been exposed to elevated CO_2] may overestimate the severity of their responses." They conclude "marine organisms may have the capacity to acclimate or adapt to elevated CO_2 over the next century."

Miller *et al.* (2009) grew larvae of two oyster species—the Eastern oyster (*Crassostrea virginica*) and the Suminoe oyster (*Crassostrea ariakensis*)—for up to 28 days in estuarine water in equilibrium with air of four CO_2 concentrations (280, 380, 560, and 800 ppm) chosen to represent atmospheric conditions in the preindustrial era, the present day, and the years 2050 and 2100, respectively, as projected by the IS92a business-as-usual scenario of IPCC. They maintained these levels by periodically aerating the aquaria with air containing 1% CO_2 , assessing larval growth via image analysis and determining calcification by means of chemical analyses of calcium in the shells of the oyster larvae.

When the larvae of both species were cultured continuously from 96 hours post fertilization for 26 to 28 days while exposed to elevated CO_2 concentrations, they "appeared to grow, calcify and develop normally with no obvious morphological deformities, despite conditions of significant aragonite undersaturation." The scientists state these findings "run counter to expectations that aragonite shelled larvae should be especially prone to dissolution at high $p\text{CO}_2$." They note, "both oyster species generated larval shells that were of similar mean thickness, regardless of $p\text{CO}_2$, Ω_{arag} [aragonite compensation point] or shell area," remarking they "interpret the pattern of similar shell thickness as further evidence of normal larval shell development."

Working with another oyster species (*Crassostrea gigas*), Havenhand and Schlegel (2009) observed and measured sperm swimming behavior and fertilization kinetics in response to lower ocean pH levels. The oysters, collected from a mixed mussel/oyster bed on the coast of western Sweden, were kept in flow-through tanks of filtered sea water the scientists maintained at either the normal ambient pH level or a level reduced by about 0.35 units they created by bubbling CO_2 through the water. In water of pH 8.15, mean sperm swimming speeds were $92.1 \pm 4.8 \mu\text{m/s}$, whereas in water of pH 7.8 they were slightly higher, at $94.3 \pm 5.5 \mu\text{m/s}$, although the difference was not statistically significant. Mean fertilization success in water of pH 8.15 was 63.4%, whereas in water of pH 7.8 it was also slightly higher, at 64.1%; this difference, too, was not statistically significant.

The Swedish scientists state “the absence of significant overall effects of pH on sperm swimming behavior and fertilization success is remarkable,” emphasizing power analyses they conducted “showed clearly that these results were not due to inadequate statistical power,” and “the absence of significant effect is likely a true reflection of the responses of *Crassostrea gigas* gametes and zygotes from the Swedish west coast to levels of CO₂-induced acidification expected by the end of this century.”

Gazeau *et al.* (2011) assessed “the impact of several carbonate-system perturbations on the growth of Pacific oyster (*Crassostrea gigas*) larvae during the first three days of development (until shelled D-veliger larvae).” They used filtered seawater obtained from the Oosterschelde (a nearby tidal inlet) with five chemistries obtained “by separately manipulating pH, total alkalinity and aragonite saturation state.” The seven scientists report “developmental success and growth rates were not directly affected by changes in pH or aragonite saturation state but were highly correlated with the availability of carbonate ions ... as long as carbonate ion concentrations were above aragonite saturation levels.” When carbonate ion concentrations dropped below aragonite saturation levels, they found growth and development “strongly decreased.”

Gazeau *et al.* conclude, “the effects of ocean acidification on larvae of *Crassostrea gigas* from the Oosterschelde estuary during the first three days of development are not significant as long as CO₃²⁻ concentrations remain above aragonite saturated conditions.” They add, “due to relatively high levels of total alkalinity in this area, it is not expected that seawater will become corrosive for aragonite following a decrease of 0.3 to 0.4 pH unit.”

The French, English, and Dutch researchers also write, “most calcifying species, including mollusks, are able to concentrate Ca²⁺ and CO₃²⁻ ions at the site of calcification (McConnaughey and Gillikin, 2008),” and the bivalves they studied “should therefore be able to regulate calcification rates under suboptimal concentrations of Ca²⁺ and CO₃²⁻.” They note, “Thomsen *et al.* (2010) have shown that blue mussels are actively growing in a bay of the Western Baltic Sea naturally enriched with high CO₂ water,” and “juvenile recruitment occurs in summer time coinciding with low pH levels and aragonite undersaturated conditions.” Thus the evidence indicates lower ocean pH levels will not seriously affect mollusks.

Ginger *et al.* (2013) note, “our knowledge of the effect of reduced pH on *C. gigas* larvae presently

relies presumptively on four short-term (< 4 days) survival and growth studies.” They studied “the effects of long-term (40 days) exposure to pH 8.1, 7.7 and 7.4 on larval shell growth, metamorphosis, respiration and filtration rates at the time of metamorphosis,” as well as the juvenile shell growth and structure of *C. gigas*. The seven scientists discovered “mean survival and growth rates were not affected by pH”; “the metabolic, feeding and metamorphosis rates of pediveliger larvae were similar, between pH 8.1 and 7.7”; “the pediveligers at pH 7.4 showed reduced weight-specific metabolic and filtration rates, yet were able to sustain a more rapid post-settlement growth rate”; and “no evidence suggested that low pH treatments resulted in alterations to the shell ultra-structures or elemental compositions (i.e., Mg/Ca and Sr/Ca ratios).” Ginger *et al.* conclude “larval and post-larval forms of the *C. gigas* in the Yellow Sea are probably resistant to elevated CO₂ and decreased near-future pH scenarios.” They note “the pre-adapted ability to resist a wide range of decreased pH may provide *C. gigas* with the necessary tolerance to withstand rapid pH changes over the coming century.”

Working with juvenile *Mytilus galloprovincialis* specimens obtained from a mussel raft in the Ria de Ares-Betanzos of Northwest Spain and reared in an experimental bivalve hatchery in Tavira, Portugal, Fernandez-Reiriz *et al.* (2012) tested the effects of three levels of seawater acidification caused by increasing concentrations of atmospheric CO₂: a natural control level plus two lesser levels of pH, one reduced by 0.3 pH unit and another reduced by 0.6 pH unit. They measured several responses of the mussels after 78 days of exposure to the three sets of pH conditions, focusing on clearance and ingestion rate, absorption efficiency, oxygen consumption, ammonia excretion, oxygen to nitrogen ratio, and scope for growth. The five researchers found no significant differences for clearance, ingestion, and respiration rates. The absorption efficiency and ammonium excretion rate of the juvenile mussels were inversely related to the 0.6 pH reduction, while the maximal scope for growth and tissue dry weight also were observed in the mussels exposed to the pH reduction of 0.6 unit. Fernandez-Reiriz *et al.* conclude their results suggest *M. galloprovincialis* “could be a tolerant ecophysiotype to CO₂ acidification, at least in highly alkaline coastal waters,” noting, “mytilids are also able to dominate habitats with low alkalinity and high pCO₂,” citing Thomsen *et al.* (2010).

Working with the same species of mussels obtained from the same location off the coast of

Northwest Spain under an identical pH regime, Range *et al.* (2012) tested the effects of seawater acidification on growth, calcification, and mortality of six-month-old juveniles. The eight researchers found the growth of the mussels, measured as relative increases in shell size and body weight during the 84 days of the experiment, “did not differ among treatments.” A tendency for faster shell growth under elevated CO₂ was apparent, “at least during the first 60 days of exposure.” They note calcification was reduced under elevated CO₂, but by only up to 9%. They state, “given that growth was unaffected, the mussels clearly maintained the ability to lay down CaCO₃, which suggests post-deposition dissolution as the main cause for the observed loss of shell mass.” They also write, “mortality of the juvenile mussels during the 84 days was small (less than 10%) and was unaffected by the experimental treatments.” The Portuguese scientists conclude “there is no evidence of CO₂-related mortalities of juvenile or adult bivalves in natural habitats, even under conditions that far exceed the worst-case scenarios for future ocean acidification (Tunnicliffe *et al.*, 2009).”

Tunnicliffe *et al.* (2009) studied *Bathymodiolus brevior*, “a vent-obligate species that relies partly on symbiotic sulphide-oxidizing bacteria for nutrition (von Cosel and Metivier, 1994)” and is found “at many sites in the western Pacific Ocean, where it occupies habitats of low hydrothermal fluid flux.” Using remotely operated vehicles to collect mussel specimens, water samples, and imagery, Tunnicliffe *et al.* examined dense clusters of the vent mussel “in natural conditions of pH values between 5.36 and 7.29 on the northwest Eifuku volcano, Mariana arc, where liquid carbon dioxide and hydrogen sulfide emerge in a hydrothermal setting.” They studied the vent mussels clusters along with mussels from “two sites in the southwestern Pacific: Hine Hina in the Lau backarc basin and Monowai volcano on the Kermadec arc,” where “the same mussel species nestles in cracks and rubble where weak fluid flow emerges.”

Based on the pH values they observed, the authors calculated saturation ratios for calcite (Ω_{calc}) ranging from 0.01 to 0.61, with an average value of only 0.18. They discovered “a dense mussel population, along with many other associated species (Limen and Juniper, 2006), on NW Eifuku, where chemosynthetic symbiosis provides an energetic benefit to living in a corrosive, low-pH environment.” Tunnicliffe *et al.* say these findings attest to “the extent to which long-term adaptation can develop tolerance to extreme conditions.” They report

discovering four-decades-old mussels living at the sites they visited, stating “the mussels’ ability to precipitate shells in such low-pH conditions is remarkable.”

In another study using extreme environmental conditions, Hammer *et al.* (2011) exposed specimens of the deep-sea bivalve *Acesta excavata* collected from cold-water reefs to water maintained in equilibrium with an atmospheric CO₂ concentration of approximately 33,000 ppm, which resulted in a pH value of 6.35—corresponding to conditions reported for water in close proximity to natural CO₂ seeps on the ocean floor—for periods of 0.5, 1, 4, 12, 24, or 96 hours, after which they returned the bivalves to normal CO₂/pH conditions for 1, 4, 12, 24, or 96 hours. The three researchers report the exposure of *A. excavata* to water in equilibrium with the super-high CO₂ concentration “induced extra- and intra-cellular acidosis that remained uncompensated during exposure,” and “oxygen consumption dropped significantly during the initial phase.” They found it “approached control values at the end of exposure” and “no mortality was observed in exposed animals.”

These observations, the researchers write, show “*A. excavata* displays higher tolerance to severe environmental hypercapnia [a condition where there is too much CO₂ in the blood] than what may be expected for deep-sea animals.” They note Tunnicliffe *et al.* (2009) “found evidence that permanent exposure to similar conditions causes reduced growth rates and shell thickness in mussels adapted to live at deep-sea vents,” and they speculate “such long-term effects may also develop in *A. excavata*.” They note previous studies on other species that mostly involved exposure of fish to moderate hypercapnia (P_{CO2} = 10,000 ppm or less) frequently observed complete compensation of extracellular acidosis, citing Heisler (1984, 1986), and “marine invertebrates are often able to partially counteract acidosis through accumulation of bicarbonate ions,” citing Lindinger *et al.* (1984), Portner *et al.* (1988), Michaelidis *et al.* (2005), Miles *et al.* (2007), Pane and Barry (2007), and Gutowska *et al.* (2010).

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Climate Change Reconsidered II: Biological Impacts

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6.3.3.2 Corals

Some scientists predict the ongoing rise in the air's CO_2 content will play havoc with Earth's coral reefs in two ways: by stimulating global warming, which has been predicted to dramatically enhance coral bleaching, and by lower ocean pH levels, which is projected to lower the calcium carbonate saturation state of seawater and thereby reduce coral calcification rates. The first of these predictions was examined in Section 6.1.2 of this chapter. The topic of lower ocean pH levels is addressed here.

Several researchers have postulated many of Earth's corals are destined to die, with some species even facing extinction, because of the hypothesized connection between the ongoing rise in the air's CO_2 content and reduced rates of coral calcification (Buddemeier, 1994; Buddemeier and Fautin, 1996a,b; Gattuso *et al.*, 1998; Buddemeier, 2001). Kleypas *et al.* (1999), for example, calculated calcification rates of tropical corals already should have declined by 6 to 11% or more since 1880, as a result of the increase in atmospheric CO_2 concentration, and they predict the reductions could reach 17 to 35% by 2100 as a result of expected increases in the air's CO_2 content in the coming decades. Langdon *et al.* (2000) calculated a decrease in coral calcification rate of up to 40% between 1880 and 2065.

IPCC claimed in its most recent assessment report:

Elevated temperature along with ocean acidification reduces the calcification rate of corals (*high confidence*), and may tip the calcium carbonate balance of reef frameworks towards dissolution (*medium evidence and agreement*).

— p. 67 of the *Technical Summary*, Working Group II, IPCC Fifth Assessment Report, dated March 28, 2013

Ocean acidification will cause a decrease of calcification of corals, which will cause not only a reduction in the coral's ability to grow its skeleton, but also in its contribution to reef building (*high confidence*).

— p. 73 of the *Technical Summary*, Working Group II, IPCC Fifth Assessment Report, dated March 28, 2013)

Ocean warming and acidification expected under RCP 8.5 will reduce calcification, elevate coral mortality and enhance sediment dissolution (*high confidence*; Manzello *et al.*, 2008). Coral reefs may stop growing and start dissolving when

Climate Change Reconsidered II: Biological Impacts

atmospheric CO₂ reaches 560 ppm due to the combined effects of both drivers (*medium evidence*).

— p. 19 of *Chapter 5. Coastal Systems and Low-Lying Areas*, Working Group II, IPCC Fifth Assessment Report, dated March 28, 2013

The research summarized below reveals the dire assessment of IPCC is tenuous at best and more likely wholly incorrect. As Idso *et al.* (2000) have noted, coral calcification is more than a physical-chemical process described by a set of well-defined equations. It is a biologically driven physical-chemical process that may not be amenable to explicit mathematical description. They state, for example, “photosynthetic activity of zooxanthellae is the chief source of energy for the energetically-expensive process of calcification,” and much evidence suggests “long-term reef calcification rates generally rise in direct proportion to increases in rates of reef primary production.” They also note “the calcium carbonate saturation state of seawater actually rises with an increase in temperature, significantly countering the direct adverse oceanic chemistry consequences of an increase in atmospheric and/or hydrospheric CO₂ concentration.” They conclude “the negative predictions of today could well be replaced by positive predictions tomorrow.”

As revealed below, numerous scientific studies point toward a much more optimistic view of the future for the planet’s corals.

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6.3.3.2.1 Laboratory Studies

Researchers have predicted rates of coral calcification, and the photosynthetic rates of their symbiotic algae, will dramatically decline in response to what is typically referred to as an “acidification” of the world’s oceans, as the atmosphere’s CO₂ concentration continues to rise. This section examines evidence to the contrary obtained from laboratory-based studies. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Larvae from *Acropora* coral species (*A. digitifera* and *A. tenuis*) “may be able to tolerate ambient pH decreases of at least 0.7 pH units.”
- “Scleractinian coral species will be able to acclimate to a high CO₂ ocean even if changes in seawater pH are faster and more dramatic than predicted.”
- Though short-term exposure to lower ocean pH levels resulted in a decline of calcification and net dissolution of calcium carbonate in *Lophelia pertusa*, longer-term (six months) exposure revealed *L. pertusa* was able to acclimate and experience slightly enhanced rates of calcification, maintaining net growth in waters sub-saturated with aragonite.
- Using “carbonate concentration or aragonite saturation state as the sole predictor of the effects of ocean acidification on coral calcification” is unreliable.

- “Other physiological mechanisms, such as a direct effect of reduced pH on calcium or bicarbonate ion transport and/or variable ability to regulate internal pH, are responsible for the variability in reported experimental effects of acidification on calcification.”
- A “firmer grasp of the biological component of biomineralization is paramount” in determining the response of corals to lower ocean pH levels .
- The future increase in oceanic bicarbonate ions may “stimulate photosynthesis and calcification in a wide variety of hermatypic corals,” reducing and potentially overcoming theoretical effects of lower ocean pH levels .
- Reef corals may mitigate the effects of seawater acidification by regulating pH in the fluid at the tissue-skeleton interface, and this mechanism “may explain how several coral species continue to calcify even in low pH seawater, which is undersaturated with respect to aragonite.”
- The fleshy tissues in octocorals may act as a protective barrier against rising levels of $p\text{CO}_2$, helping to maintain a stable internal environment that avoids the adverse effects of lower ocean pH levels .
- Based “purely on thermodynamic grounds, the predicted change in surface ocean pH in the next decades would appear to have minimal effect on the capacity of [important] acid-rich proteins to precipitate carbonates,” which suggests “these proteins will continue to catalyze calcification reactions at ocean pH values projected in the coming century.”

Suwa *et al.* (2010) employed controlled infusions of pure CO_2 to create mean pH values of 8.03, 7.64, and 7.31 in filtered seawater that flowed continuously through three sets of multiple tanks into which they had introduced the gametes of two *Acropora* coral species (*A. digitifera* and *A. tenuis*) collected during a natural spawning event. Seven days later they determined their survival percentage, and after 10 more days they documented the size of the developing polyps. After 14 days they documented the percentage of polyps that had acquired zooxanthellae the researchers had collected from the giant clam *T. crocea* and released into the several treatment tanks.

They found “*A. digitifera* larval survival rate did not differ significantly among pH treatments,” and the graphs of their data reveal survivorship in *A. tenuis* was about 18.5% greater in the lowest pH (highest CO_2) treatment than in the ambient seawater treatment. At the end of the subsequent 10-day study, polyp size was reduced in the lowest pH treatment, by about 14%, which is not too bad for an atmospheric CO_2 concentration reported by the authors to be in the range of 2,115–3,585 ppm. In the *A. tenuis* coral, this reduction in individual size was more than compensated by the greater percentage increase in survivorship. In addition, after only four days of exposure to the zooxanthellae derived from giant clams, all polyps in all treatments had acquired a full complement of the symbiotic zooxanthella.

The seven scientists say “the survival of coral larvae may not be strongly affected by pH change,” or “in other words,” as they continue, “coral larvae may be able to tolerate ambient pH decreases of at least 0.7 pH units.” A pH decrease of that magnitude is likely never to occur, as it implies atmospheric CO_2 concentrations in the range of 2,115 to 3,585 ppm. If such high concentrations ever were to occur, they would be a long, long time in coming, giving corals far more than sufficient time to acclimate—and even evolve (Idso and Idso, 2009)—to cope with the slowly developing situation.

Takahashi and Kurihara (2013) measured the rates of calcification, respiration, and photosynthesis of the tropical coral *Acropora digitifera*, along with the coral’s zooxanthellae density, under near-natural summertime temperature and sunlight conditions for five weeks. Their analysis revealed these “key physiological parameters” were not affected by either predicted mid-range CO_2 concentrations ($p\text{CO}_2 = 744$ ppm, $\text{pH} = 7.97$, $\Omega_{\text{arag}} = 2.6$) or by high CO_2 concentrations ($p\text{CO}_2 = 2,142$ ppm, $\text{pH} = 7.56$, $\Omega_{\text{arag}} = 1.1$) over the 35-day period of their experiment. They found “no significant correlation between calcification rate and seawater aragonite saturation (Ω_{arag})” and “no evidence of CO_2 impact on bleaching.”

Kreif *et al.* (2010) collected two colonies of massive *Porites* corals (which form large multi-century-old colonies and calcify relatively slowly) and four colonies of the branching *Stylophora pistillata* coral (which is short-lived and deposits its skeleton rather rapidly) from a reef adjacent to the Interuniversity Institute for Marine Science in Eilat (Israel) at the northern tip of the Red Sea. They grew fragments of these corals in 1,000-liter tanks through which they pumped Gulf of Eilat seawater adjusted to be in equilibrium with air of three CO_2 concentrations

(385, 1,904, and 3,970 ppm), which led to corresponding pH values of 8.09, 7.49, and 7.19 and corresponding aragonite saturation state (Ω_{arag}) values of 3.99, 1.25, and 0.65. After an incubation period of six months for *S. pistillata* and seven months for the *Porites* corals, the researchers sampled several fragments and analyzed them for a number of properties. Fourteen months from the start of the experiment, they analyzed fragments of each coral species from each CO₂ treatment for zooxanthellae cell density, chlorophyll *a* concentration, and host protein concentration.

They report, “following 14 months incubation under reduced pH conditions, all coral fragments survived and added new skeletal calcium carbonate, despite Ω_{arag} values as low as 1.25 and 0.65.” This occurred at a reduced rate of calcification compared to fragments growing in the normal pH treatment with a Ω_{arag} value of 3.99. Yet in spite of this reduction in skeletal growth, the scientists report, “tissue biomass (measured by protein concentration) was found to be higher in both species after 14 months of growth under increased CO₂.” They further note Fine and Tchernov (2007) observed the same phenomenon, having “reported a dramatic increase (orders of magnitude larger than the present study) in protein concentration following incubation of scleractinian Mediterranean corals (*Oculina patagonica* and *Madracis pharencis*) under reduced pH,” stating “these findings imply tissue thickening in response to exposure to high CO₂.” Krief *et al.* also report “a decrease in zooxanthellae cell density with decreasing pH was recorded in both species,” but “this trend was accompanied by an increase in chlorophyll concentration per cell at the highest CO₂ level.”

The Israeli, French, and UK researchers say “the inverse response of skeleton deposition and tissue biomass to changing CO₂ conditions is consistent with the hypothesis that calcification stimulates zooxanthellae photosynthesis by enhancing CO₂ concentration within the coelenteron (McConnaughey and Whelan, 1997),” and “since calcification is an energy-consuming process ... a coral polyp that spends less energy on skeletal growth can instead allocate the energy to tissue biomass,” citing Anthony *et al.* (2002) and Houlbreque *et al.* (2004). They suggest, “while reduced calcification rates have traditionally been investigated as a proxy of coral response to environmental stresses, tissue thickness and protein concentrations are a more sensitive indicator of the health of a colony,” citing Houlbreque *et al.* (2004).

Krief *et al.* conclude “the long acclimation time

of this study allowed the coral colonies to reach a steady state in terms of their physiological responses to elevated CO₂,” and “the deposition of skeleton in seawater with $\Omega_{\text{arag}} < 1$ demonstrates the ability of both species to calcify by modifying internal pH toward more alkaline conditions.” They further state “the physiological response to higher CO₂/lower pH conditions was significant, but less extreme than reported in previous experiments,” suggesting “scleractinian coral species will be able to acclimate to a high CO₂ ocean even if changes in seawater pH are faster and more dramatic than predicted.”

Form and Riebesell (2012) studied branches of *Lophelia pertusa*, collected from reefs off the coast of Norway, which they describe as “the most common reef framework-forming and ecosystem engineering cold-water coral with a cosmopolitan distribution (Zibrowius, 1980; Cairns, 1994; Freiwald *et al.*, 2004).” They conducted a short-term (eight-day) experiment and a long-term (178-day) experiment, in which they employed different atmospheric CO₂ treatments to create a range of water pH treatments from 8.029 to 7.768 in the eight-day study and from 7.944 to 7.755 in the 178-day study, measuring the corals’ growth rates over these intervals. They report “short-term (1-week) high CO₂ exposure resulted in a decline of calcification by 26–29% for a pH decrease of 0.1 unit and net dissolution of calcium carbonate.” In contrast, “*L. pertusa* was capable to acclimate to acidified conditions in long-term (6 months) incubations, leading to even slightly enhanced rates of calcification.” In the long-term low-pH treatment, “net growth is sustained even in waters sub-saturated with respect to aragonite.”

Crook *et al.* (2013) note “almost all tropical corals have algal symbionts (zooxanthellae),” while “most deep and cold-water corals lack zooxanthellae.” Because the latter corals have no symbionts and rely solely on heterotrophy for energy, they “provide a simplified system for exploring the roles of nutrition (and energy) in coral calcification.” Studying *Balanophyllia elegans*, a solitary azooxanthellate scleractinian coral common in shallow coastal waters around Monterey Bay, California (USA), where it is exposed seasonally to low-pH, high-*p*CO₂ upwelling waters, the five researchers conducted an eight-month factorial laboratory experiment in which they “measured the effects of three *p*CO₂ treatments (410, 770, and 1,220 μ atm) and two feeding frequencies (3-day and 21-day intervals) on ‘planulation’ (larval release) by adult *B. elegans*, and on the survival, skeletal growth and calcification of newly settled juveniles.”

Crook *et al.* report “ $p\text{CO}_2$ had no effect on the numbers of brooded planulae larvae released,” “higher food levels increased the number of larvae released by 50–200%,” and “excess food enables corals to counteract partially some of the negative impacts of lower [aragonite] saturation states under higher $p\text{CO}_2$ conditions.” They found “after 8 months of growth, high-food skeletons were up to 7 times larger (by volume) than low-food skeletons at every $p\text{CO}_2$ level,” and “in every $p\text{CO}_2$ treatment, higher food led to both greater linear extension and greater calcification (skeletal weight) over the 8-month experiment.” They also found “calcification by high- $p\text{CO}_2$, high-food corals was 4 times greater than in low-food corals at ambient $p\text{CO}_2$,” and “even feeding on planktonic crustaceans only once every 21 days was still sufficient to maintain positive growth at high $p\text{CO}_2$, albeit very slowly.” The five U.S. researchers conclude, “as long as food availability remains high, *B. elegans* may be able to largely compensate for the extra energy required for calcification at low saturations, even if calcification occurs at slightly lower rates than at modern $p\text{CO}_2$.” They reinforce this conclusion in the last sentence of their paper’s abstract, writing, “we conclude that food abundance is critical for azooxanthellate coral calcification, and that *B. elegans* may be partially protected from adverse consequences of ocean acidification in habitats with abundant heterotrophic food.”

Nash *et al.* (2012) write, “coral reef ecosystems develop best in high-flow environments,” but “their fragile frameworks are also vulnerable to high wave energy.” They say the wave-resistant algal rims, which surround many shallow coral reefs and are predominantly made of crustose coralline algae (CCA), are critical structural elements for the survival of such coral reefs. The scientists note “concerns have been growing about the susceptibility of CCA to ocean acidification, because CCA Mg-calcite skeletons are more susceptible to dissolution under low pH conditions than are coral aragonite skeletons.” They further note the recent discovery by Nash *et al.* (2011) of the stable carbonate known as dolomite in the CCA *Porolithon onkodes* necessitates a re-appraisal of the impacts of lower ocean pH levels on it and other CCAs, such as *P. pachydermum*.

The 11 researchers “carried out dissolution experiments on fragments of CCA collected fresh, but then dried, from the Heron Island reef front (Great Barrier Reef, Australia),” after which the fragments were exposed to ambient sea water as a control and an enriched CO_2 treatment, where “pH ranged from 7.85 to 8.55 (control) and 7.69–8.44 (treatment), tracking

natural diurnal changes measured in the lagoon water.” Nash *et al.* (2012) determined “dried dolomite-rich CCA have 6–10 times lower rates of dissolution than predominantly Mg-calcite CCA in both high- CO_2 (~700 ppm) and control (~380 ppm) environments.” They found this stabilizing mechanism resulted from “a combination of reduced porosity due to dolomite infilling and selective dissolution of other carbonate minerals.” Noting “the prevailing theories that Mg-calcites with higher Mg content will undergo greatest dissolution,” they write, “we were surprised to find a trend in the opposite direction.” As dolomite-rich CCA frameworks are common in shallow coral reefs globally, Nash *et al.* conclude “it is likely that they will continue to provide protection and stability for coral reef frameworks as CO_2 rises.”

Egilsdottir *et al.* (2013) note “it has been suggested that organisms presently surviving in highly variable environments are likely to be more robust to ocean acidification,” citing Moulin *et al.* (2011) and Raven (2011), and they hypothesize “the ability of organisms to tolerate significant pH/ $p\text{CO}_2$ fluctuations may be a result of adaptation (a genetic trait shared by the population) and/or acclimation (owing to phenotypic plasticity of the individual).” The authors investigated the effect of elevated $p\text{CO}_2$ “in the articulated coralline red alga *Corallina elongata* from an intertidal rock pool on the north coast of Brittany (France), where $p\text{CO}_2$ naturally varied daily between 70 and 1,000 μatm .” They grew the algae at four $p\text{CO}_2$ values (380, 550, 750, and 1,000 μatm) in laboratory mesocosms and measured several physiological responses of the coral.

The French and Icelandic researchers report “algae grown under elevated $p\text{CO}_2$ formed fewer new structures and produced calcite with a lower $m\text{Mg}/\text{Ca}$ ratio relative to those grown under 380 μatm .” They also observe “respiration, gross primary production and calcification in light and dark were not significantly affected by increased $p\text{CO}_2$.” Egilsdottir *et al.* conclude their study “supports the assumption that *C. elongata* from a tidal pool, where $p\text{CO}_2$ fluctuates over diel and seasonal cycles, [are] relatively robust to elevated $p\text{CO}_2$.” They also state these observations portend “a greater resilience” of such organisms to the projected “highly variable pH/ $p\text{CO}_2$ environments of future ocean acidification.”

Ragazzola *et al.* (2013) note coralline algae have been shown to be a major contributor to the formation and stabilization of coral reefs and in enhancing coral larvae settlement, citing Chisholm (2000). Given “their crucial role in shallow water ecosystems and

their worldwide distribution,” the scientists write, “understanding the impact of ocean acidification on calcifying algae is fundamental,” especially because “their high-Mg calcite skeleton is the most soluble polymorph of CaCO_3 (50% more soluble than calcite and 20% more soluble than aragonite).” Coralline algae are, therefore, “likely to be particularly sensitive to a reduction in Ω ,” which is the calcium carbonate saturation state of seawater, citing Ries (2011), Burdett *et al.* (2012), and Martin *et al.* (2013).

Because “species with wide geographic ranges, such as coralline algae, are in general very plastic and able to acclimatize to a variety of habitats through morphological and functional responses (Brody, 2004),” Ragazzola *et al.* cultured *Lithothamnion glaciale*, one of the main maerl-forming species in the northern latitudes, under different elevated CO_2 levels (410, 560, 840, and 1,120 ppm = 8.02, 7.92, 7.80, and 7.72 pH, respectively) for 10 months, with initial analyses of the various parameters they measured conducted at the three-month point of the study, as reported by Ragazzola *et al.* (2012). The six scientists report the growth rates of the plants in the three CO_2 -enriched treatments after the first three months of their study were not significantly different from either each other or those of the ambient-treatment plants. At the end of the 10-month experiment, however, the CO_2 -enriched plants’ growth rates were approximately 60% lower than that of the ambient-treatment plants. However, the individual cell wall thicknesses of both inter and intra filaments at the three-month point of the study were significantly thinner than those of the control plants, while at the end of the 10-month study they were equivalent to those of the control plants.

Ragazzola *et al.* (2013) note a possible explanation of their findings is “a shift from what could be termed a ‘passive’ phase during the first three months to an ‘active’ phase by the end of ten months,” whereby “during the ‘passive’ phase, the increased energy requirement for calcification due to higher CO_2 results in a reduction in the amount of calcite deposited in each cell well,” but during the “active phase,” *L. glaciale* reduces its growth rate so the cell wall structure can be better maintained. Because maintaining skeletal integrity is one of the main priorities of marine organisms living in high CO_2 environments, the German and UK researchers say “the results of this study indicate that seawater chemistry can drive phenotypic plasticity in coralline algae,” and “the ability to change the energy allocation between cell growth and structural support is a clear adaptive response of the organism,” which

“is likely to increase its ability to survive in a high CO_2 world.”

Ries *et al.* (2010) “investigated the impact of CO_2 -induced ocean acidification on the temperate scleractinian coral *Oculina arbuscula* by rearing colonies for 60 days in experimental seawaters bubbled with air- CO_2 gas mixtures of 409, 606, 903, and 2,856 ppm CO_2 , yielding average aragonite saturation states (Ω_A) of 2.6, 2.3, 1.6 and 0.8.” The authors observed “following the initial acclimation phase, survivorship in each experimental treatment was 100%,” and in regard to the corals’ rates of calcification and linear extension, “no significant difference was detected relative to the control treatment ($\Omega_A = 2.6$) for corals reared under Ω_A of 2.3 and 1.6,” with the latter values corresponding to pH reductions from current conditions of 0.08 and 0.26, respectively. Ries *et al.* “propose that the apparent insensitivity of calcification and linear extension within *O. arbuscula* to reductions in Ω_A from 2.6 to 1.6 reflects the corals’ ability to manipulate the carbonate chemistry at their site of calcification.”

Herfort *et al.* (2008) note an increase in atmospheric CO_2 will cause an increase in the abundance of HCO_3^- (bicarbonate) ions and dissolved CO_2 , and they also report several studies on marine plants have observed “increased photosynthesis with higher than ambient DIC [dissolved inorganic carbon] concentrations,” citing Gao *et al.* (1993), Weis (1993), Beer and Rehnberg (1997), Marubini and Thake (1998), Mercado *et al.* (2001, 2003), Herfort *et al.* (2002), and Zou *et al.* (2003). The three researchers employed a wide range of bicarbonate concentrations “to monitor the kinetics of bicarbonate use in both photosynthesis and calcification in two reef-building corals, *Porites porites* and *Acropora* sp.” Additions of HCO_3^- to synthetic seawater continued to increase the calcification rate of *Porites porites* until the bicarbonate concentration exceeded three times that of seawater, and photosynthetic rates of the coral’s symbiotic algae were stimulated by HCO_3^- addition until they became saturated at twice the normal HCO_3^- concentration of seawater.

Similar experiments conducted on Indo-Pacific *Acropora* sp. showed calcification and photosynthetic rates in these corals were enhanced to an even greater extent, with calcification continuing to increase above a quadrupling of the HCO_3^- concentration and photosynthesis saturating at triple the concentration of seawater. The scientists monitored calcification rates of the *Acropora* sp. in the dark, writing, “although these were lower than in the light for a given HCO_3^- concentration, they still increased dramatically with

HCO_3^- addition, showing that calcification in this coral is light stimulated but not light dependent.”

Herfort *et al.* suggest “hermatypic corals incubated in the light achieve high rates of calcification by the synergistic action of photosynthesis,” which, as they have shown, is enhanced by elevated concentrations of HCO_3^- ions caused by the rise in the air’s CO_2 content. The three researchers note over the next century the predicted increase in atmospheric CO_2 concentration “will result in about a 15% increase in oceanic HCO_3^- ,” and this development “could stimulate photosynthesis and calcification in a wide variety of hermatypic corals.”

Jury *et al.* (2010) explain why some corals show positive responses to lower ocean pH levels in laboratory studies whereas others do not. They note, “physiological data and models of coral calcification indicate that corals utilize a combination of seawater bicarbonate and (mainly) respiratory CO_2 for calcification, not seawater carbonate,” but “a number of investigators are attributing observed negative effects of experimental seawater acidification by CO_2 or hydrochloric acid additions to a reduction in seawater carbonate ion concentration and thus aragonite saturation state.” They identify “a discrepancy between the physiological and geochemical views of coral biomineralization” and report, “not all calcifying organisms respond negatively to decreased pH or saturation state.” They note, “together, these discrepancies suggest that other physiological mechanisms, such as a direct effect of reduced pH on calcium or bicarbonate ion transport and/or variable ability to regulate internal pH, are responsible for the variability in reported experimental effects of acidification on calcification.”

Jury *et al.* performed incubations with the coral *Madracis auretenra* (= *Madracis mirabilis sensu* Wells, 1973) in modified seawater chemistries, where, as they describe it, “carbonate parameters were manipulated to isolate the effects of each parameter more effectively than in previous studies, with a total of six different chemistries.” Among-treatment differences “were highly significant,” and “the corals responded strongly to variation in bicarbonate concentration, but not consistently to carbonate concentration, aragonite saturation state or pH.” They found, for example, “corals calcified at normal or elevated rates under low pH (7.6–7.8) when the sea water bicarbonate concentrations were above 1800 μM ,” and, conversely, “corals incubated at normal pH had low calcification rates if the bicarbonate concentration was lowered.”

Jury *et al.* conclude “coral responses to ocean

acidification are more diverse than currently thought,” and they question “the reliability of using carbonate concentration or aragonite saturation state as the sole predictor of the effects of ocean acidification on coral calcification,” stating “if we truly wish to decipher the response of coral calcification to ocean acidification, a firmer grasp of the biological component of biomineralization is paramount.”

Venn *et al.* (2013) also focused on how lower ocean pH levels impact the physiological mechanisms that drive calcification, to provide knowledge helpful in predicting how corals and other marine calcifiers will respond and potentially acclimate to lower ocean pH levels. In corals, the authors note, the capacity to regulate pH in the fluid at the tissue-skeleton interface [subcalicoblastic medium (SCM)] and in the calcifying cells [calicoblastic epithelium (CE)] “has been widely proposed to be important in shaping calcification responses to ocean acidification.” They studied the impact of seawater acidification on pH_{SCM} and pH_{CE} in the coral *Stylophora pistillata*, “using *in vivo* imaging of pH in corals exposed to reduced seawater pH and elevated $p\text{CO}_2$ in the laboratory for [both] long and short durations.” This work included “exposures to levels of acidification and elevated $p\text{CO}_2$ many times greater than those predicted to occur at the end of this century.”

Venn *et al.* say they “observed calcification (measured by growth of skeletal crystals and whole colonies) in all our treatments, including treatment pH 7.2, where aragonite was undersaturated.” They continue, “this finding agrees with previous work with *S. pistillata* conducted elsewhere, where net calcification was also observed over a similar range of pH and $p\text{CO}_2$ (Krief *et al.*, 2010).” Such findings suggest, they write, “*S. pistillata* may have a high tolerance to decreases in seawater pH and changes in seawater chemistry,” leading them to conclude “maintenance of elevated pH_{SCM} relative to the surrounding seawater may explain how several coral species continue to calcify even in low pH seawater, which is undersaturated with respect to aragonite (this study and Rodolfo-Metalpa *et al.* (2011) and Cohen *et al.*, (2009)).” Venn *et al.* report, “reductions in calcification rate, both at the level of crystals and whole colonies, were only observed in our lowest pH treatment [pH 7.2] when pH was significantly depressed in the calcifying cells in addition to the SCM.” “Overall,” they say their findings suggest “reef corals may mitigate the effects of seawater acidification by regulating pH in the SCM.”

Gabay *et al.* (2013) note octocorals possess “an internal calcium carbonate skeleton comprised of

microscopic sclerites embedded in their tissue,” citing Fabricius and Alderslade (2001), Jeng *et al.* (2011), and Tentori and Ofwegen (2011). They also note octocorals are “the second most important faunistic component in many reefs, often occupying 50% or more of the available substrate.” They say “it is important to predict their response to a scenario of increased $p\text{CO}_2$.”

Gabay *et al.* studied three species of octocorals from two families found in the Gulf of Aqaba at Eilat—the zooxanthellate *Ovabunda macrosciculata* and *Heteroxenia fuscens* (family Xeniidae) and *Sarcophyton* sp. (family Alcyoniidae)—which they maintained for five months under normal (8.2) and reduced (7.6 and 7.3) pH conditions, assessing their pulsation rate, protein concentration, polyp weight, density of zooxanthellae, and chlorophyll concentration per cell.

The three Israeli scientists found “no statistically significant difference between the octocorals exposed to reduced pH values compared to the control.” They say “these findings indicate that octocorals may possess certain protective mechanisms against rising levels of $p\text{CO}_2$,” and they suggest “their fleshy tissues act as a barrier, maintaining a stable internal environment and avoiding the adverse effects of the ambient elevated $p\text{CO}_2$.” That notion accords with the observations of Rodolfo-Metalpa *et al.* (2011), and Gabay *et al.* note “this suggestion is further supported by our finding that the ultrastructural features of *O. macrosciculata* sclerites are not affected by increased ambient seawater acidity.” They conclude, “octocorals might be able to acclimate and withstand rising levels of ocean acidification, even under conditions that are far beyond what is expected to occur by the end of the present century (pH 7.9).”

Mass *et al.* (2013) write, “despite the broad interest in coral calcification and the potential for climate-driven adverse effects, the molecules and biophysical mechanism responsible for the precipitation of carbonates are poorly understood.” They note, “to date, we lack both a characterization of molecules involved in calcification and a mechanistic understanding of processes that lead to and control calcification,” and this “lack of knowledge limits our ability to predict the response of corals to increasing atmospheric CO_2 .” The seven scientists “for the first time,” identified, cloned, determined the amino acid sequence of, and characterized four highly acidic proteins they derived from the expression of genes obtained from the common stony coral *Stylophora pistillata*. Each of these proteins can spontaneously catalyze the precipitation of calcium carbonate in

vitro.

They found “coral acid-rich proteins (CARPs) not only bind Ca^{2+} stoichiometrically but also precipitate aragonite in vitro in seawater at pH 8.2 and 7.6 via an electrostatic interaction with protons on bicarbonate anions.” The seven U.S. researchers conclude, “based purely on thermodynamic grounds, the predicted change in surface ocean pH in the next decades would appear to have minimal effect on the capacity of these acid-rich proteins to precipitate carbonates.” They note their findings “strongly suggest that these proteins will continue to catalyze calcification reactions at ocean pH values projected in the coming century.”

Maier *et al.* (2013) note “previous experiments examining the effect of ocean acidification on the cold-water corals *L. pertusa* and *M. oculata* have indicated that their rates of calcification remain positive even in waters where Ω_a is < 1 (Maier *et al.*, 2009; Thresher *et al.*, 2011; Form and Riebesell, 2012).” They add that Form and Riebesell (2012) and Maier *et al.* (2012, 2013) found “calcification rates of these species remained positive at a partial pressure of CO_2 ($p\text{CO}_2$) of 1000 μatm , a value that is at the high end of projected changes by 2100.” Maier *et al.* measured respiration rates “for both short and long periods of time at $p\text{CO}_2$ levels ranging from ambient (350 μatm) to elevated (1100 μatm) levels,” using “the same experimental setup as a previous study demonstrating that elevated $p\text{CO}_2$ had no effect on the rate of calcification in these two species (Maier *et al.*, 2013).”

The six scientists report, “in the range of $p\text{CO}_2$ studied so far, up to 1215 μatm , no significant change in respiration was found as a function of increasing $p\text{CO}_2$.” As for what “this means,” Maier *et al.* write, “for the maintenance of high calcification rates over a large range of $p\text{CO}_2$ of up to 1,000 ppm, there is no evidence for a direct energy allocation from food uptake to calcification in order to compensate for higher energy required to maintain calcification constant despite a decrease in pH.”

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Climate Change Reconsidered II: Biological Impacts

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6.3.3.2.2 Field Studies

Some scientists have predicted rates of coral calcification and the photosynthetic rates of their symbiotic algae will decline dramatically in response to lower ocean pH levels as the atmosphere's CO₂ concentration continues to rise. As research evidence accumulates, however, the true story appears to be just the opposite. This section examines such evidence obtained from field-based studies conducted in the natural ocean. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Theoretical calculations suggest rising atmospheric CO₂ over the past century should have led to a 6–14% decline in coral calcification via lower ocean pH levels, yet several studies show coral calcification rates have remained stable or increased.
- In contrast to model-based assumptions, the process of calcification in many corals is not correlated with aragonite saturation state or pH.
- Increases in calcification observed over the past century in many ocean regions have been shown to correlate strongly with increases in water temperature.
- Changes in pH did not affect the composition of associated microbial communities in two Mediterranean coral species.
- Cold-water corals are “likely to be much more resilient to decreasing seawater pH from ocean acidification than previously realized,” because of their ability “to ameliorate or buffer external changes in seawater pH by up-regulating their internal (extracellular) pH at the site of calcification.”
- The distribution and composition of deep-sea corals “are not constrained by carbonate levels below saturation.”
- “The drawdown of total dissolved inorganic carbon due to photosynthesis and calcification of reef communities can exceed the drawdown of

total alkalinity due to calcification of corals and calcifying algae, leading to a net increase in aragonite saturation state.” Although “carbon fluxes of benthic reef communities cannot significantly counter changes in carbon chemistry at the scale of oceans, they provide a significant mechanism of buffering ocean acidification impacts at the scale of habitat to reef.”

Field studies hold an advantage over laboratory-based studies in more aptly representing conditions in the real world, as many of those conditions are impossible or impractical to recreate in a laboratory setting. The findings produced in field studies tend to hold more weight and establish greater clarity on a scientific topic or question under investigation than findings produced in a laboratory setting. Such is the case with lower ocean pH levels. Whereas positive, negative, and neutral effects from this phenomenon have been observed on corals in laboratories, field-based studies in the ocean reveal the situation is much less dire than IPCC predicts. Many studies suggest a modest decline in oceanic pH may actually favor coral calcification and growth.

Pelejero *et al.* (2005), for example, developed a reconstruction of seawater pH spanning the period 1708–1988, based on the boron isotopic composition ($\delta^{11}\text{B}$) of a long-lived massive coral (*Porites*) from Flinders Reef in the western Coral Sea of the southwestern Pacific. They found “no notable trend toward lower $\delta^{11}\text{B}$ values” over the 300-year period investigated. They write, “the dominant feature of the coral $\delta^{11}\text{B}$ record is a clear interdecadal oscillation of pH, with $\delta^{11}\text{B}$ values ranging between 23 and 25 per mil (7.9 and 8.2 pH units),” which “is synchronous with the Interdecadal Pacific Oscillation.” They also calculated changes in aragonite saturation state from the Flinders pH record that varied between ~3 and 4.5, and these values encompass “the lower and upper limits of aragonite saturation state within which corals can survive.” They report, “skeletal extension and calcification rates for the Flinders Reef coral fall within the normal range for *Porites* and are not correlated with aragonite saturation state or pH.” Thus, contrary to claims of great sensitivity of coral calcification to changes in pH and aragonite saturation, they found large cyclical changes in these parameters had essentially no detectable effect on either coral calcification or skeletal extension rates.

In a study of historical calcification rates determined from coral cores retrieved from 35 sites on the Great Barrier Reef, Lough and Barnes (1997) observed a statistically significant correlation between

coral calcification rate and local water temperature. They found a 1°C increase in mean annual water temperature increased mean annual coral calcification rate by about 3.5 percent, but they also report there were “declines in calcification in *Porites* on the Great Barrier Reef over recent decades.” They point out their data depict several extended periods of time when coral growth rates were either above or below the long-term mean, cautioning, “it would be unwise to rely on short-term values (say averages over less than 30 years) to assess mean conditions.”

They report, “a decline in calcification equivalent to the recent decline occurred earlier this century and much greater declines occurred in the 18th and 19th centuries,” long before anthropogenic CO₂ emissions had much of an impact on the air’s CO₂ concentration. Over their entire dataset, Lough and Barnes write, “the 20th century has witnessed the second highest period of above average calcification in the past 237 years,” not exactly to be expected in light of how dangerous high water temperatures are often said to be for corals, the claim that Earth is currently warmer than it has been at any other time during the entire past millennium, and the air’s CO₂ content is currently much higher than it has been for more than a thousand years.

Bessat and Buigues (2001) reported similar findings after deriving a history of coral calcification rates, covering the period 1801–1990, from a core extracted from a massive *Porites* coral head on the French Polynesian island of Moorea. They note “recent coral-growth models highlight the enhanced greenhouse effect on the decrease of calcification rate,” but instead of relying on theoretical calculations, they wanted to work with real-world data because the records preserved in ancient corals “may provide information about long-term variability in the performance of coral reefs, allowing unnatural changes to be distinguished from natural variability.”

Bessat and Buigues found a 1°C increase in water temperature increased coral calcification rates at the site they studied by 4.5 percent. Then they found, “instead of a 6–14% decline in calcification over the past 100 years computed by the Kleypas group, the calcification has increased, in accordance with [the results of] Australian scientists Lough and Barnes.” They also observed patterns of “jumps or stages” in the record, characterized by an increase in the annual rate of calcification, particularly at the beginning of the past century “and in a more marked way around 1940, 1960 and 1976,” stating once again their results “do not confirm those predicted by the Kleypas *et al.* (1999) model.”

Lough and Barnes (2000) delivered another major blow to the Kleypas *et al.* model when they assembled and analyzed the calcification characteristics of 245 similar-sized massive colonies of *Porites* corals obtained from 29 reef sites located along the length, and across the breadth, of Australia’s Great Barrier Reef (GBR). The data spanned a latitudinal range of approximately 9° and an annual average sea surface temperature (SST) range of 25–27°C. To these data they added other published data from the Hawaiian Archipelago (Grigg, 1981, 1997) and Phuket, Thailand (Scoffin *et al.*, 1992), thus extending the latitudinal range of the expanded dataset to 20° and the annual average SST range to 23–29°C.

Lough and Barnes found the GBR calcification data were linearly related to the average annual SST data, as “a 1°C rise in average annual SST increased average annual calcification by 0.39 g cm⁻² year⁻¹.” Results were much the same for the extended dataset. They report, “the regression equation [calcification = 0.33(SST) - 7.07] explained 83.6% of the variance in average annual calcification (F = 213.59, p less than 0.00),” and “this equation provides for a change in calcification rate of 0.33 g cm⁻² year⁻¹ for each 1°C change in average annual SST.”

Lough and Barnes say their findings “allow assessment of possible impacts of global climate change on coral reef ecosystems,” and between the two 50-year periods 1880–1929 and 1930–1979, they calculate a calcification increase of 0.06 g cm⁻² year⁻¹, noting “this increase of ~4% in calcification rate conflicts with the estimated decrease in coral calcification rate of 6–14% over the same time period suggested by Kleypas *et al.* (1999) as a response to changes in ocean chemistry.” Even more stunning is their observation that between the two 20-year periods 1903–1922 and 1979–1998, “the SST-associated increase in calcification is estimated to be less than 5% in the northern GBR, ~12% in the central GBR, ~20% in the southern GBR and to increase dramatically (up to ~50%) to the south of the GBR.” Lough and Barnes conclude coral calcification rates “may have already significantly increased along the GBR in response to global climate change.”

Carricart-Ganivet (2004) developed relationships between coral calcification rate and annual average SST based on data collected from colonies of the reef-building coral *Montastraea annularis* at 12 locations in the Gulf of Mexico and Caribbean Sea. He found the calcification rate in the Gulf of Mexico increased 0.55 g cm⁻² year⁻¹ for each 1°C increase, and in the Caribbean Sea it increased 0.58 g cm⁻² year⁻¹ for each

1°C increase. Pooling these data with data regarding *M. annularis* and *M. faveolata* growing to a depth of 10 m at Carrie Bow Cay, Belize, data from reefs at St. Croix in the U.S. Virgin Islands, and data of *M. faveolata* growing to a depth of 10 m at Curacao, Antilles, Carricart-Ganivet reports a mean increase in calcification rate of $\sim 0.5 \text{ g cm}^{-2} \text{ year}^{-1}$ for each 1°C increase in annual average SST, even greater than what Lough and Barnes found for *Porites* corals.

Working at two reef sites on the northwest coast of Cuba—one in the Guanahacabibes Gulf just off the Pinar del Rio Province and the other north of Havana Bay—Carricart-Ganivet and Gonzalez-Diaz (2009) measured yearly coral extension rates and densities of the dominant Caribbean reef-building coral *Montastraea annularis* for the period 1991 to 2003, from which data they calculated annual coral calcification rates. They plotted their results against mean annual sea surface temperature (SST, obtained from the UK's Hadley Centre) and compared their results with the earlier study of Carricart-Ganivet (2004). The results of these two investigations are illustrated in Figure 6.3.3.2.2.1, where it can be seen they are completely compatible with each other.

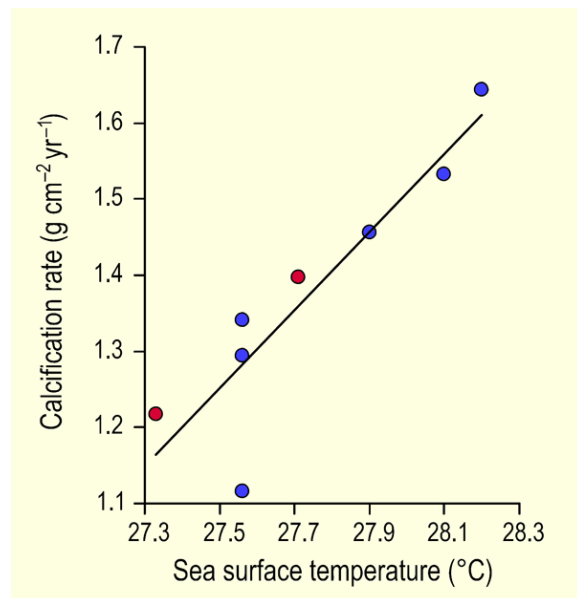


Figure 6.3.3.2.2.1. Mean yearly calcification rate of *Montastraea annularis* vs. mean annual sea surface temperature for the several sites studied by Carricart-Ganivet (2004) (blue circles) and the two sites studied by the authors (red circles). The line that has been fit to the data is defined by $\text{Calcification Rate} = 0.51 \text{ SST} - 12.85$ ($r^2 = 0.82$, $p < 0.002$). Adapted from Carricart-Ganivet and Gonzalez-Diaz (2009).

Crabbe *et al.* (2006) determined the original growth rates of long-dead Quaternary corals found in limestone deposits on islands in the Wakatobi Marine National Park of Indonesia, which they compared to the growth rates of present-day corals of the same genera living in the same area. They found the Quaternary corals grew “in a comparable environment to modern reefs”—except, of course, for the air’s CO_2 concentration, which is currently higher than it has been at any other time throughout the Quaternary, which spans the past 1.8 million years. Their measurements indicated the radial growth rates of the modern corals were 31 percent greater than those of their ancient predecessors in the case of *Porites* species, and 34 percent greater in the case of *Favites* species.

Cohen and Holcomb (2009) highlight several facts about the process of calcification in zooxanthellate corals. First, they report what is perhaps the most fundamental fact: “calcification is an active, physiological process that requires significant amounts of energy to drive it.” Second, they note “increased photosynthesis [of coral symbiotic zooxanthellae] means increased photosynthate and more energy for calcification.” Third, they report Atkinson *et al.* (1995) have shown “nutritionally replete zooxanthellate corals in naturally low [aragonite] saturation-state seawaters are capable of accreting skeletons at rates comparable to those achieved by conspecifics in high-saturation-state seawaters.” Fourth, the two researchers write, “today, several reefs, including Galapagos, areas of Pacific Panama, and Jarvis (southern Line Islands), experience levels of aragonite saturation equivalent to that predicted for the open ocean under two times and three times pre-industrial CO_2 levels (Manzello *et al.*, 2008; Kathryn Shamberger [PMEL/NOAA] and colleagues, *pers. comm.*, August 2009),” and “available data on coral colony growth rates on these reefs, albeit limited, suggest that they are equivalent to and sometimes even rival those of conspecifics in areas where aragonite saturation states are naturally high, such as the western Pacific warm pool.”

Probably the most important deduction from these observations, Cohen and Holcomb write, is “naturally elevated levels of inorganic nutrients and, consequently, high levels of primary and secondary production, may already be facilitating high coral calcification rates in regions with naturally high dissolved CO_2 levels.” This further suggests Earth’s corals, with their genetically diverse symbiotic zooxanthellae, are likely well-equipped to deal successfully with future increases in the air’s CO_2 .

content.

The same phenomenon that powers the twin processes of coral calcification and phytoplanktonic growth (photosynthesis) tends to increase the pH of marine waters (Gnaiger *et al.*, 1978; Santhanam *et al.*, 1994; Brussaard *et al.*, 1996; Lindholm and Nummelin, 1999; Macedo *et al.*, 2001; Hansen, 2002). This phenomenon has been shown to have the ability to dramatically increase the pH of marine bays, lagoons, and tidal pools (Gnaiger *et al.*, 1978; Macedo *et al.*, 2001; Hansen, 2002) and significantly enhance the surface water pH of areas as large as the North Sea (Brussaard *et al.*, 1996).

In an example of this phenomenon, Middelboe and Hansen (2007) studied the pH of a wave-exposed boulder reef in Aalsgaarde on the northern coast of Zealand, Denmark, and a sheltered shallow-water area in Kildebakkerne in the estuary Roskilde Fjord, Denmark. They report, in line with what would be expected if photosynthesis tends to increase surface-water pH, “daytime pH was significantly higher in spring, summer and autumn than in winter at both study sites,” often reaching values of 9 or more during peak summer growth periods vs. 8 or less in winter. They also found “diurnal measurements at the most exposed site showed significantly higher pH during the day than during the night,” sometimes reaching values above 9 during daylight hours but typically dipping below 8 at night, and “diurnal variations were largest in the shallow water and decreased with increasing water depth.”

Middelboe and Hansen cite the work of Pearson *et al.* (1998), who found pH averaged about 9 during the summer in populations of *Fucus vesiculosus* in the Baltic Sea; Menendez *et al.* (2001), who found maximum pH was 9 to 9.5 in dense floating macroalgae in a brackish coastal lagoon in the Ebro River Delta; and Bjork *et al.* (2004), who found pH values as high as 9.8 to 10.1 in isolated rock pools in Sweden. Noting “pH in the sea is usually considered to be stable at around 8 to 8.2,” the two Danish researchers conclude “pH is higher in natural shallow-water habitats than previously thought.”

Meron *et al.* (2012) state ocean acidification “has the potential to cause significant perturbations to the physiology of ocean organisms, particularly those such as corals that build their skeletons/shells from calcium carbonate,” and this phenomenon “could also have an impact on the coral microbial community, and thus may affect coral physiology and health.” They note most studies of declining pH effects on corals and/or their associated microbiota typically have been done under “controlled laboratory

conditions.” This approach clearly ignores any impacts declining pH values may have on the coral holobiont, some of which may be negative and some positive, which in the latter case is referred to as the probiotic hypothesis, as per Reshef *et al.* (2006).

The six scientists took advantage of a natural pH gradient off the coast of Ischia (Gulf of Naples, Italy) created by an underwater CO₂ flux from volcanic vents (Hall-Spencer *et al.*, 2008). They examined the potential impacts of a range of pH conditions (7.3 to 8.1) on coral microbial communities living under real-world conditions, focusing on two Mediterranean coral species: *Balanophyllia europaea* and *Cladocora caespitosa*.

The research team reports “pH did not have a significant impact on the composition of associated microbial communities in both coral species.” They note “corals present at the lower pH sites exhibited only minor physiological changes” and “no microbial pathogens were detected.” They conclude “at least for these two coral species, reduced pH does not seem to significantly reduce coral health,” which suggests some of the contrary results obtained in laboratory studies could be due to the fact “laboratory environments cannot mimic the dynamism and microbial diversity present in nature,” and the possibility “aquarium conditions themselves contribute to stress or disturbance in the microbial community.” This view is supported in part by the finding of Kooperman *et al.* (2007), who noted, “the same coral species has different associated microbial communities in the laboratory compared with field conditions.”

Shamberger *et al.* (2011) deployed “auto-samplers” to collect water samples from the barrier coral reef of Kaneohe Bay, Oahu, Hawaii, every two hours for six 48-hour periods, two each in June 2008, August 2009, and January/February 2010. Based on these seawater measurements, they calculated net ecosystem calcification (NEC) and net photosynthesis (NP) rates for these periods. The six scientists found “daily NEC was strongly negatively correlated with average daily pCO₂, which ranged from 421 to 622 ppm.” They report, “daily NEC of the Kaneohe Bay barrier reef is similar to or higher than daily NEC measured on other coral reefs, even though Ω_{arag} levels (mean $\Omega_{\text{arag}} = 2.85$) are some of the lowest measured in coral reef ecosystems.” Shamberger *et al.* conclude “it appears that while calcification rate and Ω_{arag} are correlated within a single coral reef ecosystem,” as in the case of the barrier reef of Kaneohe Bay, “this relationship does not necessarily hold between different coral reef systems,” and it can

thus be expected “ocean acidification will not affect coral reefs uniformly and that some may be more sensitive to increasing $p\text{CO}_2$ levels than others.” That implies (taking a more positive view of the subject) some coral reefs may be less sensitive to increasing $p\text{CO}_2$ than others.

McCulloch *et al.* (2012) state “for cold-water corals, which are already living at low levels of carbonate saturation, the shoaling of the saturation horizon as carbonate saturation states decrease [in response, for example, to rising atmospheric CO_2 concentrations] has the potential to cause dramatic declines in rates of calcification, or the dissolution of the carbonate skeletons of those living at or close to the saturation horizon.” Since these corals are indeed living there, they speculate “they may have evolved adaptive strategies to counter the effects of low carbonate saturation states,” one of which is to up-regulate their internal pH to a value that allows calcification to occur.

McCulloch *et al.* extended the novel approach of Trotter *et al.* (2011), based on boron isotopic systematics, to determine the relationship between seawater pH and the internal (extracellular) pH_{cf} at the site of calcification for several azooxanthellate cold-water scleractinian corals, collected from a large range of depths and geographically disparate sites, including southeast Australia, Chile’s Comau Fjord, the Marmara Sea, a number of sites in the Mediterranean Sea, the northeast Atlantic Ocean, and the northwestern Hawaiian Islands.

The suite of “aragonitic cold-water coral species,” as the 11 researchers describe them, “collectively show an overall trend of higher ΔpH [= pH_{cf} - seawater pH] values that is anti-correlated with seawater pH, with systematics generally consistent with biologically controlled pH up-regulation.” This result indicates, “like symbiont-bearing tropical corals (Trotter *et al.*, 2011), they have the ability to ameliorate or buffer external changes in seawater pH by up-regulating their pH_{cf} at the site of calcification.”

McCulloch *et al.* conclude “cold-water corals are likely to be much more resilient to decreasing seawater pH from ocean acidification than previously realized,” because, as they see it, “decreasing seawater pH alone will only marginally affect calcification rates since this process would be largely countered by pH_{cf} up-regulation in cold-water corals, together with enhanced calcification rates from warming of the deep oceans.”

Jantzen *et al.* (2013) write ocean acidification “is thought to negatively affect most marine-calcifying organisms, notably cold-water corals (CWC),” which

might be expected to be especially sensitive due to the deep and cold waters in which they are typically found. They measured water profiles with a CTD (conductivity, temperature, depth) multi-probe profiler along the Comau fjord, extending down to 50–60 meters in 2010 and down to 225 meters in 2011, which allowed them to detect and describe the spatial distribution of the cold-water coral *Desmophyllum dianthus*.

The seven scientists determined *D. dianthus* grows along the fjord over its entire pH range, where “it occurs in shallow depths (below 12 m, pH 8.1) as part of a deep-water emergence community, but also in [water of] 225 m depth at a pH of 7.4.” They report the cold-water coral thrives close to the aragonite saturation horizon and even below it, where they found “flourishing coral banks.”

Jantzen *et al.* note other studies “question reduced calcification rates of corals in environments with lowered aragonite saturation state (Ω_{arg}),” citing Marubini *et al.* (2008) and Jury *et al.* (2010), but they note “very recent studies hint at a higher acclimatization potential of cold-water corals to ocean acidification,” citing Rodolfo-Metalpa *et al.* (2010), Trotter *et al.* (2011), Form and Riebesel (2012), and McCulloch *et al.* (2012a,b).

Thresher *et al.* (2011) state concerns about the effects of lower ocean pH levels on marine ecosystems “are based primarily on modeling studies and short-term laboratory exposure to low-carbonate conditions,” citing Riegl *et al.* (2009), Veron *et al.* (2009), and Ries *et al.* (2010). They say “their relevance to long-term exposure in the field and the potential for ecological or evolutionary adjustment are uncertain,” citing Maynard *et al.* (2008). In an effort “to determine the sensitivity of corals and allied taxa to long-term exposure to very low carbonate concentrations,” Thresher *et al.* examined “the depth distribution and life-history characteristics of corals and other shell-forming megabenthos along the slopes of deep-sea seamounts and associated structure in the SW Pacific,” where the gradient of water chemistry ranged from super-saturated in the case of aragonite and high-magnesium calcite (HMC) to under-saturated with calcite.

The five researchers “found little evidence that carbonate under-saturation to at least -30% affected the distribution, skeletal composition, or growth rates of corals and other megabenthos on Tasmanian seamounts.” They found “both solitary scleractinian corals and colonial gorgonians were abundant at depths well below their respective saturation horizons and appeared healthy,” and HMC echinoderms were

common as deep as they sampled (4,011 m), in water approximately 45% under-saturated. They also report, “for both anthozoan and non-anthozoan taxa, there was no obvious difference in species’ maximum observed depths as a function of skeletal mineralogy.” In other words, the community “was not obviously shifted towards taxa with either less soluble or no skeletal structure at increasing depth.” They conclude, “it is not obvious from our data that carbonate saturation state and skeletal mineralogy have any effect on species’ depth distributions to the maximum depth sampled,” and they saw “little evidence of an effect of carbonate under-saturation on growth rates and skeletal features.”

Thresher *et al.* write, “the observation that the distributions of deep-sea corals are not constrained by carbonate levels below saturation is broadly supported by the literature,” noting “solitary scleractinians have been reported as deep as 6 km (Fautin *et al.*, 2009) and isidid gorgonians as deep as 4 km (Roark *et al.*, 2005).” They say their own data also “provide no indication that conditions below saturation per se dictate any overall shifts in community composition.”

Explaining these results, the researchers note one or more cell membranes may envelop the organisms’ skeletons, largely isolating the calcification process and its associated chemistry from the bulk seawater, citing McConnaughey (1989), Adkins *et al.* (2003), and Cohen and McConnaughey (2003), and this phenomenon could presumably protect “the skeleton itself from the threat of low carbonate dissolution.” In addition, Thresher *et al.* note, “calcification is energetically expensive, consuming up to 30% of the coral’s available resources, and ... normal calcification rates can be sustained in relatively low-carbonate environments under elevated feeding or nutrient regimes,” as described in detail by Cohen and Holcomb (2009). Thresher *et al.* conclude, “Although saturation levels in those studies are considerably higher than those experienced by the deep-sea taxa we observed, the principle that elevated food availability could compensate for the higher costs of calcification in heterotrophic deepsea species appears plausible.”

Thresher *et al.* say their data clearly suggest, whatever the cause, “a change in carbonate saturation horizons per se as a result of ocean acidification is likely to have only a slight effect on most of the live deep-sea biogenic calcifiers.”

Anthony *et al.* (2011) used “a carbon flux model for photosynthesis, respiration, calcification and dissolution coupled with Lagrangian transport to

examine how key groups of calcifiers (zooxanthellate corals) and primary producers (macroalgae) on coral reefs contribute to changes in the seawater carbonate system as a function of water residence time.” The examination showed “the carbon fluxes of corals and macroalgae drive Ω_a in opposing directions,” and “areas dominated by corals elevate pCO_2 and reduce Ω_a , thereby compounding ocean acidification effects in downstream habitats, whereas algal beds draw CO_2 down and elevate Ω_a , potentially offsetting ocean acidification impacts at the local scale.” They also report simulations for two significantly elevated CO_2 scenarios (600 and 900 ppm CO_2) suggest “a shift in reef community composition from coral to algal dominance in upstream areas under ocean acidification will potentially improve conditions for calcification in downstream areas.”

Kleypas *et al.* (2011) provided field validation of the simulations of Anthony *et al.* by examining the roles of three key members of benthic reef communities—corals, macroalgae, and sand—in modifying the chemistry of open-ocean source water. They found “the drawdown of total dissolved inorganic carbon due to photosynthesis and calcification of reef communities can exceed the drawdown of total alkalinity due to calcification of corals and calcifying algae, leading to a net increase in aragonite saturation state.” They note there were no seagrasses on the reef flat they studied, and “research suggests that seagrasses may have an additional impact on reef seawater chemistry because they enhance the alkalinity flux from sediments (Burdige and Zimmerman, 2002), and they respond to CO_2 fertilization (Palacios and Zimmerman, 2007).”

These observations suggest reef communities gradually could alter their spatial compositions in a CO_2 -accreting world to the point where seagrasses and other macroalgae take up residence in upstream regions, while corals and other calcifying organisms lay claim to downstream regions. Anthony *et al.* (2011) conclude, “although the carbon fluxes of benthic reef communities cannot significantly counter changes in carbon chemistry at the scale of oceans, they provide a significant mechanism of buffering ocean acidification impacts at the scale of habitat to reef.”

Manzello *et al.* (2012) note although many people expect future ocean acidification (OA) resulting from rising atmospheric CO_2 concentrations to reduce the calcification rates of marine organisms, we have little understanding of how OA will manifest in dynamic, real-world systems, because “natural CO_2 , alkalinity, and salinity gradients can significantly alter local

carbonate chemistry, and thereby create a range of susceptibility for different ecosystems to OA.” “To determine if photosynthetic CO₂ uptake associated with seagrass beds has the potential to create OA refugia,” Manzello *et al.* repeatedly measured carbonate chemistry across an inshore-to-offshore gradient in the upper, middle, and lower Florida Reef Tract over a two-year period.

During times of heightened oceanic vegetative productivity, the five U.S. researchers found, “there is a net uptake of total CO₂ which increases aragonite saturation state (Ω_{arag}) values on inshore patch reefs of the upper Florida Reef Tract,” and “these waters can exhibit greater Ω_{arag} than what has been modeled for the tropical surface ocean during preindustrial times, with mean Ω_{arag} values in spring equaling 4.69 ± 0.10 .” They report Ω_{arag} values on offshore reefs “generally represent oceanic carbonate chemistries consistent with present day tropical surface ocean conditions.”

Manzello *et al.* hypothesize the pattern described above “is caused by the photosynthetic uptake of total CO₂ mainly by seagrasses and, to a lesser extent, macroalgae in the inshore waters of the Florida Reef Tract.” They conclude these inshore reef habitats are “potential acidification refugia that are defined not only in a spatial sense, but also in time, coinciding with seasonal productivity dynamics,” which further implies “coral reefs located within or immediately downstream of seagrass beds may find refuge from ocean acidification.” They cite Palacios and Zimmerman (2007), whose work they describe as indicating “seagrasses exposed to high-CO₂ conditions for one year had increased reproduction, rhizome biomass, and vegetative growth of new shoots, which could represent a potential positive feedback to their ability to serve as ocean acidification refugia.”

Noonan *et al.* (2013) write, “ocean acidification (OA) is expected to negatively affect coral reefs,” but “little is known about how OA will change the coral-algal symbiosis on which reefs ultimately depend.” They state, “to date it remains unknown if corals are able to respond to rising CO₂ concentrations by changing to better adapted dominant *Symbiodinium* types after long-term exposure to elevated pCO₂ in the field,” the field being the ocean, in this case. Noonan *et al.* investigated “the dominant types of *Symbiodinium* associating with six species of scleractinian coral that were exposed to elevated partial pressures of carbon dioxide (pCO₂) *in situ* from settlement and throughout their lives.” They did so “at three naturally occurring volcanic CO₂ seeps

(pCO₂ ~500 to 900 ppm, pH_{Total} 7.8–7.9) and adjacent control areas (pCO₂ ~390 ppm, pH_{Total} ~8.0–8.05) in Papua New Guinea,” and “*Symbiodinium* associated with corals living in an extreme seep site (pCO₂ >1000 ppm) were also examined.”

In five of the six species studied, the researchers report, “85–95% of samples exhibited the same *Symbiodinium* type across all sites, with remaining rare types having no patterns attributable to CO₂ exposure.” The sixth species of coral did display “site specific differences in *Symbiodinium* types,” but these were “unrelated to CO₂ exposure.” The scientists write, “*Symbiodinium* types from the coral inhabiting the extreme CO₂ seep site were found commonly throughout the moderate seeps and control areas.” These findings suggest the six species of coral Noonan *et al.* studied, plus the various *Symbiodinium* types they encountered, were able not only to survive but to function well throughout the full range of CO₂-induced pH values to which they had been exposed.

Wall and Edmunds (2013) note laboratory studies “typically are performed under conditions that do not replicate the natural environment perfectly, notably by providing light at a constant low intensity throughout the day, and with a spectral composition differing from ambient sunlight,” citing Kinzie *et al.* (1984) and Schlacher *et al.* (2007). “Also of great importance,” they write, “is the hydrodynamic regime of reef environments (Monismith, 2007), which is difficult to recreate in tanks and yet is critical for multiple aspects of coral physiology (Dennison and Barnes, 1988; Patterson *et al.*, 1991).”

Wall and Edmunds collected juvenile *Porites* spp. from 2–3 m depths on the back reef of Moorea, attached them to plastic bases with epoxy, and after allowing them to recover in a 1,000-L flow-through tank placed them in nine 150-L reservoirs consisting of three replicates each of filtered seawater maintained at three conditions: Treatment 1 (unmanipulated seawater), Treatment 2 (seawater equilibrated with pCO₂ at 98.9 Pa), and Treatment 3 (same as Treatment 2 but augmented with baking soda to increase [HCO₃⁻] to 2730 $\mu\text{mol kg}^{-1}$ at a pH_T of 7.69). They conducted three experiments on 4, 6, and 8 February 2012, where in each case the custom-cast, UV-transparent acrylic chambers they created remained on the reef for 28 hours.

They found no differences between the behaviors of the juvenile massive *Porites* corals in Treatments 1 and 2, but calcification was enhanced by fully 81% in Treatment 3 relative to Treatments 1 and 2. The two U.S. researchers conclude, “these findings indicate that juvenile massive *Porites* spp. are resistant to

short exposures to OA *in situ*,” and “they can increase calcification at low pH and low Ω_{arg} if $[\text{HCO}_3^-]$ is elevated.” The latter finding leads them also to suggest calcification of juvenile *Porites* spp. may “be limited by dissolved inorganic carbon under ambient pCO₂ condition.”

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Climate Change Reconsidered II: Biological Impacts

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6.3.3.3 Crustaceans

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on marine crustaceans. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Survival of shrimp larvae was not reduced by lower ocean pH levels .
- At reduced seawater pH the velvet swimming crab was able to “buffer changes to extra-cellular pH over 30 days exposure” and do so “with no evidence of net shell dissolution.” In addition, “tolerance to heat, carapace mineralization, and aspects of immune response were not affected by hypercapnic conditions.”
- The early life larval stages of the bay barnacle “are generally tolerant to near-future levels of ocean acidification,” and this observation “is in line with findings for other barnacle species.” In addition, its “substantial genetic variability in response to low pH may confer adaptive benefits under future ocean acidification.”
- Vertically migrating adult Arctic copepods daily cross a pCO₂ range of less than 140 μatm and show

“only minor responses to manipulated high CO₂,” suggesting “the natural range of pCO₂ experienced by an organism determines its sensitivity to future OA.”

Noting “there is a particular need to study effects of OA [ocean acidification] on organisms living in cold-water environments due to the higher solubility of CO₂ at lower temperatures,” Bechmann *et al.* (2011) maintained shrimp (*Pandalus borealis*) larvae, from day 1 through day 36 post-hatching, under the OA scenario predicted for the year 2100 (pH 7.6) and compared them against batches of larvae held under the current oceanic pH of 8.1 (the control treatment), while water temperature was kept at a constant 5°C. Bechmann *et al.* report survival of the larvae was not reduced at any time during the experiment, but there was “a significant delay in zoeal progression (development time),” which “may increase the chance of loss by predation.” They note “a multi-generation experiment with the copepod *Acartia tonsa* showed that effects of OA observed in the first generation were no longer present in the second and third generation (Dupont and Thorndyke, 2009),” implying that could also prove true in the situation they investigated. The eight Norwegian researchers conclude, “there are different opinions about how to extrapolate the effects of OA from a single species examined in relatively short-term experiments to the population and ecosystem level,” noting “all agree that more data from relevant long-term experiments are needed to better predict effects at higher levels of biological organization,” citing Dupont *et al.* (2010a,b), Hendriks and Duarte (2010), and Hendricks *et al.* (2010).

Small *et al.* (2010) investigated the potential effects of lower ocean pH levels on the velvet swimming or “devil” crab (*Necora puber*). Working with adult individuals collected from the lower intertidal zone of Mount Batten Beach, Plymouth, UK, the authors tested the effect of 30 days’ exposure of the crabs to seawater maintained in 4-L aquaria at pH values of 8.0 (control), 7.3, and 6.7. They found “*Necora puber* was able to buffer changes to extracellular pH over 30 days exposure,” and to do so “with no evidence of net shell dissolution.” They report, “tolerance to heat, carapace mineralization, and aspects of immune response were not affected by hypercapnic conditions”—i.e., conditions that lead to more than the normal level of carbon dioxide in an organism’s blood. About the only negative finding was a decline in whole-animal oxygen consumption, which they described as being “marginal” between

the control and medium hypercapnic conditions, but “significant” at the unrealistic future pH value of 6.7. Small *et al.* conclude their results “confirm that most physiological functions in *N. puber* are resistant to low pH/hypercapnia over a longer period than previously investigated.”

In two experiments conducted over two successive years, Pansch *et al.* (2013) first assessed larval survival and development of the bay barnacle *Amphibalanus improvisus* while rearing nauplius larvae in six-well plates over 10 days in response to three pH treatments (8.02, 7.80, and 7.59). In the second experiment they assessed larval stage and size by rearing nauplius larvae in 5-L glass bottles over six days with two pH treatments (8.09 and 7.80). The three scientists report the “larval development of the barnacle was not significantly affected by the level of reduced pH that has been projected for the next 150 years,” noting, “after 3 and 6 days of incubation, we found no consistent effects of reduced pH on developmental speed or larval size at pH 7.8 compared with the control pH of 8.1.” They write, “after 10 days of incubation, there were no net changes in survival or overall development of larvae raised at pH 7.8 or 7.6 compared with the control pH of 8.0.” In their many individual trials, they determined “there was significant variation in responses between replicate batches (parental genotypes) of some larvae,” with some batches responding positively to reduced pH.

Pansch *et al.* say their results suggest “the non-calcifying larval stages of *A. improvisus* are generally tolerant to near-future levels of ocean acidification,” and “this result is in line with findings for other barnacle species and suggests that barnacles do not show the greater sensitivity to ocean acidification in early life history reported for other invertebrate species.” They also state the barnacle’s “substantial genetic variability in response to low pH may confer adaptive benefits under future ocean acidification.”

According to Lewis *et al.* (2013), “copepods comprise the dominant Arctic zooplankton; hence, their responses to OA [ocean acidification] have important implications for Arctic ecosystems, yet there is little data on their current under-ice winter ecology on which to base future monitoring or make predictions about climate-induced change.” Lewis *et al.* examined “the natural distributions of the dominant Arctic copepods found under winter sea ice in relation to the current seawater carbonate chemistry conditions and compared these with their short-term responses to future high CO₂ conditions.” They conducted this work “at the temporary Catlin Arctic

Survey Ice Base (CIB) during late winter to early spring in 2011,” where “the zooplankton were dominated by adult calanoid copepods, comprising mainly the Arctic endemics *Calanus glacialis* and *Calanus hyperboreus* but also the smaller, globally occurring *Oithona similis*, together with the nauplii of various copepod species.” They conducted a series of OA experiments “using these copepod species and life history stages to compare their response to future high CO₂ conditions with natural under-ice pCO₂ exposures.”

The five researchers’ data revealed “species and life stage sensitivities to manipulated conditions were correlated with their vertical migration behavior and with their natural exposures to different pCO₂ ranges,” and “vertically migrating adult *Calanus* spp. crossed a pCO₂ range of >140 µatm daily and showed only minor responses to manipulated high CO₂,” whereas “*Oithona similis*, which remained in the surface waters and experienced a pCO₂ range of <75 µatm, showed significantly reduced adult and nauplii survival in high CO₂ experiments.”

Lewis *et al.* conclude, “the natural range of pCO₂ experienced by an organism determines its sensitivity to future OA,” adding, “certainly, ubiquitous species in their adult form, living across a range of physicochemical conditions, are likely capable of surviving change.” They also note the “larvae of many marine organisms are released at very specific times to coincide with favorable environmental or food conditions,” and it seems logical to conclude the same would hold true in the future, making it easier for copepod larvae to survive future OA conditions as well.

Pedersen *et al.* (2013) investigated “the impact of medium-term exposure to CO₂ acidified seawater on survival, growth and development ... in the North Atlantic copepod *Calanus finmarchicus*.” Using a custom-developed experimental system, “fertilized eggs and subsequent development stages were exposed to normal seawater (390 ppm CO₂) or one of three different levels of CO₂-induced acidification (3,300, 7,300, 9,700 ppm CO₂).” The four Norwegian researchers report, “following the 28-day exposure period, survival was found to be unaffected by exposure to 3,300 ppm CO₂, but significantly reduced at 7,300 and 9,700 ppm CO₂,” values far beyond any atmospheric concentration predicted under even the most extreme of circumstances. Pedersen *et al.* conclude, “the absence of any apparent reduction in the overall survival during the present medium-term exposure to 3,300 ppm CO₂, indicates that survival of *Calanus* eggs and nauplii may be robust against the

direct effects of the worst-case CO₂ scenario predicted for year 2300.”

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6.3.3.4 Echinoderms

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on marine echinoderms. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- The common sea star *C. papposus* is “positively impacted by ocean acidification,” as “larvae and juveniles raised at low pH grow and develop faster, with no negative effect on survival or skeletogenesis.”
- Adults of the sea star *Luidia clathrata* exposed to end-of-century pH conditions “are relatively unimpaired in their regenerative capacity,” which “encompasses not only their ability to re-grow their arms, but their ability to allocate materials and energy to regenerated somatic body components.”
- “*Paracentrotus lividus* appears to be extremely resistant to low pH, with no effect on fertilization success or larval survival.”
- “Polar and sub-polar sea urchin larvae can show a certain degree of resilience to acidification” and do not appear to be more susceptible to lower seawater pH than their temperate and tropical counterparts.
- Gametes from *Sterechinus neumayeri* are “relatively robust to pH change, especially to changes within the range predicted for the near future (i.e. a decrease of 0.3–0.5 pH units).”
- “Sea urchins inhabiting stressful intertidal environments produce offspring that may better resist future ocean acidification.”
- In studies designed to reveal the effects of atmospheric CO₂ enrichment upon marine life, treatment comparisons should be made at equivalent development stages of the organism being studied. At such points along the life cycle, studies have shown there to be no significant physical differences between individuals raised under control or CO₂-enriched conditions.

- Lower ocean pH levels induced a developmental delay in *P. lividus*, yet “at a given developmental state (or size), larvae present the same calcium incorporation rate regardless of pH.”
- *Strongylocentrotus purpuratus* sea urchins “demonstrate the capacity for rapid evolution in the face of ocean acidification and show that standing genetic variation could be a reservoir of resilience to climate change in [a] coastal upwelling ecosystem.”

According to Dupont *et al.* (2010), “echinoderms are among the most abundant and ecologically successful groups of marine animals (Micael *et al.*, 2009), and are one of the key marine groups most likely to be impacted by predicted climate change events,” presumably because “the larvae and/or adults of many species from this phylum form skeletal rods, plates, test, teeth, and spines from an amorphous calcite crystal precursor, magnesium calcite, which is 30 times more soluble than normal calcite (Politi *et al.*, 2004).” This fact normally would be thought to make it much more difficult for echinoderms (relative to most other calcifying organisms) to produce calcification-dependent body parts.

Dupont *et al.* studied naturally fertilized eggs of the common sea star *Crossaster papposus*, which they collected and transferred to five-liter culture aquariums filled with filtered seawater (a third of which was replaced every four days). They regulated the pH of the tanks to values of either 8.1 or 7.7 by adjusting environmental CO₂ levels to either 372 ppm or 930 ppm, documenting settlement success as the percentage of initially free-swimming larvae that affixed themselves to the aquarium walls, larval length at various time intervals, and degree of calcification. The three researchers report results the opposite of what is often predicted: The echinoderm larvae and juveniles were “positively impacted by ocean acidification.” They found “larvae and juveniles raised at low pH grow and develop faster, with no negative effect on survival or skeletogenesis within the time frame of the experiment (38 days).” They report the sea stars’ growth rates were “two times higher” in the low pH seawater, and “*C. papposus* seem to be not only more than simply resistant to ocean acidification, but are also performing better.”

The Swedish scientists conclude, “in the future ocean, the direct impact of ocean acidification on growth and development potentially will produce an increase in *C. papposus* reproductive success,” and “a

decrease in developmental time will be associated with a shorter pelagic period with a higher proportion of eggs reaching settlement,” leading the sea stars to become “better competitors in an unpredictable environment.”

Schram *et al.* (2011) investigated the effects of lower ocean pH levels on another sea star, *Luidia clathrata*. They write, “two groups of sea stars, each with two arms excised, were maintained on a formulated diet in seawater bubbled with air alone (pH 8.2, approximating a $p\text{CO}_2$ of 380 ppm) or with a controlled mixture of air/ CO_2 (pH 7.8, approximating a $p\text{CO}_2$ of 780 ppm),” and “arm length, total body wet weight, and righting responses were measured weekly.” After 97 days, “a period of time sufficient for 80% arm regeneration,” they state “protein, carbohydrate, lipid and ash levels were determined for body wall and pyloric caecal tissues of intact and regenerating arms of individuals held in both seawater pH treatments.”

The four U.S. researchers report, “adults of the common soft bottom predatory sea star *Luidia clathrata* exposed to end-of-century conditions of ocean acidification (pH 7.8) are relatively unimpaired in their regenerative capacity,” which “encompasses not only their ability to re-grow their arms, but their ability to allocate materials and energy to regenerated somatic body components.” They found “no discernable pattern arising from exposure to a reduced seawater pH of 7.8 for 97 days on righting behavior,” which they say is “an integrative measure of stress.” Schram *et al.* conclude, “the demonstration of an organism’s ability to sustain normal functions under these conditions is as equally important to document as those that are negatively impacted,” because “this information will be critical to future assessments of prospective impacts of ocean acidification at the community level.”

Schlegel *et al.* (2012) note “environmental factors directly affect populations by selecting resilient individuals,” and “selection at the gametic level, or during early life, has strong and immediate effects at the population level, carrying over into subsequent life stages,” as “heritability of this resilience leads to cascading adaptive effects in subsequent generations.” As an example of this process, they report, “in free-spawning marine organisms, sperm selection during fertilization plays a key role by determining the nature and diversity of genotypes in the subsequent generation (Levitan, 1996; 2008) and thus their resilience to environmental change.”

Schlegel *et al.* investigated “the effects of CO_2 -induced ocean acidification on the early life history

stages in the Australasian sea urchin *Heliocidaris erythrogramma*, focusing on intra-specific variation in responses, which can be highly variable for this species (Evans and Marshall, 2005).” They followed “the A1FI-scenario from IPCC’s 4th assessment report” and “compared the effects of present day conditions for southeast Australia with the end-of-century scenario ($p\text{CO}_2=970$ ppm; pH=0.3 unit reduction) and a high- CO_2 scenario ($p\text{CO}_2=1600$ ppm; pH=0.5 unit reduction).” They write, “observed effects on sperm swimming behavior were applied within an established fertilization kinetics modeling framework (Vogel *et al.*, 1982; Styan *et al.*, 2008) to predict fertilization outcomes of single urchin pairs at each $p\text{CO}_2$ level.” These results “were then compared to observed results from fertilization experiments conducted in the laboratory.”

Schlegel *et al.* found “acidification significantly decreased the proportion of motile sperm but had no effect on sperm swimming speed,” and the four researchers state the subsequent fertilization experiments “showed strong inter-individual variation in responses to ocean acidification, ranging from a 44% decrease to a 14% increase in fertilization success.” They say their results indicate “some individuals will exhibit enhanced fertilization success in acidified oceans, supporting the concept of ‘winners’ and ‘losers’ of climate change at an individual level.” If these differences are heritable, they say, it is likely “ocean acidification will lead to selection against susceptible phenotypes as well as to rapid fixation of alleles that allow reproduction under more acidic conditions,” and these phenomena “may ameliorate the biotic effects of climate change if taxa have sufficient extant genetic variation upon which selection can act.”

Moulin *et al.* (2011) supplied real-world data indicating phenotypic adaptation to seawater of lower pH by conducting a field experiment on the sea urchin *Paracentrotus lividus* in an attempt “to compare the effect of pH on the progeny of individuals collected from the same shore, i.e., same population, but from distinct tide pools: one where night pH was significantly reduced and the other where this decline was not so important.” The four Belgian researchers report the pH of coastal seawater at the site they studied (Aber, Crozon peninsula, southern Brittany, France) was 8.14, but they say at the end of the night low tides, tide pools 1 (subtidal) and 2 (intertidal) had pH values of, respectively, 7.8 and 7.4. Under these conditions, they detected “no significant difference in gonad maturity between individuals from the two tide pools,” and “the offspring of sea urchins from the tide

pool with higher pH decrease (tide pool 2) showed a better resistance to acidification at pH 7.4 than that of sea urchins from the tide pool with low pH decrease (tide pool 1) in terms of fertilization, viz. a reduction of over 30% [for tide pool 1] compared to about 20% for tide pool 2.”

Moulin *et al.* conclude “sea urchins inhabiting stressful intertidal environments produce offspring that may better resist future ocean acidification.” They also note “the fertilization rate of gametes whose progenitors came from the tide pool with higher pH decrease was significantly higher,” suggesting “a possible acclimation or adaptation of gametes to pH stress.”

Martin *et al.* (2011) write, “ocean acidification is predicted to have significant effects on benthic calcifying invertebrates, in particular on their early developmental states,” and “echinoderm larvae could be particularly vulnerable to decreased pH, with major consequences for adult populations.” The authors explored the effect of a gradient of decreasing pH from 8.1 to 7.0—corresponding to atmospheric CO₂ concentrations of ~400 ppm to ~6,630 ppm—on the larvae of the sea urchin *Paracentrotus lividus*, a common, economically and ecologically important species widely distributed throughout the Mediterranean Sea and the northeast Atlantic from Ireland to southern Morocco. The scientists used “multiple methods to identify the response of *P. lividus* to CO₂-driven ocean acidification at both physiological (fertilization, growth, survival and calcification) and molecular (expression of genes involved in calcification and development) levels.”

They found “*Paracentrotus lividus* appears to be extremely resistant to low pH, with no effect on fertilization success or larval survival.” They reported “larval growth was slowed when exposed to low pH,” as larvae of *P. lividus* “collected at pH 7.5 at 46 hours post-fertilization (real age) were smaller than in the control treatment [pH 8.1] and corresponded to a virtual age of 36 hours (a delay in development of 10 hours).” They further report, “down to a pH of 7.25, the larvae at Day 3 have a normal morphology but are delayed in development,” so the apparent decrease in calcification at that point in time is, as they put it, “simply an indirect consequence of the impact of low pH on developmental rate.” They continue, “at a given developmental state (or size), larvae present the same calcium incorporation rate regardless of pH.” The scientists also report “genes involved in development and biomineralization were upregulated by factors of up to 26 at low pH,” which suggests “plasticity at the gene expression level” in *P. lividus*

“allows a normal, but delayed, development under low pH conditions.”

Ericson *et al.* (2010) note in polar latitudes “the effects of changing pCO₂ and pH on gametes may be influenced by the carbonate chemistry of cold water, such as the already higher pCO₂ and lower seawater pH,” and “it has also been predicted that ocean acidification effects on organisms may be more apparent and appear earliest in polar waters.” Ericson *et al.* “investigated the effects of present-day pH 8.0, predicted ocean surface pH for the years 2100 and 2300 (pH 7.7 and pH 7.3, respectively) and an extreme pH (pH 7.0) on fertilization and embryogenesis in the Antarctic nemertean worm *Parborlasia corrugatus* and sea urchin *Sterechinus neumayeri*.”

The four researchers found “fertilization success was not affected by pH in *P. corrugatus* across a range of sperm concentrations,” and “fertilization success in *S. neumayeri* declined significantly in pH 7.0 and 7.3 seawater, but only at low sperm concentration.” They observe, “seawater pH had no effect on the rate of egg cleavage in *S. neumayeri*, or the proportion of abnormal embryos 1-day post-fertilization,” and “*P. corrugatus* embryogenesis was also relatively robust to pH changes, with a significant effect detected only when the seawater pH was decreased to 7.0.” Ericson *et al.* conclude, “as in a number of other studies (see reviews by Byrne *et al.*, 2010; Dupont *et al.*, 2010), that gametes appeared relatively robust to pH change, especially to changes within the range predicted for the near future (i.e. a decrease of 0.3–0.5 pH units),” and they say their initial findings “do not support a view that polar species are more affected by lowered pH compared with temperate and tropical counterparts (as has also been shown for the later developmental stages of *S. neumayeri* (Clark *et al.*, 2009)).”

Yu *et al.* (2013) tested the effects of high CO₂/low pH on early development and larval growth by exposing *Sterechinus neumayeri* to environmental levels of CO₂ in McMurdo Sound (control: 410 ppm) and mildly elevated CO₂ levels, both near the level of the aragonite saturation horizon (510 ppm), and to under-saturating conditions (730 ppm). Over the course of development from egg to late four-arm pluteus, they found, “(1) early embryological development was normal with the exception of the hatching process, which was slightly delayed, (2) the onset of calcification as determined by the appearance of CaCO₃ spicule nuclei was on schedule, (3) the lengths of the spicule elements, and the elongation of the spicule nuclei into the larval skeleton, were significantly shorter in the highest CO₂ treatment four

days after the initial appearance of the spicule nuclei, and (4) finally, without evidence of true developmental delay, larvae were smaller overall under high CO₂ treatments; and arm length, the most plastic morphological aspect of the echinopluteus, exhibited the greatest response to high CO₂/low pH/low carbonate conditions.” Yu *et al.* conclude, “effects of elevated CO₂ representative of near future climate scenarios are proportionally minor on these early development stages.”

Yu *et al.* (2011) raised larvae of the purple sea urchin (*Strongylocentrotus purpuratus*) in seawater maintained at pCO₂ levels ranging from ambient to 1,000 and 1,450 ppm CO₂ (pH 7.7 and 7.5, respectively) while measuring, after three and six days of development, “total larval length (from the spicule tip of the postoral arm to the spicule tip of the aboral point) along the spicules, to assess effects of low pH upwelling water on morphology.” They found “even at the highest pCO₂ treatments, larval development was normal in terms of timing and morphological appearance,” although at both days 3 and 6 larvae in the 1,450 ppm CO₂ treatment were 7–13% smaller than control larvae. Yu *et al.* also report “the observed developmental progression and survival of cultures was within the norm typically observed for this species at this temperature range.” They note, “a lack of developmental deformities at early stages for pCO₂ ~1000 ppm has been previously reported for this species (Todgham and Hofmann, 2009), and another local species, *Lytechinus pictus*, with a similar overlapping portion of its range in southern California (O'Donnell *et al.*, 2010).” They also remark, “there are even reports survival is increased in this species and its congener *S. droebachiensis* under some low pH conditions (Dupont and Thorndyke, 2008).”

Yu *et al.* conclude, “the effects of small magnitude in these urchin larvae are indicative of a potential resilience to near-future levels of ocean acidification.”

Stumpp *et al.* (2011a) evaluated the impacts of elevated seawater pCO₂ (1,264 ppm vs. 375 ppm) on the early development of, and the larval metabolic and feeding rates of, *Strongylocentrotus purpuratus*. The researchers assessed growth and development daily, for three weeks, in terms of total body length, body rod length, postoral rod length, and postero-lateral rod length, as well as mortality and feeding and metabolic rates. They found daily mortality rate (DMR) was higher under control conditions (DMR = 2.7% per day) than under high seawater pCO₂ (DMR = 2.2% per day). They also observed, in the elevated

CO₂ treatment, larval development was about 8% slower, such that it took slightly longer for the organisms to reach equivalent development stages in the high CO₂ treatment.

As a result of the slower development of the larvae in the high CO₂ treatment, at any given time the individuals in this treatment were smaller and less well-developed than those in the control treatment, and if that were the only comparison made in this study, the effects of elevated CO₂ would seem to be negative. However, the researchers also made comparisons on the basis of development stage, and they found there were no long-term physical differences between the larvae living in the high and low CO₂ treatments.

Thus in studies designed to reveal the effects of atmospheric CO₂ enrichment on various species of marine life, treatment comparisons should be made at equivalent development stages of the organism being studied. At such points along the life cycle of the purple sea urchin, there were no significant physical differences between individuals raised in the control and CO₂-enriched conditions. Stumpp *et al.* conclude, “we suggest that body length is a useful scale of reference for studies in sea urchin larvae where a morphological delay in development occurs,” and “using time post-fertilization as a reference may lead to misinterpretation of data”—by wrongfully assuming a negative result when in fact there may be no deleterious effect of lower ocean pH levels. Stumpp *et al.* (2011b) reached essentially the same conclusion in a companion paper, writing, “in studies in which a stressor induces an alteration in the speed of development, it is crucial to employ experimental designs with a high time resolution in order to correct for developmental artifacts,” as this protocol “helps prevent misinterpretation of stressor effects on organism physiology.”

Pespeni *et al.* (2013) note “little is known about the adaptive capacity of species to respond to an acidified ocean,” and, as a result, “predictions regarding future ecosystem responses remain incomplete.” They demonstrated lower ocean pH levels generate striking patterns of genome-wide selection in purple sea urchins (*Strongylocentrotus purpuratus*) cultured under CO₂ levels of 400 and 900 ppm. Working with seven populations collected along a 1,200 km mosaic of coastal upwelling-driven acidification of the California Current System, Pespeni *et al.* combined sequencing across the transcriptome of the purple sea urchin, growth measurements under experimental acidification, and tests of frequency shifts in 19,493 polymorphisms

during development, detecting in the process “the widespread occurrence of genetic variation to tolerate ocean acidification.”

Although larval development and morphology showed little response to elevated CO₂, the 11 researchers found “substantial allelic change in 40 functional classes of proteins involving hundreds of loci.” They state “pronounced genetic changes, including excess amino acid replacements, were detected in all populations and occurred in genes for biomineralization, lipid metabolism, and ion homeostasis—gene classes that build skeletons and interact in pH regulation.” They note “such genetic change represents a neglected and important impact of ocean acidification that may influence populations that show few outward signs of response to acidification.” The researchers conclude “our results demonstrate the capacity for rapid evolution in the face of ocean acidification and show that standing genetic variation could be a reservoir of resilience to climate change in this coastal upwelling ecosystem.”

Catarino *et al.* (2012) studied the development of larvae produced by adults of the *Arbacia dufresnei* urchin, which they collected from a sub-Antarctic population in the Straits of Magellan near Punta Arenas, Chile, immersed in high (8.0), medium (7.7), and low (7.4) pH seawater. The five scientists found “the proportion of abnormal larvae did not differ according to [pH] treatment.” Although “lower pH induced a delay in development,” which also was noted by Dupont *et al.* (2010), it “did not increase abnormality.” Catarino *et al.* report, “even at calcium carbonate saturation states <1, skeleton deposition occurred,” and they note specimens of *Heliocidaris erythrogramma* also “seem not to be affected by a pH decrease (until 7.6),” citing Byrne *et al.* (2009a,b). They note the Antarctic *Sterechinus neumayeri* is thought to be “more robust to ocean acidification than tropical and temperate sub-tidal species,” citing Clark *et al.* (2009) and Ericson *et al.* (2010). The findings of Catarino *et al.*, and those of the other researchers they cite, indicate “polar and sub-polar sea urchin larvae can show a certain degree of resilience to acidification.” They conclude *A. dufresnei* has the potential to “migrate and further colonize southern regions.”

Sunday *et al.* (2011) note the presumed acidification of Earth’s oceans is predicted to impact marine biodiversity via “physiological effects impacting growth, survival, reproduction and immunology, leading to changes in species abundances and global distributions.” They point out “the degree to which these changes will play out

critically depends on the evolutionary rate at which populations will respond to natural selection imposed by ocean acidification,” and this phenomenon “remains largely unquantified,” citing Stockwell *et al.* (2003) and Gienapp *et al.* (2008). Sunday *et al.* measured the potential for an evolutionary response to lower ocean pH levels in the larval development rate of the two coastal invertebrates, a sea urchin (*Strongylocentrotus franciscanus*) and a mussel species (*Mytilus trossulus*).

The four researchers report their experiment revealed “the sea urchin species *Strongylocentrotus franciscanus* has vastly greater levels of phenotypic and genetic variation for larval size in future CO₂ conditions compared to the mussel species *Mytilus trossulus*.” They demonstrate “*S. franciscanus* may have faster evolutionary responses within 50 years of the onset of predicted year-2100 CO₂ conditions despite having lower population turnover rates.” Sunday *et al.* conclude their comparisons suggest “information on genetic variation, phenotypic variation, and key demographic parameters, may lend valuable insight into relative evolutionary potentials across a large number of species,” thereby also indicating simplistic climate envelope models of species redistributions in a future CO₂-enriched and possibly warmer world are not up to the task of providing an accurate picture of future biological reality. They note “a genetic basis for variation in CO₂ responses has been found in the three previous studies in which it has been sought (Langer *et al.*, 2009; Parker *et al.*, 2011; Pistevos *et al.*, 2011), supporting the notion that genetic variation exists at some level for almost all quantitative characters (Roff, 1997).”

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6.3.3.5 Fish

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on marine fish. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Negative effects of lower ocean pH levels on fish are generally not manifested until the water reaches pH concentrations associated with atmospheric CO₂ levels several times the present value.
- Otoliths of fish grown in seawater of lower pH and aragonite saturation associated with higher CO₂ conditions are usually significantly larger than those of fish grown under present-day conditions.
- “CO₂-induced acidification up to the maximum values likely to be experienced over the next 100 years had no noticeable effect on embryonic duration, egg survivorship and size at hatching for *A. percula*, and tended to have a positive effect on the length and weight of larvae.”
- “Most shallow-water fish tested to date appear to compensate fully their acid-base balance within several days of exposure to mild hypercapnia.”
- “Future ocean acidification will probably not pose a problem for sperm behavior, and hence fertilization success, of Baltic cod.”
- Lower ocean pH levels “neither affected the embryogenesis nor the hatch rate” of Atlantic herring. It also “showed no linear relationship between CO₂ and total length, dry weight, yolk sac area and otolith area of the newly hatched larvae.”
- “Cobia exhibited resistance to treatment effects on growth, development, swimming ability, and swimming activity at 800 and 2100 μ atm pCO₂,” whereas “these scenarios resulted in a significant increase in otolith size (up to 25% larger area).”
- The larval clown fish “is robust to levels of ocean chemistry change that may occur over the next 50–100 years.”

Climate Change Reconsidered II: Biological Impacts

- Lower ocean pH levels significantly increased the size, density, and relative mass of larval cobia otoliths, which changes “could affect auditory sensitivity including a ~50% increase in hearing range at 2100 ppm CO₂.”
- Lower ocean pH levels “did not appear to negatively affect size or condition of early larval walleye pollock.” It induced “a trend toward larger body sizes among fish reared at elevated CO₂ levels.”

Ishimatsu *et al.* (2005) note fish “constitute a major protein source in many countries,” and the “potential reduction of fish resources by high-CO₂ conditions due to the diffusion of atmospheric CO₂ into the surface waters ... can be considered as another potential threat to the future world population.” They conducted a survey of the scientific literature regarding the potential negative consequences for the health of marine fish of atmospheric CO₂ enrichment that could arise from continued anthropogenic CO₂ emissions.

Focusing on the possible threat of hypercapnia—a condition characterized by an excessive amount of CO₂ in the blood that typically results in acidosis, a serious and sometimes fatal condition—they say their survey revealed “hypercapnia acutely affects vital physiological functions such as respiration, circulation, and metabolism, and changes in these functions are likely to reduce growth rate and population size through reproduction failure.” Although this potential threat sounds dire, it represents an egregious flight of the imagination away from what could realistically be expected to happen to fish in the future.

Ishimatsu *et al.* report “predicted future CO₂ concentrations in the atmosphere are lower than the known lethal concentrations for fish,” noting “the expected peak value is about 1.4 torr [just under 1,850 ppm CO₂] around the year 2300 according to Caldeira and Wickett (2003).” As to just how far below the lethal CO₂ concentration for fish 1.4 torr is, in the case of short-term exposures on the order of a few days, Ishimatsu *et al.* cite a number of studies that yield median lethal concentrations ranging from 37 to 50 torr, values 26 and 36 times greater than the maximum CO₂ concentration expected some 300 years from now.

Regarding long-term exposures, the results are even more comforting. Ishimatsu *et al.* report Fivelstad *et al.* (1999) observed only 5 and 8% mortality at the end of 62 days of exposure to CO₂

concentrations of 5 and 9 torr, respectively, for freshwater Atlantic salmon smolts, and mere 1 and 5% mortalities for seawater postsmolts of the same species at 12 and 20 torr after 43 days (Fivelstad *et al.*, 1998). Ishimatsu *et al.* note Smart *et al.* (1979) found little difference in mortality for freshwater rainbow trout reared for 275 days at 4 to 17 torr, and no mortality occurred by the tenth week of exposure of juvenile spotted wolf fish to 20 torr (Foss *et al.*, 2003).

Fish embryos and larvae are often more vulnerable to environmental stresses than are adult fish. Yet even here, Ishimatsu *et al.* report the 24-hour median lethal concentration of CO₂ for eggs and larvae of several marine fish studied by Kikkawa *et al.* (2003) “ranged widely from 10 torr to 70 torr among species,” with the smaller of these two values being more than seven times greater than the CO₂ concentration expected 300 years from now.

Ishimatsu *et al.*’s review reveals growth reductions of 24 to 48%, but again the CO₂ concentrations that induced those growth reductions ranged from 17 to 20 torr, or 12 to 14 times more than the CO₂ concentration expected 300 years from now. Consequently, Ishimatsu *et al.*’s scientific literature review suggests both freshwater and marine fish will most likely never experience any ill effects from elevated atmospheric CO₂ concentrations.

Melzner *et al.* (2009) state several of Earth’s 30,000 species of teleost fish, which include virtually all the important sport and commercial fishes, have been shown able to “fully compensate extra cellular fluid pH” and “maintain oxygen consumption rates and growth performance under ocean acidification conditions (e.g. Larsen *et al.*, 1997; Foss *et al.*, 2003; Fivelstad *et al.*, 1998, 2003; Deigweier *et al.*, 2008).” Noting no studies of these phenomena have lasted for more than a few days, they maintained a group of Atlantic Cod (*Gadus morhua*) for four months in a recirculating aquaculture system of 15 cubic meters at an atmospheric CO₂ partial pressure of 0.3 kPa (~3,000 ppm) and another group for 12 months at a CO₂ partial pressure of 0.6 kPa (~6,000 ppm). They then investigated the fishes’ swimming metabolism in a swim-tunnel respirometer and took tissue samples of their gills for various chemical analyses, including gill Na⁺/K⁺-ATPase capacity, which serves as a general indicator for ion regulatory effort.

The six German scientists report, “motor activity in adult Atlantic Cod is not compromised by long-term exposure to water pCO₂ levels of 0.3–0.6 kPa,” which are “scenarios exceeding the 0.2 kPa value

predicted for surface ocean waters around the year 2300 (Caldeira and Wickett, 2003).” Melzner *et al.* conclude “adults of active fish species with a high ion regulatory capacity [which is employed to eliminate metabolic CO₂] are well equipped to cope with projected scenarios of global climate change.”

Checkley *et al.* (2009) report on their work with fish otoliths—bony structures consisting of aragonite-protein bilayers which fish use to sense orientation and acceleration. Noting atmospheric CO₂ enrichment had been calculated to decrease the saturation state of carbonate minerals such as aragonite in the world’s oceans, the six scientists “hypothesized that otoliths in eggs and larvae reared in seawater with elevated CO₂ would grow more slowly than they do in seawater with normal CO₂.” To test this hypothesis, they “grew eggs and pre-feeding larvae of white sea bass (*Atractoscion nobilis*) under a range of CO₂ concentrations [380, 993 and 2,558 ppm] and measured the size of their sagittal otoliths.”

“Contrary to expectations,” Checkley *et al.* write, “the otoliths of fish grown in seawater with high CO₂, and hence lower pH and aragonite saturation, were significantly larger than those of fish grown under simulations of present-day conditions.” They found “for 7- to 8-day-old fish grown under 993 and 2558 ppm CO₂, the areas of the otoliths were 7 to 9% and 15 to 17% larger, respectively, than those of control fish grown under 380 ppm CO₂.” The marine researchers note young fish are “able to control the concentration of ions (H⁺ and Ca²⁺) ... in the endolymph surrounding the otolith,” where “with constant pH, elevated CO₂ increases CO₃²⁻ concentration and thus the aragonite saturation state, accelerating formation of otolith aragonite.”

Munday *et al.* (2009) note “there is concern that continued increases in atmospheric CO₂ over the next century could have significant impacts on a wide range of marine species, not just those with calcified skeletons.” In the case of fish, which “control their tissue pH by bicarbonate buffering and the exchange of ions, mostly across the gills,” they write, “small changes in internal or external pH can readily be compensated (Heisler, 1989; Claiborne *et al.*, 2002).” Fish embryos and young larvae are possibly “more sensitive to pH changes than are juveniles and adults,” and “significant effects of ocean acidification are most likely to be detected in these early life stages.”

Munday *et al.* grew wild-caught pairs of the orange clownfish (*Amphiprion percula*) in a 70,000-liter recirculating seawater system at James Cook University’s experimental marine aquarium facility.

They filled 70-liter tanks with seawater simulating a range of ocean acidification scenarios for the next 50–100 years—390 (current day), 550, 750, and 1,030 ppm atmospheric CO₂—while documenting egg, embryo, and larval development. The four researchers from the School of Marine and Tropical Biology of Australia’s James Cook University determined “CO₂ acidification had no detectable effect on embryonic duration, egg survival and size at hatching,” and it “tended to increase the growth rate of larvae.” They observed, for example, 11 days after hatching, “larvae from some parental pairs were 15 to 18 per cent longer and 47 to 52 per cent heavier in acidified water compared to controls.” There was a “positive relationship between length and swimming speed,” and, they note, “large size is usually considered to be advantageous for larvae and newly settled juveniles.”

Munday *et al.* note “the most common prediction is that ocean acidification could [negatively] affect individual performance (e.g. development, growth, survival, swimming ability),” especially during the early life history of the fish. However, they write, “contrary to expectations,” their findings indicate “CO₂-induced acidification up to the maximum values likely to be experienced over the next 100 years had no noticeable effect on embryonic duration, egg survivorship and size at hatching for *A. percula*, and tended to have a positive effect on the length and weight of larvae.” As for adult fish, they state “most shallow-water fish tested to date appear to compensate fully their acid-base balance within several days of exposure to mild hypercapnia,” citing Michaelidis *et al.* (2007) and Ishimatsu *et al.* (2008).

Frommel *et al.* (2010) state, “elevated CO₂ concentrations can disturb the acid-base regulation, blood circulation, and respiration, as well as the nervous system of marine organisms, leading to long term effects such as reduced growth rates and reproduction,” especially in fish, because most “are external fertilizers, and sperm are activated by seawater as they are expelled into the open ocean during a spawning event,” citing Westin and Nissling (1991). Frommel *et al.* collected sperm from ripe adult male cod fish (*Gadus morhua*) caught during an August cruise through their spawning grounds in the Baltic Sea’s Bornholm Basin. They exposed the fish to seawater that had been brought into equilibrium (by bubbling) with air of either 380 or 1,400 ppm CO₂ (leading to seawater pH values of 8.080 and 7.558, respectively), and they recorded sperm swimming behavior during the exposure period using a digital camera.

The scientists “found no significant effect of decreased pH on sperm speed, rate of change of direction or percent motility for the population of cod analyzed.” Frommel *et al.* conclude “future ocean acidification will probably not pose a problem for sperm behavior, and hence fertilization success, of Baltic cod.”

Franke and Clemmesen (2011) conducted a study in which eggs of Atlantic herring (*Clupea harengus* L.) were fertilized and incubated in artificially acidified seawater corresponding to atmospheric CO₂ concentrations of 1,260, 1,859, 2,626, 2,903, and 4,635 ppm and compared to a control treatment of 480 ppm CO₂ until the main hatch of the herring larvae occurred. “The development of the embryos was monitored daily and newly hatched larvae were sampled to analyze their morphometrics.” The scientists report elevated CO₂ “neither affected the embryogenesis nor the hatch rate,” and “the results showed no linear relationship between CO₂ and total length, dry weight, yolk sac area and otolith area of the newly hatched larvae.” Franke and Clemmesen conclude “herring eggs can cope at current temperature conditions with an increase in CO₂,” even one “exceeding future predictions of CO₂-driven ocean acidification.”

Bignami *et al.* (2013a) state “there is a critical need to understand the effects of acidification on the vulnerable larval stages of marine fishes, as there is a potential for large ecological and economic impacts on fish populations and the human economies that rely on them.” They studied “the larvae of *Rachycentron canadum* (cobia), a large, highly mobile, pelagic-spawning, widely distributed species with a life history and fishery value contrasting other species studied to date.” Bignami *et al.* raised larval cobia through the first three weeks of ontogeny under conditions of predicted future ocean pH levels to determine effects on somatic growth, development, swimming ability, swimming activity, and the formation of otoliths.

The three U.S. researchers report “cobia exhibited resistance to treatment effects on growth, development, swimming ability, and swimming activity at 800 and 2100 μ atm pCO₂,” and “these scenarios resulted in a significant increase in otolith size (up to 25% larger area).” Bignami *et al.* conclude, “this study demonstrates that cobia is unlikely to experience a strong negative impact from CO₂-induced acidification predicted to occur within the next several centuries,” which they speculate “may be due to the naturally variable environmental conditions this species currently encounters throughout ontogeny

in coastal environments,” and “may lead to an increased acclimatization ability even during long-term exposure to stressors.”

Munday *et al.* (2011a) state “in general, marine fish appear to be relatively tolerant to mild increases in ambient CO₂, presumably because well-developed mechanisms for acid-base regulation allow them to compensate for cellular acidosis caused by exposure to elevated pCO₂ (Portner *et al.*, 2005; Ishimatsu *et al.*, 2008; Melzner *et al.*, 2009).” However, because “fish otoliths (earbones) are composed of aragonite,” there is a concern they “could be susceptible to the declining carbonate ion concentrations associated with ocean acidification.” Such an effect could be quite serious because “fish ears detect sound, body orientation and acceleration from the position of the otoliths in the inner ear and movement of the otoliths over sensory hair cells (Helfman *et al.*, 1997; Popper and Lu, 2000).”

Munday *et al.* reared larvae of the marine clown fish *Amphiprion percula* throughout their larval phase at three pH levels—ambient or control conditions (CO₂ ~ 390 ppm, pH ~ 8.15) and higher CO₂/lower pH conditions (CO₂ ~ 1,050 ppm, pH ~ 7.8; CO₂ ~ 1,721 ppm, pH ~ 7.6) representative of conditions predicted to prevail in AD 2100 and AD 2200–2300, respectively—to ascertain whether the elevated CO₂/reduced pH conditions would alter otolith size, shape, symmetry (between left and right otoliths), or chemistry compared to current conditions. The four researchers report “there was no effect of the intermediate treatment on otolith size, shape, symmetry between left and right otoliths, or otolith elemental chemistry, compared with controls.” In the more extreme treatment, otolith area and maximum length were slightly larger than for the controls, and “no other traits were significantly affected.” Munday *et al.* state the larval clown fish appears “capable of regulating endolymphic fluid chemistry even in waters with pH values significantly lower than open ocean values,” and they conclude “the larval clown fish is robust to levels of ocean chemistry change that may occur over the next 50–100 years.” This conclusion is similar to that reached by Munday *et al.* (2011b), who “detected no effects of ~850 ppm CO₂ on size, shape or symmetry of otoliths on juvenile spiny damselfish, a species without a larval phase.”

Miller *et al.* (2013) assessed the impact of lower ocean pH levels on the breeding success of cinnamon anemone fish. They employed three 8,000-L recirculating aquarium systems, each set to a different CO₂ and corresponding pH level. The treatments consisted of a current-day Control CO₂ (430 μ atm), a

mid-century Moderate CO₂ (584 μ atm), and an end-of-century High CO₂ (1,032 μ atm). They placed 18 pairs of cinnamon anemone fish (*Amphiprion melanopus*) collected from Australia's Great Barrier Reef into each of these three aquariums after all individuals had been weighed and measured for length. At the start of the experiment, they placed pairs of fish in individual 45-L tubs with continuous water flow at winter non-breeding temperatures and ambient pCO₂ values, which the scientists gradually adjusted over a two-week period to the desired levels. Then, they increased temperature by 0.5°C per week, until the average summer breeding temperature was reached, after which they kept the pairs of fish in these conditions for a nine-month period that included the summer breeding season, and the researchers recorded various assessments of breeding success.

The four Australian researchers report, “unexpectedly, increased CO₂ dramatically stimulated breeding activity.” More than twice as many pairs of the fish bred in the Moderate and High CO₂ treatments (67% and 55%) compared to the Control treatment (27%). In addition, “pairs in the High CO₂ group produced double the number of clutches per pair and 67% more eggs per clutch compared to the Moderate and Control groups.” The researchers determined “reproductive output in the High group was 82% higher than that in the Control group and 50% higher than that in the Moderate group.” They note, “despite the increase in reproductive activity, there was no difference in adult body condition among the three treatment groups,” and “there was no significant difference in hatchling length between the treatment groups.” Miller *et al.* conclude “this study provides the first evidence of the potential effects of ocean acidification on key reproductive attributes of marine fishes and, contrary to expectations, demonstrates an initially stimulatory effect in response to increased pCO₂.”

Bignami *et al.* (2013b) write, “the days- to month-long pelagic larval period is an ecologically vital ontogenetic phase in marine fishes because it constitutes the primary mode of dispersal in many species (Cowen and Sponaugle, 2009) and represents the life stage most susceptible to mortality (Houde, 1997).” They say, “during this phase, the sensory abilities of larval fishes are important determinants of survival (Montgomery *et al.*, 2006) and ultimately influence the persistence of viable populations.” The five researchers “used new 3D microcomputed tomography to conduct *in situ* analysis of the impact of ocean acidification on otolith (ear stone) size and density of larval cobia (*Rachycentron canadum*), a

large, economically important pantropical fish species that shares many life history traits with a diversity of high-value, tropical pelagic fishes.”

According to the researchers, at an atmospheric partial pressure of 2,100 ppm CO₂ there was a significant increase in otolith size (up to 49% greater volume and 58% greater relative mass) and a 6% increase in otolith density, and the estimated relative mass of larval cobia otoliths in an end-of-century 800 ppm CO₂ treatment was 14% greater. Bignami *et al.* demonstrate “these changes could affect auditory sensitivity including a ~50% increase in hearing range at 2100 ppm CO₂.” They say “this is a potentially optimistic result, indicating some resistance to acidification and suggesting that under near-future scenarios these impacts may be most relevant in habitats already experiencing high pCO₂ levels.”

Hurst *et al.* (2013) examined the direct effects of projected ocean pH levels on the eggs and larvae of walleye pollock in a series of laboratory experiments to determine the effects of elevated CO₂ levels on size-at-hatch and early larval growth rates. They selected treatments to reflect ambient conditions and conditions predicted to occur in high latitude seas in the next century (a 400–600 ppm increase), as well as a significantly higher CO₂ treatment (~1,200 ppm). The three U.S. researchers report, “ocean acidification did not appear to negatively affect size or condition of early larval walleye pollock.” They found “a trend toward larger body sizes among fish reared at elevated CO₂ levels,” and they note this trend also has been observed in experiments with orange clownfish (Munday *et al.*, 2009) and in a study of juvenile walleye pollock conducted by Hurst *et al.* (2012). Such findings, the authors write, suggest “the growth dynamics of early life stages of walleye pollock are resilient to projected levels of ocean acidification.”

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6.3.3.6 Miscellaneous Animal Studies

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on other marine animals not discussed in prior subsections. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- For the common cuttlefish (*Sepia officinalis*), a decrease in pH to 7.85 “should lead to some possibly beneficial effects, such as a larger egg and presumably hatchling size and a better incorporation of the essential element[s] such as Zn in the embryonic tissue,” and these phenomena “may improve the survival [of] the newly hatched juveniles.”
- Adults of the branched calcitic bryozoan *Myriapora truncata* “are able to up-regulate their

calcification rates and survive in areas with higher levels of pCO₂ than are predicted to occur due to anthropogenic ocean acidification.”

- The gastropod *Concholepas concholepas* demonstrates “the ability to maintain calcification even at pCO₂ levels of 1036 μ atm.” In addition, exposure to elevated pCO₂ during their early ontogeny “may actually increase the likelihood of *C. concholepas* surviving after being overturned by an exogenous cause.”
- Juveniles of the Arctic pteropod *Limacina helicina* are able to extend their shells at an aragonite saturation state as low as 0.6, which may result from “the presence of a thin periostracal layer covering the calcareous surface” that might act to protect the shell in seawater of reduced pH.
- “Copepods, as a group, may be well equipped to deal with the chemical changes associated with ocean acidification.”
- Sea anemone abundance along a natural seawater pH gradient of 8.2–7.6 was observed to be higher at the lowest pH.
- Lower ocean pH levels will have no impact on the oceans’ “transparency to sound.”

Lacoue-Labarthe *et al.* (2009) placed fertilized eggs of the common cuttlefish (*Sepia officinalis*) in five-liter plastic bottles filled with filtered and UV-sterilized Mediterranean seawater pumped from a depth of 30 meters at a site adjacent to Monaco Bay, after which the eggs were maintained throughout their full development time at controlled conditions of temperature (16 or 19°C) and pH (8.1, 7.85 or 7.6), with the latter values maintained within ± 0.05 of a pH unit by periodically bubbling pure CO₂ into the bottles (which were continuously aerated with CO₂-free air), resulting in mean CO₂ concentrations of the air in contact with the surface of the water of 400, 900, or 1,400 ppm.

According to the authors, “decreasing pH resulted in higher egg weight at the end of development at both temperatures ($p < 0.05$), with maximal values at pH 7.85 (1.60 ± 0.21 g and 1.83 ± 0.12 g at 16°C and 19°C, respectively).” They found “hatchlings were smaller when they developed at 16°C than at 19°C ($p < 0.05$).” They also observed zinc (Zn) accumulation “was higher at pH 7.85 during the full developmental period,” when “high embryonic requirements for Zn

are not fully covered by the maternal pool,” so the higher accumulation of Zn “was associated with a greater rate of growth of both egg and embryo.” Concurrently, there was a greater accumulation of potentially detrimental silver in the tissues of the hatchlings, but any deleterious effects of the extra silver apparently were overcome by the positive effects of lowered pH on beneficial zinc accumulation. Toxic cadmium accumulation was reduced in the lower pH (higher CO₂) treatments.

The seven scientists conclude, “decreasing pH until 7.85,” as could be expected to occur in air enriched with carbon dioxide to a concentration of 900 ppm, “should lead to some possibly beneficial effects, such as a larger egg and presumably hatchling size and a better incorporation of the essential element[s] such as Zn in the embryonic tissue.” These phenomena, they write, “may improve the survival [of] the newly hatched juveniles.” They note Gutowska *et al.* (2008) demonstrated “calcification was enhanced in sub-adult cuttlefish reared at 6,000 ppm CO₂.”

Gutowska *et al.* found, over a six-week test period, “juvenile *S. officinalis* maintained calcification under ~4000 and ~6000 ppm CO₂, and grew at the same rate with the same gross growth efficiency as did control animals,” gaining approximately 4% body mass daily and increasing the mass of their calcified cuttlebone by more than 500%. Gutowska *et al.* conclude “active cephalopods possess a certain level of pre-adaptation to long-term increments in carbon dioxide levels,” and they suggest our “understanding of the mechanistic processes that limit calcification must improve before we can begin to predict what effects future ocean acidification will have on calcifying marine invertebrates.”

Rodolfo-Metalpa *et al.* (2010) conducted “the first coastal transplant experiment designed to investigate the effects of naturally acidified seawater on the rates of net calcification and dissolution of the branched calcitic bryozoan *Myriapora truncata*.” Bryozoans or “moss animals” are a geologically important group of small animals that resemble corals; they are major calcifiers found on rocky shores in cool-water areas of the planet, where they comprise a significant component of the carbonate sediments in shallow sublittoral habitats, and where they form long-lived three-dimensional structures that provide attachment sites for numerous epifauna and trap sediment and food for a variety of infauna.

Rodolfo-Metalpa *et al.* transplanted colonies of the species to normal (pH 8.1), high (pH 7.66), and

extremely high (pH 7.43) CO₂ conditions at gas vents located just off Italy’s Ischia Island in the Tyrrhenian Sea. They calculated the net calcification rates of live colonies and the dissolution rates of dead colonies by weighing them before and after 45 days of *in situ* residence in May–June (when seawater temperatures ranged from 19 to 24°C) and after 128 days of *in situ* residence in July–October (when seawater temperatures ranged from 25–28°C). They found throughout the first and cooler observation period, “dead *M. truncata* colonies dissolved at high CO₂ levels (pH 7.66), whereas live specimens maintained the same net calcification rate as those growing at normal pH.” At the extremely high CO₂ level, the net calcification rate of the live specimens was reduced to only about 20% of what it was at normal pH, though the moss animals survived. Throughout the second and warmer observation period, by contrast, calcification ceased in both the normal and the high CO₂ treatments, and in the extremely high CO₂ treatment the transplants died.

The five scientists conclude, “at moderate temperatures,” such as those to which they are currently adapted, “adult *M. truncata* are able to up-regulate their calcification rates and survive in areas with higher levels of pCO₂ than are predicted to occur due to anthropogenic ocean acidification, although this ability broke down below mean pH 7.4.” That level is far below what even IPCC predicts will occur in response to continued burning of fossil fuels.

According to Manriquez *et al.* (2013), in Chile “the gastropod *Concholepas concholepas* is both an economically and ecologically important species inhabiting subtidal and intertidal marine habitats.” In these rocky environments, “the gastropods are often exposed to highly turbulent conditions,” during which times they adhere tightly to the rock surface with their foot. The scientists note, “when feeding and handling prey items the foot of *C. concholepas* is often removed from the rock leaving it vulnerable to being dislodged.” Thus it is in the gastropod’s best interests to right itself as quickly as possible whenever this occurs.

To explore the impact of lower ocean pH levels on this self-preservation response, as well as the more basic phenomena of growth and calcification, Manriquez *et al.* collected small individuals of *C. concholepas* from a rocky intertidal area in northern Chile, transported them to a laboratory, and reared them in natural seawater for one month, after which 10 individuals were randomly assigned to one of three pCO₂ concentrations: 388 µatm (current), 716 µatm (medium), or 1,036 µatm (high). There they

remained, under well-fed conditions, for 83 days, while the researchers made various measurements on days 0, 11, 45, 52, 62, 73, and 83 after the beginning of treatments.

At the end of the study period, the 11 researchers report, there were no significant among-treatment differences in peristomal length, wet weight, or buoyant weight, nor the shell weight of empty shells. They also determined, “on average, self-righting time was three times faster in individuals reared under increased $p\text{CO}_2$ levels than under normal seawater conditions.” Manriquez *et al.* conclude “*C. concholepas* have the ability to maintain calcification even at $p\text{CO}_2$ levels of 1036 μatm ... in agreement with similar results reported in the literature for other invertebrates (Ries *et al.*, 2009; Manzello, 2010; Rodolfo-Metalpa *et al.*, 2011).” And they state, “during their early ontogeny, exposure to elevated $p\text{CO}_2$ may actually increase the likelihood of *C. concholepas* surviving after being overturned by an exogenous cause.”

Citing Hunt *et al.* (2008), authors Comeau *et al.* (2012) write, “pteropods are pelagic mollusks that play an important role in the food web of extensive oceanic regions, particularly at high latitudes, where they are a major dietary component for zooplankton and higher predators, such as herring, salmon, whales and birds.” Comeau *et al.* investigated the effect of lower ocean pH levels “using juveniles of the Arctic pteropod *Limacina helicina* from the Canada Basin of the Arctic Ocean,” where they caught and extracted overwintering individuals from depths of 100 to 200 meters through a hole in the ice, thereafter maintaining the mollusks at three pH levels (8.05, 7.90, and 7.75) for eight days, after which they assessed them for mortality and shell growth.

Comeau *et al.* found pH did not impact the mortality of the pteropods, but the degree of linear extension of their shells decreased as pH declined. Nevertheless, the pteropods were able to extend their shells at an aragonite saturation state as low as 0.6, suggesting “the presence of a thin periostracal layer covering the calcareous surface, as shown on the Antarctic pteropod *Limacina helicina antarctica* (Sato-Okoshi *et al.*, 2010), might, among other mechanisms, protect the shell from a corrosive environment.” Although much remains to be known about pteropod responses to a potential decline in seawater pH, these findings indicate pteropods possess a certain degree of adaptability to low pH levels, and the results of similar studies of other calcifying sea creatures suggest pteropods may be able to evolve in their ability to cope with declining

seawater pH.

Weydmann *et al.* (2012) note the Arctic copepod *Calanus glacialis* “can comprise up to 70–80% of the zooplankton biomass in Arctic shelf seas (Blachowiak-Samolyk *et al.*, 2008; Conover, 1988; Hirche and Mumm, 1992), and is a key herbivore (Mumm *et al.*, 1998; Soreide *et al.*, 2008; Tande, 1991) as well as an important prey item for other zooplankton species (Falk-Petersen *et al.*, 2002, 2004), fish (Fortier *et al.*, 2001), and seabirds (Karnovsky *et al.*, 2003; Weslawski *et al.*, 1999; Wojczulanis *et al.*, 2006).” Noting “testing the potential impacts of ocean acidification on *C. glacialis* reproduction is vital,” they investigated “how the reduction of sea surface pH from present day levels (pH 8.2) to a realistic model-based level of pH 7.6, and to an extreme level of pH 6.9, would affect the egg production and hatching success of *C. glacialis* under controlled laboratory conditions,” where “reduced pH seawater was prepared by bubbling compressed CO_2 through filtered seawater, until the appropriate level of pH was reached.”

The four researchers report, “ CO_2 -induced seawater acidification had no significant effect on *C. glacialis* egg production,” and a reduction in pH to 6.9 only delayed hatching at what they called this “extreme level of pH.” They also state there was no significant effect “on the survival of adult females”; this observation, they write, “is in agreement with previous studies on other copepod species,” citing Mayor *et al.* (2007) and Kurihara and Ishimatsu (2008). Weydmann *et al.* conclude their results are “in agreement with previous studies on other copepod species and would indicate that copepods, as a group, may be well equipped to deal with the chemical changes associated with ocean acidification.”

Suggett *et al.* (2012) state “non-calcifying anthozoans such as soft corals and anemones, play important ecological and biogeochemical roles in reef environments (e.g. Fitt *et al.*, 1982; Bak and Borsboom, 1984; Muller-Parker and Davy, 2001).” They collected pertinent data from 11–26 May 2011 on a sea anemone (*Anemonia viridis*) along a natural seawater pH gradient of 8.2–7.6—which would be expected to prevail across an atmospheric CO_2 gradient of 365–1,425 ppm—produced by a shallow cold vent system (Johnson *et al.*, 2011; 2012) that released CO_2 to coastal waters near Vulcano, Italy, about 25 km northeast of Sicily. The nine researchers found an increase in gross maximum photosynthesis, respiration rates, and dinoflagellate endosymbiont abundance (but unchanged diversity) with increasing CO_2 . Sea anemone abundance increased with CO_2 and

“dominated the invertebrate community at high CO₂ conditions.” The enhanced productivity in the sea anemones they studied, Suggett *et al.* write, implies “an increase in fitness that may enable non-calcifying anthozoans to thrive in future environments, i.e. higher seawater CO₂.” As they declare in the title of their paper, “Sea anemones may thrive in a high CO₂ world.”

Meron *et al.* (2013) studied the physiology of *Anemonia viridis* growing naturally along a CO₂-vent-induced pH gradient near Ischia, Italy, also studying the nature of the associated microbial community (bacteria and endosymbiotic *Symbiodinium*), focusing on two specific locations that could be characterized as ambient (pCO₂ 330 ppm, pH 8.1) and very CO₂-enriched (pCO₂ 9,341 ppm, pH 7.0). Although the four researchers found reduction in pH had an impact on the composition and diversity of the anemones’ associated microbial communities, “no significant changes were observed in *A. viridis* physiology, and no microbial stress indicators (i.e., pathogens, antibacterial activity, etc.) were detected.” Meron *et al.* conclude, “it appears that elevated CO₂ does not have a negative influence on *A. viridis* that live naturally in the [very CO₂-enriched] site.” They say “this suggests that natural long-term exposure and dynamic diverse microbial communities may contribute to the acclimation process of the host in a changing pH environment.”

Mukherjee *et al.* (2013) “investigated the proteomic response of metamorphosing larvae of the tubeworm *Hydroides elegans*, challenged with two climate change stressors, ocean acidification (pH 7.6) and hypoxia (2.8 mg O₂ per liter),” as well as with both of the stressors combined. The seven scientists found concomitant exposure to the two climate change stressors “caused several proteins involved in energy metabolism, calcification and stress tolerance to be differentially expressed.” This phenomenon “seemed to allow the tubeworm larvae to successfully metamorphose and carry out calcification.” Mukherjee *et al.* conclude “the aragonite tube-forming tubeworm larvae have a high tolerance to hypoxia and may possess the capacity to acclimate over time, even in the face of ocean acidification.” Some researchers have recently looked at the possible effects of lower ocean pH levels on the oceans’ “transparency to sound.” Reeder and Chiu (2010) state “it has been reported that, given a 0.3 reduction in pH, from 8.1 to 7.8, a reduction in the acoustic absorption at low frequencies could result, suggesting a significant increase in ocean noise,” and more recently “it has been suggested that low-frequency

sound will travel farther due to the ocean pH reduction expected by 2050,” and most recently, researchers have suggested “in an ocean more transparent to sound, the resultant changes in propagation range will be noticeable in the operation of scientific, commercial and naval applications that are based on ocean acoustics.”

Reeder and Chiu reviewed “the fundamental principles of acoustic transmission loss in the ocean and how the multiple transmission loss mechanisms impact ocean noise levels within the context of changing ocean pH.” They conducted “an analytical analysis involving physical and empirical models of all relevant transmission loss mechanisms,” focusing on “three ocean acoustic environments ... to elucidate the expected change in ocean noise level from sources at the surface as a function of frequency: shallow water, the acoustic surface duct and the deep ocean.”

The two researchers in the Department of Oceanography of the Naval Postgraduate School in Monterey California (USA) report for even a large reduction in ocean pH from 8.1 to 7.4, there was “no observable change in ocean noise in the shallow water and surface duct environments for all frequencies—two environments which host a large portion of the marine mammal population.” They also found “a negligible change in ocean noise level in the deep water environment for all frequencies ... which also provides an upper bound to the maximum expected increase in ocean noise level due to the fact that it does not fully account for the range-dependent water column sound speed, bottom topography and distributed sources.”

Putting their results in the context of average background ocean noise levels as represented by Wenz (1962) curves, they found “a statistically insignificant change compared to the inherent variability of ocean noise associated with shipping and surface-generated mechanisms.” Thus, “after 250 years,” they write, “there would still be no significant modifications to the Wenz curves,” which suggests lower ocean pH levels will have no negative impact on ocean noise.

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Climate Change Reconsidered II: Biological Impacts

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6.3.3.7 Multiple Animal Studies

The studies reviewed in this section examine what scientists have learned about potential impacts of lower ocean pH levels on animals as obtained from studies in which multiple species are discussed. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages

in quotation marks in the bullet points are included in the main body of the section.)

- The impact of elevated atmospheric CO₂ on marine calcification “is more varied than previously thought.”
- Different stress effects on interacting species resulting from lower ocean pH levels “may not only enhance but also buffer community level effects.”
- “Biological processes can provide homeostasis against changes in pH in bulk waters of the range predicted during the 21st century.”
- The world’s marine biota are “more resistant to ocean acidification than suggested by pessimistic predictions identifying ocean acidification as a major threat to marine biodiversity” and “may not be the widespread problem conjured into the 21st century.”

Ries *et al.* (2009) “reared 18 calcifying species for 60 days in isothermal (25°C) experimental seawaters equilibrated with average [atmospheric] CO₂ values of 409, 606, 903 and 2856 ppm, corresponding to modern CO₂, and ~2, 3 and 10 times pre-industrial levels (~280 ppm), respectively, and yielding average seawater saturation states of 2.5, 2.0, 1.5 and 0.7 with respect to aragonite,” after which “the organisms’ net rates of calcification (total calcification minus total dissolution) under the various CO₂ treatments were estimated from changes in their buoyant weight and verified with dry weight measurements after harvesting.” The three Woods Hole Oceanographic Institution (USA) researchers report, “in ten of the 18 species (temperate corals, pencil urchins, hard clams, conchs, serpulid worms, periwinkles, bay scallops, oysters, whelks, soft clams), net calcification decreased with increasing CO₂,” and “in six of the ten negatively impacted species (pencil urchins, hard clams, conchs, periwinkles, whelks, soft clams) [they] observed net dissolution of the shell in the highest CO₂ treatment.”

They continue, “in four of the 18 species (limpets, purple urchins, coralline red algae, calcareous green algae), net calcification increased relative to the control under intermediate CO₂ levels (605 and 903 ppm), and then declined at the highest CO₂ level (2856 ppm).” Finally, they write, “in three species (crabs, lobsters, and shrimps), net calcification was greatest under the highest level of CO₂ (2856 ppm),”

and “one species, the blue mussel, exhibited no response to elevated CO₂.”

Ries *et al.* conclude “the impact of elevated atmospheric CO₂ on marine calcification is more varied than previously thought,” with responses ranging from negative to neutral to positive.

Kurihara *et al.* (2007) extracted sedimentary mud from the seafloor of Tanabe Bay on the Kii Peninsula of Japan and incubated it in marine microcosms continuously aerated for 56 days with air of either 360 or 2,360 ppm CO₂ while they periodically measured the abundance and biomass of different members of the meiobenthic community contained in the sediments. Meiofauna are small benthic invertebrates larger than microfauna but smaller than macrofauna; they are metazoan animals that can pass through a 0.5–1 mm mesh but are retained by a 30–45 µm mesh. In marine environments, they typically are found between grains of damp sand on the seashore or in muddy sediments at the bottoms of water bodies.

The authors “observed no significant differences in the abundance of total meiofauna, nematodes, harpacticoid copepods (including adults and copepodites) and nauplii by the end of the experiment.” They say there “may have been successful recruitments under elevated CO₂ conditions” and “elevated CO₂ had not impacted the reproduction of nematodes and harpacticoid copepods.” These observations, the three researchers write, “suggest that the projected atmospheric CO₂ concentration in the year 2300 does not have acute effects on the meiofauna.”

Appelhans *et al.* (2012) note “the impact of seawater acidification on calcifying organisms varies at the species level,” and “if the impact differs between predator and prey in strength and/or sign, trophic interactions may be altered.” This consequence, if true, could play havoc with many marine ecosystems as currently constituted. In a study designed to explore the potential for such interactions in the brackish western Baltic Sea, Appelhans *et al.* investigated the impacts of three seawater pCO₂ levels (650, 1,250 and 3,500 ppm) on the growth of two predatory species (the common sea star *Asterias rubens* and the shore crab *Carcinus maenas*), also determining whether the conditions affected the quantity or size of prey consumed (the blue mussel *Mytilus edulis*). The five German scientists found “growth of *Mytilus edulis* was generally very low and not significantly affected by acidification.” They write, “a trend toward a lower shell mass with increasing seawater pCO₂ was observed,” and “the mean maximum breaking resistance of mussel shells

was significantly lowered by ~20% at the highest level of 3500 ppm.”

As for the predators, they report, “acidification did not provoke a measurable shift in prey size preferred by either predator.” They also found intermediate acidification levels (corresponding to 1,250 ppm CO₂) “had no significant effect on growth or consumption in either predator species,” but the highest acidification level (corresponding to 3,500 ppm CO₂) “reduced feeding and growth rates in sea stars by 56%, while in crabs a 41% decrease in consumption rates of mussels could be demonstrated.” “Interestingly,” Appelhans *et al.* conclude, “the enhanced vulnerability of mussels seems to be neutralized by the decreased consumption of the predators under high acidification.” They write, “these results illustrate that different stress effects on interacting species may not only enhance but also buffer community level effects,” noting, “when stress effects are similar (and weak) on interacting species, biotic interactions may remain unaffected.”

Hurd *et al.* (2011) observe, “most ocean acidification studies so far have been simplistic” because they have not “jointly considered physical, chemical and biological interactions.” They note “the emerging discipline of marine ecomechanics (Denny and Helmuth, 2009; Denny and Gaylord, 2010) provides a valuable framework in which such inter-disciplinary research can be conducted.” The old experimental approach, they write, “overlooks the existence of a discrete micro-layer (i.e., diffusion boundary layer, DBL) at the surface of many aquatic organisms that buffers them from the surrounding mainstream seawater (Vogel, 1996).” This is achieved by metabolic processes that alter the water chemistry within the DBL, with photosynthesis increasing pH, and calcification and respiration reducing pH (Hurd *et al.*, 2009). They continue, “the chemical environment within the DBL differs from that in the mainstream seawater just micrometers away, with implications for both the dissolution of, and formation of, calcium carbonate (Borowitzka and Larkum, 1976; Ries *et al.*, 2009).”

In a study employing the still-evolving eco-mechanic approach, Hurd *et al.* used pH micro-electrodes and oxygen micro-optodes to measure the DBL thickness at the surface of the coralline seaweed *Sporolithon durum*, the sea urchin *Evechinus chloroticus*, and the abalone *Haliotis iris*, at a range of seawater velocities (0–10 cm/sec) that reflected those found within a temperate reef in Southern New Zealand (45.38°S) that may be vulnerable to ocean acidification (OA). For *S. durum*, they also deter-

mined whether DBL thickness would be affected when mainstream seawater pH was reduced to 7.5, the projected worst-case scenario for the year 2215 as calculated by Caldeira and Wickett (2003). In addition, they measured pH fluctuations at the surface of *S. durum* on a timescale of hours at ambient seawater pH and pH 7.5 at two different flows (1.5 and 6.3 cm/sec), and for the invertebrates they measured surface pH fluctuations at ambient pH and a flow of 1.5 cm/sec.

The seven scientists determined coralline seaweeds encounter a wide range of pH values over each daily cycle, but they are able to increase their pH substantially due to photosynthesis and to withstand periods of very low pH (relative to the present day and comparable to values predicted for coming centuries) under low flows. As to sea urchins, the scientists found they are currently subjected to—and readily survive—very low pH values (7.5) at their surfaces in slow seawater flows, values equivalent to those predicted to occur in the future. And abalone, the researchers write, “have a very thin DBL and hence their outer surface is subjected to the pH in the mainstream seawater, in all flow conditions,” yet they too persist, probably because they are “internal calcifiers” and “the reduced pH predicted for future oceans may not directly alter their rates of calcification.”

Hurd *et al.* conclude their findings “support the view that although the role of chemistry on OA is well understood, the biological responses to OA will be complex,” citing their own work and that of Fabry *et al.* (2008). They also note, “both the site of calcification and the ecomechanics of the biota, i.e., the interactions between their morphology, physiology and the surrounding hydrodynamic environment, must be considered.” Their work suggests marine calcifiers are much more robust to OA than originally thought.

Findlay *et al.* (2011) provide further evidence of the importance of biology in controlling calcification. They note, “calcifying marine organisms such as molluscs and foraminifera, crustaceans, echinoderms, corals and coccolithophores are predicted to be most vulnerable to decreasing oceanic pH (ocean acidification).” They point out there is a possibility for “increased or maintained calcification under high carbon dioxide conditions,” and their experiment demonstrates the reality of this phenomenon in different types of calcifying marine animals. Working with five calcifying organisms—two gastropods (the limpet *Patella vulgata* and the periwinkle *Littorina littorea*), a bivalve mussel (*Mytilus edulis*), one

crustacean (the cirripede *Semibalanus balanoides*), and one echinoderm (the brittlestar *Amphiura filiformis*)—Findlay *et al.* “measured either the calcium (Ca^{2+}) concentration in the calcified structures or shell morphological parameters as a proxy for a net change in calcium carbonate in live individuals exposed to lowered pH,” where the lower pH of the seawater employed was created by the bubbling of CO_2 into header tanks.

“Contrary to popular predictions,” they write, the results indicated “the deposition of calcium carbonate can be maintained or even increased in acidified seawater.” In fact, four of the five species they studied actually exhibited increased levels of calcium in low pH conditions. In the case of *Littorina littorea*, for example, all morphological shell parameters—width, height, thickness, area, perimeter, aperture area, and aperture perimeter—“increased in low pH treatments compared to the control,” and “there was ~67% more growth in shell height, ~30% more growth in shell width and ~40% more growth in shell thickness under low pH conditions compared to the control.” They also observed a large amount of dissolution taking place on isolated shells and arms of the creatures they studied, but they found “the presence of a live animal within its calcium carbonate structure offset this dissolution.”

Findlay *et al.* say their findings demonstrate “there is a great degree of biological control on calcification with complex links to other physiological processes,” and “increasing evidence in the literature agrees with the results of [our] study,” noting, “McDonald *et al.* (2009) showed calcification in another barnacle species (*Amphibalanus amphitrite*) to continue, and possibly even increase, under low pH conditions (pH 7.4); Arnold *et al.* (2009) demonstrated larval lobsters (*Homarus gammarus*) were able to lay down calcium carbonate structure in pH conditions 0.3 units below the control levels; Checkley *et al.* (2009) showed young fish have enhanced aragonite otolith growth when grown under elevated CO_2 ; Maier *et al.* (2009) showed that, although there was a decrease in calcification in cold-water corals, overall they showed a positive net calcification at aragonite saturation states below 1, and longer-term experiments suggest these corals may actually maintain or even increase calcification over longer timescales at low pH (Schubert *et al.*, 2010).”

In what was at the time the most comprehensive analysis ever conducted of experimental studies that have explored the effects of rising atmospheric CO_2 concentrations on marine biota, Hendriks *et al.* (2010) assembled a database of 372 experimentally evaluated

responses of 44 marine species to lower ocean pH levels induced by equilibrating seawater with CO₂-enriched air. They note, “warnings that ocean acidification is a major threat to marine biodiversity are largely based on the analysis of predicted changes in ocean chemical fields,” which are derived from theoretical models that do not account for numerous biological phenomena and have only “limited experimental support.”

Of the published reports they scrutinized, only 154 assessed the significance of responses relative to controls. Of those reports, 47 reported no significant response, so “only a minority of studies” demonstrated “significant responses to acidification.” When the results of that minority group of studies were pooled, there was no significant mean effect. Nevertheless, the three researchers found some types of organisms and certain functional processes did exhibit significant responses to lower seawater pH levels.

Since their analyses to this point had included some extremely high acidification treatments, they repeated their analyses for only those pH levels induced by atmospheric CO₂ concentrations of 2,000 ppm or less, as that concentration had been predicted to occur around the year 2300 by Caldeira and Wickett (2003). In this second analysis, Hendriks *et al.* once again found the overall response, including all biological processes and functional groups, was not significantly different from that of the various control treatments, although calcification was reduced by $33 \pm 4.5\%$ and fertility by $11 \pm 3.5\%$ across groups, whereas survival and growth showed no significant overall responses. When the upper limiting CO₂ concentrations were in the range of 731–759 ppm, just below the value predicted by IPCC (2007) for the end of the twenty-first century (790 ppm)—calcification rate reductions of only 25% were observed.

The three researchers say this decline “is likely to be an upper limit, considering that all experiments involve the abrupt exposure of organisms to elevated pCO₂ values, while the gradual increase in pCO₂ that is occurring in nature may allow adaptive and selective processes to operate,” citing Widdicombe *et al.* (2008) and noting “these gradual changes take place on the scale of decades, permitting adaptation of organisms even including genetic selection.”

Even this mitigating factor is not the end of the good news, for Hendriks *et al.* also write, “most experiments assessed organisms in isolation, rather than [within] whole communities,” and the responses of other entities and processes within the community

may buffer the negative impacts of CO₂-induced acidification. As an example, they note “sea-grass photosynthetic rates may increase by 50% with increased CO₂, which may deplete the CO₂ pool, maintaining an elevated pH that may protect associated calcifying organisms from the impacts of ocean acidification.”

Describing another phenomenon that benefits corals, the researchers write, “seasonal changes in pCO₂ are in the range of 236–517 ppm in the waters of the northern East China Sea (Shim *et al.*, 2007),” and “metabolically-active coastal ecosystems experience broad diel changes in pH, such as the diel changes of >0.5 pH units reported for sea grass ecosystems (Invers *et al.*, 1997),” which they say represent “a broader range than that expected to result from ocean acidification expected during the 21st century.” They note these fluctuations also “offer opportunities for adaptation to the organisms involved.”

Hendriks *et al.* additionally state the models on which the ocean “acidification” threat is based “focus on bulk water chemistry and fall short of addressing conditions actually experienced by [marine] organisms,” which are “separated from the bulk water phase by a diffusive boundary layer” and “photosynthetic activity”—such as that of the zooxanthellae hosted by corals—“depletes pCO₂ and raises pH (Kuhl *et al.*, 1995) so that the pH actually experienced by organisms may differ greatly from that in the bulk water phase (Sand-Jensen *et al.*, 1985).”

Hendriks *et al.* also note “calcification is an active process where biota can regulate intracellular calcium concentrations,” so “marine organisms, like calcifying coccolithophores (Brownlee and Taylor, 2004), actively expel Ca²⁺ through the ATPase pump to maintain low intracellular calcium concentrations (Corstjens *et al.*, 2001; Yates and Robbins, 1999).” They note, “as one Ca²⁺ is pumped out of the cell in exchange for 2H⁺ pumped into the cell, the resulting pH and Ca²⁺ concentrations increase the CaCO₃ saturation state near extracellular membranes and appear to enhance calcification (Pomar and Hallock, 2008)” —so much so, in fact, that “there is evidence that calcification could even increase in acidified seawater, contradicting the traditional belief that calcification is a critical process impacted by ocean acidification (Findlay *et al.*, 2009).”

Hendriks *et al.* note the world’s marine biota are “more resistant to ocean acidification than suggested by pessimistic predictions identifying ocean acidification as a major threat to marine biodiversity,” and thus this phenomenon “may not be the widespread

problem conjured into the 21st century” by the world’s climate alarmists, echoing a similar conclusion reached at the turn of the last millennium (Idso *et al.*, 2000). Hendriks *et al.* conclude, “biological processes can provide homeostasis against changes in pH in bulk waters of the range predicted during the 21st century.”

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6.4 Freshwater “Acidification”

The vast majority of studies of the effects of lower pH levels examine the topic as it pertains to marine life. However, a growing body of research investigates its potential effects on aquatic species inhabiting the world’s freshwater lakes, rivers, and streams. That research suggests there may be great benefits in store for such aquatic life as the air’s CO₂ concentration continues to rise.

6.4.1 Algae

The studies reviewed in this section examine what scientists have learned about potential impacts of falling freshwater pH levels on algae. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- A “doubled atmospheric CO₂ concentration would affect the growth of *C. pyrenoidosa* when it grows under bright solar radiation, and such an effect

would increase by a great extent when the cell density becomes high.”

- The effects of lower freshwater pH levels on algal production could be such that a “doubling of atmospheric CO₂ may result in an increase of the productivity of more than 50%.”
- “Contrary to the dominating hypotheses in the literature,” lower freshwater pH levels may lead to “positive, bottom-up effects on secondary production in some stream food webs.”
- Lower freshwater pH levels may prevent bloom development and ambient toxicity of certain harmful algae.

Xia and Gao (2003) cultured cells of the freshwater alga *Chlorella pyrenoidosa* in Bristol’s solution within controlled environment chambers maintained at low and high light levels (50 and 200 μmol/m²/s) during 12-hour light periods followed by 12-hour dark periods for a total of 13 days, while the solutions in which the cells grew were continuously aerated with air of either 350 or 700 ppm CO₂. When they harvested the cells (in the exponential growth phase) at the conclusion of this period, they found the biomass (cell density) of the twice-ambient CO₂ treatment was 10.9% and 8.3% greater than that of the ambient-air treatment in the low- and high-light regimes, respectively, although only the high-light result was statistically significant. The two scientists conclude a “doubled atmospheric CO₂ concentration would affect the growth of *C. pyrenoidosa* when it grows under bright solar radiation, and such an effect would increase by a great extent when the cell density becomes high.” Their data also suggest the same may happen, perhaps only to a lesser extent, when the alga grows under less-bright conditions.

Andersen and Andersen (2006) placed six 1.5-m-diameter flexible plastic cylinders in the littoral zone of Lake Hampen in central Jutland, Denmark. Three of the cylinders were maintained at the ambient CO₂ concentration of the air and three were enriched to 10 times ambient, and the researchers measured the CO₂-induced growth response of a mixture of several species of filamentous freshwater algae dominated by *Zygnema* species but also containing some *Mougeotia* and *Spirogyra*. After one full growing season (May to November), they determined the biomass of the microalgal mixture in the CO₂-enriched cylinders was increased by 220% in early July, by 90% in mid-August, and by 3,750% in mid-November.

Schippers *et al.* (2004a) note “it is usually thought that unlike terrestrial plants, phytoplankton will not show a significant response to an increase of atmospheric CO₂,” but “most analyses have not examined the full dynamic interaction between phytoplankton production and assimilation, carbon-chemistry and the air-water flux of CO₂,” and “the effect of photosynthesis on pH and the dissociation of carbon (C) species have been neglected in most studies.”

Schippers *et al.* developed “an integrated model of phytoplankton growth, air-water exchange and C chemistry to analyze the potential increase of phytoplankton productivity due to an atmospheric CO₂ elevation.” As a test of their model, they let the freshwater alga *Chlamydomonas reinhardtii* grow in 300 ml bottles filled with 150 ml of a nutrient-rich medium at enclosed atmospheric CO₂ concentrations of 350 and 700 ppm maintained at two air-water exchange rates characterized by CO₂ exchange coefficients of 2.1 and 5.1 m day⁻¹, as Shippers *et al.* (2004b) describe it, periodically measuring the biovolume of the solutions by means of an electronic particle counter.

The results of this effort, they write, “confirm the theoretical prediction that if algal effects on C chemistry are strong, increased phytoplankton productivity because of atmospheric CO₂ elevation should become proportional to the increased atmospheric CO₂,” which suggests algal productivity “would double at the predicted increase of atmospheric CO₂ to 700 ppm.” Although “strong algal effects (resulting in high pH levels) at which this occurs are rare under natural conditions,” they predict effects on algal production in freshwater systems could be such that a “doubling of atmospheric CO₂ may result in an increase of the productivity of more than 50%.”

Collins *et al.* (2006) propagated 10 replicate lines from each of two clones of *Chlamydomonas reinhardtii* within a phytotron by batch-culturing them in flasks through which air of 430 ppm CO₂ was continuously bubbled or air of gradually increasing CO₂ concentration was bubbled over the course of development of 600 generations of the microalga, when a concentration of 1,050 ppm was reached and maintained throughout the development of 400 more algal generations. They grew each of these sets of plants (low-CO₂-adapted and high-CO₂-adapted) for a short period of time at both 430 and 1,050 ppm CO₂ and determined their steady-state CO₂ uptake rates.

For the algae whose atmospheric CO₂ concentration had been continuously maintained at 430 ppm,

Collins *et al.* report abruptly increasing it to a value of 1,050 ppm led to a 143% increase in steady-state CO₂ uptake rate. For the algae that had experienced the gradual CO₂ increase from 430 to 1,050 ppm, there was a 550% increase in CO₂ uptake rate when the rate in the 1,050-ppm air was compared to the rate that prevailed when the air’s CO₂ concentration was abruptly lowered to 430 ppm. For the algae experiencing the most realistic scenario—gradually going from a state of continuous 430-ppm CO₂ exposure to one of 1,050 ppm exposure over a period of 600 generations and then maintaining the higher CO₂ level for a further 400 generations, the increase in steady-state CO₂ uptake rate due to the long-term 620-ppm increase in atmospheric CO₂ concentration was a more modest 50%, which roughly translates to a 25% increase in growth for the more typical 300 ppm increase in atmospheric CO₂ concentration employed in numerous CO₂ enrichment studies of terrestrial plants.

If the results obtained by Collins *et al.* for the freshwater *Chlamydomonas reinhardtii* are typical of what to expect of marine microalgae—which Field *et al.* suggest may provide nearly half of the primary production of the planet—the totality of Earth’s plant life may provide a significant brake upon the rate at which the air’s CO₂ content may increase in the future, as well as the ultimate level to which it may rise. Collins *et al.* provide a rough indication of just how powerful this phenomenon may be when they note, “mathematical simulations have estimated that pre-industrial levels of CO₂ would have been as high as 460 ppm” without the operation of the well-known “biological pump” (Sarmiento and Toggweiler, 1984) by which dying phytoplankton sink carbon into deep ocean sediments, “whereas pre-industrial atmospheric CO₂ levels were [actually] around 280 ppm (Etheridge *et al.*, 1996),” or 180 ppm less.

Logothetis *et al.* (2004) note “the function and structure of the photosynthetic apparatus of many algal species resembles that of higher plants (Plumley and Smidt, 1984; Brown, 1988; Plumley *et al.*, 1993),” and “unicellular green algae demonstrate responses to increased CO₂ similar to those of higher plants in terms of biomass increases (Muller *et al.*, 1993).” Noting “little is known about the changes to their photosynthetic apparatus during exposure to high CO₂,” they grew batches of the unicellular green alga *Scenedesmus obliquus* (wild type strain D3) autotrophically in liquid culture medium for several days in a temperature-controlled water bath of 30°C at low (55 μmol m⁻² s⁻¹) and high (235 μmol m⁻² s⁻¹) light intensity while continuously aerating the water

with air of either 300 or 100,000 ppm CO₂. Exposure to the latter high CO₂ concentration produces a “reorganization of the photosynthetic apparatus” and “leads to enhanced photosynthetic rates, which ... leads to an immense increase of biomass.” After five days under low light conditions, the CO₂-induced increase in biomass was approximately 300%, and under high light conditions it was approximately 600%.

Hargrave *et al.* (2009) “used free air CO₂ enrichment to compare effects of eCO₂ (i.e., double ambient ~ 720 ppm) relative to ambient CO₂ (aCO₂ ~ 360 ppm) on several ecosystem properties and functions in large, outdoor, experimental mesocosms that mimicked shallow sand-bottom prairie streams.” They found the primary productivity of benthic algae inhabiting the streams “was about 1.6, 1.9, 2.5, and 1.3 times greater in the eCO₂ treatment on days 30, 45, 60, and 75, respectively.” The carbon/phosphorus (C/P) ratio of the algae was on average 2 and 1.5 times greater in the eCO₂ treatment than in the aCO₂ treatment on days 45 and 90, respectively, implying a reduced availability of phosphorus, which would make the algae less nutritious and, therefore, less beneficial for its consumers.

However, the researchers observed eCO₂ “had positive effects on benthic invertebrates, significantly increasing chironomid density, biomass, and average size.” Hargrave *et al.* state “chironomid density was about 3, 5, and 2.5 times greater in the eCO₂ treatment than in the aCO₂ treatment on days 30, 60, and 90, respectively,” “biomass was about 4, 3, and 3 times greater in the eCO₂ treatment than in the aCO₂ treatment on days 30, 60, and 90, respectively,” and “individual mass was about two times greater on days 30 and 60.” Thus, “contrary to the dominating hypotheses in the literature,” Hargrave *et al.* conclude “eCO₂ might have positive, bottom-up effects on secondary production in some stream food webs.” They state their experimental findings and “the large literature from terrestrial and marine ecosystems suggests that future [i.e., higher] atmospheric CO₂ concentrations are likely to have broad reaching effects on autotrophs and consumers across terrestrial and aquatic biomes.”

Joint *et al.* (2011) write “marine and freshwater assemblages have always experienced variable pH conditions,” noting “phytoplankton blooms can rapidly reduce pCO₂, with a concomitant increase in pH,” which subsequently declines as the blooms die out, demonstrating “pH is naturally variable and that marine organisms—particularly microbes—must already be capable of adapting to rapid and some-

times large changes in pH.” They note “oceanic pH can change by up to 0.06 pH unit during the year even in the oligotrophic Central Pacific, which does not experience the dramatic phytoplankton blooms of temperate oceans.”

In the case of freshwater ecosystems, Joint *et al.* report, “Maberly (1996) showed that diel variations in a lake can be as much as 2–3 pH units,” and “Talling (2006) showed that in some English lakes, pH could change by >2.5 pH units over a depth of only 14 m.” They note, “phytoplankton, bacteria, archaea and metazoans are all present in lakes, and appear to be able to accommodate large daily and seasonal changes in pH.”

Noting the “the impacts of elevated atmospheric CO₂ on freshwater habitats are still poorly understood,” Wu *et al.* (2012) isolated specimens of the freshwater N₂-fixing cyanobacterium *Cylindrospermopsis raciborskii* from a pond near Dianchi Lake in Kunming (China). They cultured them semi-continuously for 18 days at low and high inorganic phosphorus (Pi) levels (0.022 µM and 22 µM, respectively) in contact with air of either 380 or 1,000 ppm CO₂, while measuring several important physiological functions of the cyanobacterium.

In the case of light-saturated net photosynthesis, the 620-ppm increase in the air’s CO₂ content resulted in 37% and 74% increases in the low and high Pi treatments, respectively. The CO₂ increase resulted in 26% and 23% increases in biomass in the low and high Pi treatments, respectively. And the CO₂ increase resulted in 36% and 14% increases in nitrogen fixation in the low and high Pi treatments, respectively. Wu *et al.* say the cyanobacterial growth increase they observed “confirms previous studies with other algae (Burkhardt and Riebesell, 1997; Burkhardt *et al.*, 1999; Clark and Flynn, 2000; Kim *et al.*, 2006; Posselt *et al.*, 2009; Kranz *et al.*, 2010),” as well as the finding of Chinnasamy *et al.* (2009) that “the nitrogenase activity of *Anabaena fertilissima* increased with increasing levels of CO₂.”

Prosser *et al.* (2012) write, “harmful algal blooms of *Prymnesium parvum* are global phenomena occurring in marine, estuarine and inland ecosystems,” citing Moestrup (1994), Edvardsen and Paasche (1998), and Lundholm and Moestrup (2006). They note *P. parvum*, commonly known as “golden algae” or “Texas tide,” is “a mixotrophic flagellated haptophyte known to produce toxins that may severely impact aquatic organisms,” citing Brooks *et al.* (2010). Prosser *et al.* evaluated “whether pH influences *P. parvum* bloom development and ambient toxicity” by manipulating pH levels (7, 7.5,

8.5) of *in situ* experimental enclosures during 21-day pre-bloom development experiments in Lake Granbury, Texas (USA).

The 10 U.S. researchers report neutral pH levels preempted *P. parvum* bloom development, as “population densities never reached bloom proportions and no ambient toxicity to fish or cladocerans resulted.” They found “higher pH (8.5) allowed bloom formation to occur” and “resulted in ambient toxicity,” whereas at the other end of the pH spectrum, “reducing pH to 7 and 7.5 did not adversely affect phytoplankton or zooplankton biomass.”

The results of the studies reviewed above are encouraging, suggesting the growth and productivity of freshwater algae may be enhanced as the air’s CO₂ concentration rises and the pH levels of freshwater lakes, rivers, and streams decline, while also making it more difficult for blooms of some harmful algae to occur.

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Aquatic Life

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6.4.2 Macrophytes

The studies reviewed in this section examine what scientists have learned about potential impacts of lower freshwater pH levels on macrophytes—aquatic plants. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- The ongoing rise in the air's CO_2 content will likely induce significant positive impacts on most freshwater macrophytes, including submersed, floating, and emergent species.
- The CO_2 -induced growth enhancement of Corkscrew vallisneria (*Vallisneria spiralis*) has been observed to increase linearly out to CO_2 concentrations 10 times the ambient value.
- Total biomass accumulation of *Vallisneria spiralis* plants grown at an elevated CO_2 concentration of 1,000 ppm was “2.3 times that of plants grown in ambient CO_2 , with biomass of leaves, roots, and rhizomes increasing by 106%, 183%, and 67%, respectively.”
- A tenfold increase in aquatic CO_2 concentration enhanced the biomass production of *Littorella uniflora* by 78% across an entire growing season.
- A 300 ppm increase in CO_2 produced a 3.7-fold increase in total dry matter production in the water lily *Nymphaea marliac*.
- In a CO_2 enrichment study of the common water fern *Azolla pinnata*, “the debilitating effects of high temperatures were [found to be] reduced: in one case to a much less severe negative growth rate, in another case to merely a short period of zero growth rate, and in a third case to no discernible ill effects whatsoever—in spite of the fact that the ambient treatment plants in this instance all died.”
- Elevated CO_2 and temperature—both singly and in combination—positively impacted root growth of water horsetail (*Equisetum fluviatile*).

Idso (1997) grew specimens of corkscrew vallisneria (*Vallisneria spiralis*) for several multiweek periods in several 10- and 29-gallon glass tanks (containing 10-cm bottom-layers of common aquarium gravel) filled with tap water maintained within 0.5°C of either 18.2°C or 24.5°C . He maintained the semi-sealed air spaces above these “poor man’s biospheres,” as he named them, at a number of CO_2 concentrations. Upon harvesting the plants at the end of the study, he found the CO_2 -induced growth enhancement was linear, and this linear relationship extended to the highest atmospheric CO_2 concentration studied: 2,100 ppm. In addition, he found the CO_2 -induced growth increase of the plants in the higher of the two water

temperature treatments (a 128% increase in going from an atmospheric CO₂ concentration of 365 ppm to one of 2,100 ppm) was 3.5 times greater than that of the plants in the lower water temperature treatment. Idso reports Titus *et al.* (1990), who studied the closely related *Vallisneria americana*, “observed that the biomass of their experimental plants also rose linearly with the CO₂ content of the air above the water within which they grew, and that [it] did so from the value of the [then] current global mean (365 ppm) to a concentration fully ten times larger.”

Yan *et al.* (2006) collected turions of *Vallisneria spirulosa* from Liangzi Lake, Hubei Province (China) and planted them in tanks containing 15-cm-deep layers of fertile lake sediments, topped with 40 cm of lake water, placed in two glasshouses—one maintained at the ambient atmospheric CO₂ concentration of 390 ppm and the other at an elevated concentration of 1,000 ppm. They allowed the plants to grow for 120 days, harvested them, and determined the dry weights of their various organs. They found the “total biomass accumulation of plants grown in the elevated CO₂ was 2.3 times that of plants grown in ambient CO₂, with biomass of leaves, roots, and rhizomes increasing by 106%, 183%, and 67%, respectively.” They report, “turion biomass increased 4.5-fold,” because “the mean turion numbers per ramet and mean biomass per turion in elevated CO₂ were 1.7–4.3 and 1.9–3.4 times those in ambient CO₂.”

Andersen *et al.* (2006) studied small, slow-growing evergreen perennials called isoetids that live submersed along the shores of numerous freshwater lakes. They obtained specimens of *Littorella uniflora* from sediment cores removed from Lake Hampen, Denmark, which they grew in 75-liter tanks with 10-cm overburdens of filtered lake water for 53 days. They measured various plant, water, and sediment properties throughout the experiment’s duration, and then the researchers destructively harvested the plants and measured their biomass. Throughout this period, half of the tanks had ambient air bubbled through their waters, while the other half were similarly exposed to a mixture of ambient air and pure CO₂ that produced a tenfold increase in the air’s CO₂ concentration. This ultra-CO₂-enrichment led to a 30% increase in plant biomass and “higher O₂ release to the sediment which is important for the cycling and retention of nutrients in sediments of oligotrophic softwater lakes.” When the ultra-CO₂-enrichment was maintained for an entire growing season (May–November), Andersen and Andersen (2006a) report the tenfold increase in aquatic CO₂ concentration

enhanced the biomass production of *Littorella uniflora* by 78%.

Andersen and Andersen (2006b) propagated *Littorella uniflora* under sterile conditions in the absence of symbiotic arbuscular mycorrhizal fungi (AMF), after which they re-infected half of the plants with AMF and allowed both groups to grow for 60 days in water of either high (150 μM) or low (ambient, about 15 μM) CO₂ concentration in conditions where concentrations of NO₃⁻ and PO₄³⁻ were low enough to limit plant growth. Under this experimental setup, the authors report, “both in treatments with and without AMF, high CO₂ concentration resulted in a significantly higher total biomass of *L. uniflora*, and the same was observed for both shoots and roots,” although “the biomass of roots increased more than the biomass of shoots.” They report, “in treatments without AMF, increasing the CO₂ concentration 10 times resulted in a change from a slightly negative growth to a twofold increase in biomass over the 60-day period,” and “in treatments with AMF, the increase in CO₂ concentration resulted in a fourfold increase in biomass.”

The researchers’ work also demonstrated “*L. uniflora*’s symbiosis with mycorrhiza improved the retention of N and P in the plants at very low nutrient concentrations in the water.” Consequently, as they observed “hyphal infection increased fivefold under the raised CO₂ concentration,” it is evident elevated aquatic CO₂ concentrations may also help isoetids by enhancing the magnitude and stability of their AMF symbiosis, which helps them retain vital nutrients.

Idso *et al.* (1990) studied an “in-between” type of plant—water lily (*Nymphaea marliac*)—which has submersed roots and rhizomes anchored in water-body sediments but also has floating leaves on the surface of the water and emergent flowers that protrude above the water surface. The water lilies were grown for two consecutive years in sunken metal stock tanks located out-of-doors at Phoenix, Arizona (USA) and enclosed within clear-plastic-wall open-top chambers through which air of either 350 or 650 ppm CO₂ was continuously circulated. In addition to the leaves of the plants being larger in the CO₂-enriched treatment, there were 75% more of them than in the ambient-air tanks at the conclusion of the initial five-month-long growing season, the scientists report. Each of the plants in the high-CO₂ tanks also produced twice as many flowers as the plants growing in ambient air, and the flowers that blossomed in the CO₂-enriched air were more substantial than those that bloomed in the air of ambient CO₂ concentration—they had more petals, the petals were

longer, and they had a greater percent dry matter content, so the flowers weighed on average about 50% more than those in the ambient-air treatment. In addition, the stems that supported the flowers were slightly longer in the CO₂-enriched tanks, and the percent 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%.

There were also noticeable differences just above the surface of the soil that covered the bottoms of the tanks. Plants in the CO₂-enriched tanks had more and bigger basal rosette leaves, which were attached to longer stems of greater percent dry matter content, which led to the total biomass of these portions of the plants being 2.9 times greater than the total biomass of the corresponding portions of the plants in the ambient-air tanks. In addition, plants in the CO₂-enriched tanks had more than twice as many unopened basal rosette leaves.

The greatest differences of all, however, were within the soil that covered the bottoms of the stock tanks. When half of the plants were harvested at the conclusion of the first growing season, the number of new rhizomes produced over that period was 2.4 times greater in the CO₂-enriched tanks than in the ambient-air tanks, and the number of major roots produced there was 3.2 times greater. The percent dry matter contents of the new roots and rhizomes were also greater in the CO₂-enriched tanks. Overall, the total dry matter production within the submerged soils of the water lily ecosystems was 4.3 times greater in the CO₂-enriched tanks than in the ambient-air tanks, and the total dry matter production of all plant parts—those in the submerged soil, those in the free water, and those in the air above—was 3.7 times greater in the high-CO₂ enclosures.

Over the second growing season, the growth enhancement in the high-CO₂ tanks was somewhat less, but the plants in those tanks were so far ahead of the plants in the ambient-air tanks that in their first five months of growth they produced what it took the plants in the ambient-air tanks fully 21 months to produce.

Idso (1997) focused on an exclusively floating freshwater macrophyte, growing many batches of the common water fern (*Azolla pinnata*) over a wide range of atmospheric CO₂ concentrations at two water temperatures (18.2°C and 24.5°C) for periods of several weeks. A 900 ppm increase in the CO₂ concentration of the air above the tanks led to a 19% increase in the biomass production of the plants

floating in the cooler water, but a 66% biomass increase in the plants floating in the warmer water.

In another study of *Azolla pinnata*, Idso *et al.* (1989) conducted three separate two- to three-month experiments in which they grew batches of the floating fern out-of-doors in adequately fertilized water contained in sunken metal stock tanks located within clear-plastic-wall open-top chambers continuously maintained at atmospheric CO₂ concentrations of either 340 or 640 ppm. At weekly intervals, the researchers briefly removed the plants from the water and weighed them, and they measured their photosynthetic rates at hourly intervals from dawn to dusk on selected cloudless days. They found the photosynthetic and growth rates of the plants growing in ambient air “first decreased, then stagnated, and finally became negative when mean air temperature rose above 30°C.” In the high CO₂ treatment, they found “the debilitating effects of high temperatures were reduced: in one case to a much less severe negative growth rate, in another case to merely a short period of zero growth rate, and in a third case to no discernible ill effects whatsoever—in spite of the fact that the ambient treatment plants in this instance all died.”

Ojala *et al.* (2002) studied an emergent freshwater macrophyte, growing water horsetail (*Equisetum fluviatile*) plants at ambient and double-ambient atmospheric CO₂ concentrations and ambient and ambient + 3°C air temperatures for three years, although the plants were subjected to the double-ambient CO₂ condition only for approximately five months of each year. The increase in air temperature boosted maximum shoot biomass by 60%, but the elevated CO₂ had no effect on this aspect of plant growth. Elevated CO₂ and temperature—both singly and in combination—positively impacted root growth, which was enhanced by 10, 15, and 25% by elevated air temperature, CO₂, and the two factors together, respectively.

The experimental findings discussed here indicate the ongoing rise in the air’s CO₂ content likely will have significant positive impacts on most freshwater macrophytes, including submersed, floating, and emergent species.

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6.5 Simultaneous Ocean Warming and “Acidification”

6.5.1 Effects on Marine Plants

The studies reviewed in this section examine what scientists have learned about potential impacts of rising ocean temperatures and lower ocean pH levels on various types of marine phytoplankton and macroalgae. The key findings, which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Strains of one phytoplankton species, and even of a single population, can yield responses opposite

to changes in temperature and CO₂, which can lead to contrasting predictions about the future.

- Laboratory experiments suggest increases in the air's temperature and CO₂ content may improve the productivity of two dominating filamentous cyanobacteria species of the Baltic Sea.
- Future ocean warming and acidification will significantly increase the biological extraction of nitrogen and carbon dioxide from the atmosphere by diazotrophic cyanobacteria.
- Atmospheric CO₂ enrichment and sea-surface warming likely will have a large positive influence on the growth of *Emiliania huxleyi*, based on findings of laboratory studies.
- Consistent with findings of laboratory experiments, over the past 220 years of warming and lower ocean pH levels, there has been a 40% increase in average *E. huxleyi* coccolith mass in the subpolar North Atlantic Ocean, based on analyses of real-world sediment-core data.
- Sediment cores taken from the Santa Barbara Basin on the North American Pacific margin indicate an approximate 33% increase in mean coccolith weight over the 87-year period 1917–2004.
- Modern *Coccolithus* populations in the Southern Ocean are, on average, more heavily calcified than their fossil counterparts from the Last Glacial Maximum (21.6–19.9 ka), the Holocene (4.2–3.1 ka), and the Transition between the two periods (16.2–15.6 ka).
- A literature review of experiments conducted on more than 100 marine macroalgae (macro-autotrophs) species finds “photosynthetic and growth rates of marine macro-autotrophs are likely to increase under elevated CO₂ similar to terrestrial C₃ species.”

Fiorini *et al.* (2011) note coccolithophores “are considered to be the most productive calcifying organisms on the planet,” and “they play a crucial role in the marine carbon cycle through calcification and photosynthetic carbon production (Rost and Riebesell, 2004).” They also note coccolithophores “contribute significantly to the flux of organic matter from the sea surface to deep waters and sediments

(Klaas and Archer, 2002)” and are “responsible for about half of the global surface ocean calcification.”

Fiorini *et al.* (2011) examined the effects of the $p\text{CO}_2$ and temperature levels projected for the end of this century on photosynthesis, growth, and calcification during both life stages (haploid and diploid) of strain AC418 of the coccolithophore *Syracosphaera pulchra*, via a series of culture studies conducted in the laboratory, where they focused on both particulate inorganic carbon (PIC) and particulate organic carbon (POC). The three researchers report “neither the rate of calcification (production of particulate inorganic carbon) nor the PIC:POC ratio were significantly affected by elevated $p\text{CO}_2$, temperature or their interaction.” They further state, “our results confirm that the expected 3°C increase in the present seawater temperature will not strongly affect the physiology of this eurythermal species” and “the effect of an elevated $p\text{CO}_2$ in seawater will not be significant on calcification or on the PIC:POC ratio in either life stage.”

Feng *et al.* (2008) grew *Emiliana huxleyi*, which they isolated from the Sargasso Sea, by semi-continuous culture methods at two light intensities (low 50 and high 400 $\mu\text{mol photons/m}^2/\text{sec}$), two temperatures (low 20 and high 24°C), and two CO_2 concentrations (low 375 and high 750 ppm). They found in the low-light environment, the chlorophyll *a*-normalized photosynthetic rates of the coccolithophores in all four temperature/ CO_2 treatments attained maximum values at an irradiance of approximately 200 $\mu\text{mol photons/m}^2/\text{sec}$. The maximum photosynthetic rate was lowest in the low-temperature, low- CO_2 (ambient) treatment, but was significantly increased by elevated temperature alone (by 55%) and by elevated CO_2 alone (by 95%). In the high-temperature, high- CO_2 (greenhouse) treatment the maximum photosynthetic rate was increased by 150% relative to the ambient treatment.

In the high-light environment, the chlorophyll *a*-normalized photosynthetic rates did not max out below the maximum irradiance tested (900 $\mu\text{mol photons/m}^2/\text{sec}$) for any but the ambient treatment. Consequently, the equations fit to the data of the other treatments were extrapolated to their respective photosynthetic maxima, which produced corresponding maximum photosynthetic rate increases of 58%, 67%, and 92% for the elevated temperature alone, elevated CO_2 alone, and greenhouse treatments, respectively.

In the high-light greenhouse treatment characteristic of the expected future condition of Earth, the maximum photosynthetic rate was 178% greater than

in the low-light ambient treatment characteristic of the present. The seven researchers say their results indicate “future trends of CO_2 enrichment, sea-surface warming and exposure to higher mean irradiances from intensified [surface water] stratification will have a large influence on the growth of *Emiliana huxleyi*.”

Another important group of phytoplankton are diatoms, which Sobrino *et al.* (2008) say “are responsible for almost 40% of the ocean primary productivity (Nelson *et al.*, 1995).” According to Kremp *et al.* (2012), “most of the laboratory studies investigating the effects of climate stressors on phytoplankton have been performed on single strains,” and “the significant effects often found in such experiments are contrasted by the general lack of clear responses in natural populations,” citing Engel *et al.* (2008). They hypothesize the “contradictory responses to changed climate conditions sometimes observed within the same species might be partly attributable to strain variability between or within populations,” citing Langer *et al.* (2009) and noting these observations emphasize “the need to consider variability in studies aiming to understand the effects of climate change on phytoplankton species.”

Kremp *et al.* studied “the effects of increased temperature and CO_2 availability, as predicted consequences of global change, on 16 genetically different isolates of the diatom *Skeletonema marinoi* from the Adriatic Sea and the Skagerrak (North Sea), and on eight strains of the PST (paralytic shellfish toxin)-producing dinoflagellate *Alexandrium ostenfeldii* from the Baltic Sea.” They assessed maximum growth rates of acclimated isolates grown in batch cultures for five to 10 generations in a factorial design at 20 and 24°C , and present-day and next-century atmospheric CO_2 concentrations (385 and 750 ppm), respectively. The seven scientists found strains of one species, and even of a single population, “can be impacted in very different ways by climate stressors,” noting “a particularly wide response range was found in the population of *S. marinoi* from the NW Adriatic sea, where temperature and CO_2 caused positive, negative or no effect at all.”

Kremp *et al.* conclude, “depending on the strain of choice,” experiments using single isolates of the population they studied “could have given opposite response patterns,” which likely would have led to “contrasting predictions” about the future. Therefore, they write, “responses observed in single strain experiments may not be representative” of the species or population in question, and predictions for specific

species behavior under future climatic conditions must “be treated with caution.”

Noting “cyanobacteria such as *Synechococcus* and *Prochlorococcus* have a major impact on the global carbon cycle and contribute up to 50% of fixed carbon in marine systems (Partensky *et al.*, 1999),” Fu *et al.* (2007) studied “how CO₂ and temperature individually and together affect the physiology of these two species under identical growth conditions.” They grew stock cultures of the two picocyanobacteria in one-liter bottles of autoclaved and filtered seawater maintained at temperatures of either 20 or 24°C in equilibrium with air of either 380 or 750 ppm CO₂. The five researchers discovered the growth rate and maximum photosynthetic rate in *Synechococcus* increased about 2.3-fold and 4-fold, respectively, in the high-temperature and high-CO₂ treatment relative to ambient conditions, but they remained unchanged in *Prochlorococcus*.

Fu *et al.* say their observations “could be taken to mean that in the future, rising temperature and CO₂ would stimulate growth or photosynthesis of [the] *Synechococcus* isolate but would have much less effect on [the] *Prochlorococcus* strain,” and such a result could “potentially influence competition between particular *Synechococcus* and *Prochlorococcus* ecotypes.” However, they add, “we need to be very cautious about inferring ecosystem-scale shifts in broad taxonomic groups like picocyanobacteria from studies using only two isolates.” They report stimulation of algal growth rates by elevated CO₂ also has been observed by Burkhardt and Riebesell (1997), Burkhardt *et al.* (1999), Yang and Gao (2003), Beardall and Raven (2004), and Kim *et al.* (2006).

Hutchins *et al.* (2007) note *Trichodesmium* species and other diazotrophic cyanobacteria support a large fraction of the total biological productivity of Earth’s tropical and subtropical seas, and they exert a significant influence on the planet’s carbon cycle by supplying much of the nitrogen that enables marine phytoplankton to maintain a level of productivity that removes vast amounts of CO₂ from the atmosphere. They hypothesized that if an increase in the air’s CO₂ content or its temperature led to an increase in oceanic N₂ fixation, it also could lead to the biological extraction of more CO₂ from the atmosphere and a tempering of the CO₂ greenhouse effect via this negative feedback process.

To explore this possibility, the eight researchers grew cultures of Pacific and Atlantic Ocean isolates of *Trichodesmium* ecotypes across a range of atmospheric CO₂ concentrations characteristic of Earth’s past (150 ppm), its current state (380 ppm), and

possible future conditions (750, 1,250, and 1,500 ppm) at two temperatures (25 and 29°C) and at sufficient and limiting phosphorus concentrations (20 and 0.2 μmol L⁻¹ of phosphate, respectively), in situations where the carbonate buffer system parameters in their artificial seawater culture media were “virtually identical to those found in natural seawater across the relevant range of CO₂ values.”

Hutchins *et al.* found, at atmospheric CO₂ concentrations projected for the year 2100 (750 ppm), “N₂ fixation rates of Pacific and Atlantic isolates increased 35–100%, and CO₂ fixation rates increased 15–128% relative to present day CO₂ conditions (380 ppm).” In what they call one of their “most striking results,” they found “increased CO₂ enhanced N₂ and CO₂ fixation and growth rates even under severely phosphorus-limited steady-state growth conditions.” They also report “neither isolate could grow at 150 ppm CO₂,” but “N₂ and CO₂ fixation rates, growth rates, and nitrogen:phosphorus ratios all increased significantly between 380 and 1500 ppm,” and, “in contrast, these parameters were affected only minimally or not at all by a 4°C temperature change.”

Hutchins *et al.* note current global estimates of N₂ fixation by *Trichodesmium* are about 60 × 10⁹ kg N yr⁻¹, and if their experimental results can be extrapolated to the world’s oceans, by 2100 this amount could increase to 81–120 × 10⁹ kg N yr⁻¹. “If these estimates are coupled with modeling predictions of a 27% warming-induced expansion of suitable habitat (Boyd and Doney, 2002), calculations suggest that global N₂ fixation by *Trichodesmium* alone could range from 103–152 × 10⁹ kg N yr⁻¹ by the end of this century,” which is to be compared to recent estimates for total pelagic N₂ fixation of 100–200 × 10⁹ kg N yr⁻¹ (Galloway *et al.*, 2004). They also note free-living unicellular cyano-bacteria in the ocean are believed to fix at least as much nitrogen as *Trichodesmium* (Montoya *et al.*, 2004), and endosymbiotic cyanobacteria also contribute substantially to N₂ fixation. Hence they conclude, “if N₂ fixation rates in these groups show commensurate increases with rising CO₂, the cumulative effect on the global nitrogen cycle could be considerably larger (e.g., a doubling).” In addition, they state their results indicate “like N₂ fixation, CO₂ fixation by *Trichodesmium* should also increase dramatically in the future because of CO₂ enrichment.”

Hutchins *et al.* conclude, “many of our current concepts describing the interactions between oceanic nitrogen fixation, atmospheric CO₂, nutrient biogeochemistry, and global climate may need re-evaluation

to take into account these previously unrecognized feedback mechanisms between atmospheric composition and ocean biology.”

Karlberg and Wulff (2013) investigated the ramifications of potential future increases in the air's CO₂ content on the productivity of two dominating filamentous cyanobacteria species of the Baltic Sea (*Nodularia spumigena* and a mix of *Aphanizomenon* sp.) during the summer bloom of the Baltic Proper. The pair of researchers set out to experimentally determine the response of these two species to changes in that region's environment predicted to occur in response to IPCC's business-as-usual A1FI scenario described by Meehl *et al.* (2007): a temperature increase of 4°C, an atmospheric pCO₂ increase from 380 to 960 ppm, and a reduction in salinity from 7 to 4. Working in the laboratory, Karlberg and Wulff measured numerous responses of the two species of cyanobacteria, growing both separately and together, to different combinations of these environmental changes.

The two researchers report “increased temperature, from 12 to 16°C, had a positive effect on the biovolume and photosynthetic activity of both species,” and “compared when growing separately, the biovolume of each species was lower when grown together.” They also note “decreased salinity, from 7 to 4, and elevated levels of pCO₂, from 380 to 960 ppm, had no effect on the biovolume, but on [the photosynthetic activity] (Fv/Fm) of *N. spumigena* with higher Fv/Fm in salinity 7.” Karlberg and Wulff say their results suggest “the projected A1FI scenario might be beneficial for the two species dominating the extensive summer blooms in the Baltic Proper.” They caution their results “further stress the importance of studying interactions between species.” They conclude, “long-term studies together with multifactorial and mesocosm/field experiments are needed to elucidate the future impact of climate change effects on Baltic filamentous cyanobacteria.”

Grelaud *et al.* (2009) investigated “the morphometry (size, weight) of selected species of the order Isochrysidales (i.e., *E. huxleyi*, *G. muelleriae* and *G. oceanica*) to understand how coccolithophores' carbonate mass is influenced by recent oceanographic global changes.” They analyzed sediment cores taken from “the deep center of the Santa Barbara Basin (SBB) on the North American Pacific margin in the interval from AD 1917 to 2004.” They found “morphometric parameters measured on *E. Huxleyi*, *G. muelleriae* and *G. oceanica* indicate increasing coccolithophore shell carbonate mass from ~1917 until 2004 concomitant with rising pCO₂ and

sea surface temperature in the region of the SBB.” Specifically, they note “a >33% increase in mean coccolith weight was determined for the order Isochrysidales over 87 years from ~1917 until 2004.”

The three researchers note “the last century has witnessed an increasing net influx of atmospheric carbon dioxide into the world's oceans, a rising of pCO₂ of surface waters, and under-saturation with respect to aragonite, especially along the North American Pacific margin,” which was the site of their study. They note those concerned about lower ocean pH levels predicted such conditions will “result in reduced coccolithophore carbonate mass and a concomitant decrease in size and weight of coccoliths.” They discovered just the opposite appears to have occurred in the real world, even in places where the predicted calcification reductions were expected to be greatest.

Iglesias-Rodriguez *et al.* (2008) grew several batch incubations of the coccolithophore species *Emiliania huxleyi* in the laboratory, bubbling air of a number of different atmospheric CO₂ concentrations through the culture medium and determining the amounts of particulate inorganic carbon (PIC) and particulate organic carbon (POC) produced by the coccolithophores within the CO₂ treatments. In addition, they determined the change in average coccolithophore mass of *Emiliania huxleyi* over the past 220 years in the real world of nature, based on data they obtained from a sediment core extracted from the subpolar North Atlantic Ocean, over which period of time temperatures increased and the air's CO₂ concentration rose by approximately 90 ppm. The 13 researchers from the United Kingdom, France, and United States observed an approximate doubling of both PIC and POC between the culture media in equilibrium with air of today's CO₂ concentration and air of 750 ppm CO₂. They report the field evidence obtained from the deep-ocean sediment core they studied “is consistent with these laboratory conclusions, indicating that over the past 220 years there has been a 40% increase in average coccolith mass.”

Cubillos *et al.* (2012) set out to adapt “an existing method to estimate coccolith calcite weight using birefringence (Beaufort, 2005),” which they decided was needed “to suit the large coccoliths of *Coccolithus pelagicus*,” focusing “only on the central area, which is the thickest and most robust part of the coccolith.” They applied this technique “to fossil and sediment trap material from the South Tasman Rise area of the Southern Ocean,” based on three sediment samples each from the Last Glacial Maximum (21.6–19.9 ka), the Holocene (4.2–3.1 ka), and the

Transition between the two periods (16.2–15.6 ka), as well as modern-day trap samples. “Most strikingly,” the five researchers report, “it appears that modern *Coccolithus* populations in the Southern Ocean are, on average, more heavily calcified than their fossil counterparts,” a positive and encouraging finding. Cubillos *et al.* say their work reveals “substantial non-linearity and independency of variations (plasticity) in coccolith size, shape and volumetric weight between the investigated time intervals.” They say they hope to study these phenomena “in more detail” in order to “unravel what environmental conditions are related to intra-specific phenotypic variability in ancient and modern coccolithophores.”

Koch *et al.* (2013) write, “although seagrasses and marine macroalgae (macro-autotrophs) play critical ecological roles in reef, lagoon, coastal and open-water ecosystems, their response to ocean acidification (OA) and climate change is not well understood.” They reviewed the scientific literature on these subjects, examining “marine macro-autotroph biochemistry and physiology relevant to their response to elevated dissolved inorganic carbon (DIC), carbon dioxide (CO₂), and lower carbonate (CO₃²⁻) and pH,” and also exploring “the effects of increasing temperature under climate change and the interactions of elevated temperature and CO₂.”

The four researchers determined their “literature review of >100 species revealed marine macro-autotroph photosynthesis is overwhelmingly C₃ (>=85%) with most species capable of utilizing HCO₃⁻,” and “most are not saturated at current ocean DIC.” They conclude, “photosynthetic and growth rates of marine macro-autotrophs are likely to increase under elevated CO₂ similar to terrestrial C₃ species.” In addition, as “the photosynthesis of the majority of the species examined was not saturated at the current levels of DIC in the ocean and responded to an increase in CO₂,” they conclude seagrasses and many marine macroalgae have the potential to respond positively, in terms of photosynthesis and growth, under elevated ocean CO₂ and OA.

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6.5.2 Effects on Marine Animals

6.5.2.1 Corals

6.5.2.1.1 Review Papers

Few studies have investigated the interactive effects of lower ocean pH levels and rising temperature. This section examines what scientists have learned from such studies, focusing on the impacts of these variables on coral reefs as reported in review papers on the topic. The key findings, all of which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- “Neither climate nor sea-level nor chemical changes in the oceans can elucidate the waxing and waning of reefs” throughout their history on Earth. The “boom and bust pattern” observed through geologic time is “impossible to explain by linear responses to physicochemical changes.”
- Shallow water tropical reef organisms existed throughout the entire 540 million years of the Phanerozoic, which included times when sea surface temperatures were more than 7°C higher than those of today and the air’s CO_2 concentration was as much as 6,000 ppm higher.
- Although the Paleocene-Eocene Thermal Maximum, some 55.8 million years ago, was “characterized by rapid sea surface temperature rise and a similar order of magnitude of CO_2 increase as present,” there is evidence “reef assemblages in at least one oceanic setting were

unaffected.” Other reefs also have shown “greater resilience to past rapid warming and acidification than previously thought.”

- Emerging evidence indicates there is variability in the coral calcification response to lower seawater pH levels, geographical variation in bleaching susceptibility and recovery, and potential adaptation to rapid warming and declining pH, supporting “an alternative scenario in which reef degradation occurs with greater temporal and spatial heterogeneity than current projections suggest.”

Kiessling (2009), from the Museum fur Naturkunde of the Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University in Berlin, reviewed the state of knowledge of the long-term effects of changes in ocean temperature and the atmosphere’s CO₂ concentration on the vigor of the planet’s coral reefs as of 2009. With respect to global warming, Kiessling reports, “on geologic timescales, there is little evidence for climate change affecting reefs in a linear fashion,” and “changes in mean global temperature as reconstructed from stable oxygen isotopes and the distribution of non-reef climate-sensitive sediments do not correspond to changes in reef abundance or latitudinal distribution,” citing some of his own analyses of the subject (Kiessling, 2001a, 2002). He also states, “reports linking reef expansions and declines to climate change fail to explain why other changes in temperature did not lead to a similar response in reefs and why the reported (fairly modest) temperature changes would have such a dramatic effect.”

Regarding lower ocean pH levels, the German researcher reports, “just like temperature,” it is currently receiving much attention as “a control of reef development,” but “the boom and bust pattern of reefs and hyper-calcifiers is difficult to explain with inferred long-term changes in the saturation state of ocean water, at least if the major trigger is atmospheric pCO₂,” because “previous analyses failed to find any significant cross-correlation between changes in pCO₂ and changes in reef attributes,” citing Kiessling (2001b, 2002).

In light of these and many other observations, Kiessling concludes “neither climate nor sea-level nor chemical changes in the oceans can elucidate the waxing and waning of reefs” throughout their history on Earth, and their “boom and bust pattern” is “impossible to explain by linear responses to physico-chemical changes.” Furthermore, Kiessling writes,

“ecologically complex reef systems have been around for hundreds of millions if not billions of years,” and “geologic models of CO₂ concentrations in the atmosphere suggest that these were much greater during most of Earth’s history than today.” This further suggests something other than CO₂-induced global warming and lower ocean pH levels must have been responsible for their prior “boom and bust” pattern of behavior.

In a major review article published in *Science*, Pandolfi *et al.* (2011) summarize “the most recent evidence for past, present and predicted future responses of coral reefs to environmental change, with emphasis on rapid increases in temperature and lower ocean pH levels and their effects on reef-building corals.” They note, “many physiological responses in present-day coral reefs to climate change are interpreted as consistent with the imminent disappearance of modern reefs globally because of annual mass bleaching events, carbonate dissolution and insufficient time for substantial evolutionary responses.” All of these interpretations, they demonstrate, may be incorrect.

The four researchers report shallow water tropical reef organisms existed throughout the entire 540 million years of the Phanerozoic, which included times when sea surface temperatures (SSTs) were more than 7°C higher than those of today and the air’s CO₂ concentration was as much as 6,000 ppm higher. As to what they call “the most recent reef crisis,” they report “the Paleocene-Eocene Thermal Maximum (PETM; 55.8 million years ago), was characterized by rapid SST rise and a similar order of magnitude of CO₂ increase as present,” yet there is evidence “reef assemblages in at least one oceanic setting were unaffected (Robinson, 2011)” and other reefs also have shown “greater resilience to past rapid warming and acidification than previously thought.”

More recently, during the Holocene, Pandolfi *et al.* state, “evidence from high-resolution proxy records suggests that tropical SSTs had the potential to repeatedly warm over centennial to millennial time scales (Rosenthal *et al.*, 2003; Schmidt *et al.*, 2004).” In one location, they report, SSTs rose “at rates comparable to those projected for the coming century (Lea *et al.*, 2003),” yet “none of these post-Last Glacial Maximum warming episodes appear to have interrupted reef growth.”

As for current coral responses to SST increases, the four scientists note “numerous characteristics of coral hosts have the potential to confer differences in bleaching susceptibility,” and “these characteristics vary substantially within and among coral species

(Baird *et al.*, 2009a; Csaszar *et al.*, 2010).” They note “some coral species also harbor multiple strains of zooxanthellae, which confer differential susceptibility of their hosts to bleaching (Rowan, 2004).” They note there is also “substantial variation in reef recovery in the aftermath of bleaching events (Baker *et al.*, 2008).”

The story is much the same regarding coral responses to lower ocean pH levels. Pandolfi *et al.* note, for example, studies have shown calcification has “increased under moderately elevated partial pressure of CO₂ (Rodolfo-Metalpa *et al.*, 2010; Jury *et al.*, 2010; Reynaud *et al.*, 2003), as has also been observed for some coralline algae, crustacea and echinoderms (Ries *et al.*, 2009).” They also note sensitivity of calcification to lower ocean pH levels “appears to be reduced when (i) studies are conducted over weeks or months (Ries *et al.*, 2009; Rodolfo-Metalpa *et al.*, 2010; Marubini *et al.*, 2001; Reynaud *et al.*, 2003) as opposed to less than one day (Langdon and Atkinson, 2005; Ohde and Hossain, 2004) or (ii) corals are reared under nutritionally replete conditions by feeding or elevating inorganic nutrient concentrations (Langdon and Atkinson, 2005; Ries *et al.*, 2009).”

The four researchers write, “because bleaching-susceptible species often have faster rates of recovery from disturbances, their relative abundances will not necessarily decline” in the future. They continue, “such species could potentially increase in abundance, depending on how demographic characteristics and competitive ability are correlated with thermal tolerance and on the response of other benthic taxa, such as algae.” They further note “the shorter generation times typical of more-susceptible species (Baird *et al.*, 2009b) may also confer faster rates of evolution of bleaching thresholds, which would further facilitate maintenance of, or increases to, the relative abundance of thermally sensitive but faster-evolving species (Baskett *et al.*, 2009).”

Pandolfi *et al.* state emerging evidence for variability in the coral calcification response to lower ocean pH levels, geographical variation in bleaching susceptibility and recovery, responses to past climate change, and potential rates of adaptation to rapid warming “supports an alternative scenario in which reef degradation occurs with greater temporal and spatial heterogeneity than current projections suggest.” Further noting “non-climate-related threats already confronting coral reefs are likely to reduce the capacity of coral reefs to cope with climate change,” they conclude “the best and most achievable thing we can do for coral reefs currently to deal with climate

change is to seek to manage them well” by reducing more direct anthropogenic impacts such as fishing, pollution, and habitat destruction, which fragment populations or decrease population sizes and reduce the potential of coral reefs to adapt to warmer, lower pH conditions.

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6.5.2.1.2 A Model-based Study

This section reviews one model-based study that focuses on the impact of lower ocean pH levels in combination with higher temperatures on coral reefs.

Couce *et al.* (2013) note “there is concern that the growing frequency and severity of mass bleaching episodes may lead to species composition shifts and functional collapse in coral reefs in the near future.” They also note global warming “has the potential to improve currently marginal environmental conditions and extend the range of tropical coral reefs into higher latitudes,” as is “demonstrated in the fossil record in response to warmer geological periods (e.g., Lighty *et al.*, 1978; Veron, 1992; Precht and Aronson, 2004; Greenstein and Pandolfi, 2008; Woodroffe *et al.*, 2010; Kiessling *et al.*, 2012).” Less is known about the interacting effects of global warming and lower ocean pH levels, although these phenomena are projected to occur concurrently.

Couce *et al.* employed “a suite of statistical models based on the environmental factors thought to be limiting to the present equilibrium distribution of shallow-water coral reefs, perturbing them with Earth System Model projected future sea surface temperatures and aragonite saturation changes (the simulations used in Turley *et al.*, 2010),” while considering “a range of potential future CO₂ emissions scenarios” but focusing on “the consequences of the ‘A2’ scenario (characterized by regionally oriented economic development and high population growth, expecting ca. 850 ppm CO₂ by 2100).”

The three UK researchers write of their model-based results, “contrary to expectations, the combined impact of ocean surface temperature rise and acidification leads to little, if any, degradation in future habitat suitability across much of the Atlantic and areas currently considered ‘marginal’ for tropical corals, such as the eastern Equatorial Pacific.” They note, “these results are consistent with fossil evidence of range expansions during past warm periods.” Such findings, Couce *et al.* conclude, “present important implications for future coral reef management, as they suggest that more emphasis should be placed on conservation efforts on marginal reefs as they are not necessarily a ‘lost cause’.”

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6.5.2.1.3 Laboratory Studies

Several laboratory studies have focused on the combined impacts of rising temperatures and falling ocean pH levels on coral reefs. The key findings, all of which challenge the alarming and negative projections of IPCC, are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- The “enhanced kinetics of calcification owing to higher temperatures has the potential to counter the effects of ocean acidification.”
- The conventional belief that calcification rates will be affected by lower ocean pH levels may be unfounded for temperate zone corals.
- The study of a Mediterranean zooxanthellate coral, *Cladocora caespitosa*, revealed “an increase in CO₂, alone or in combination with elevated

temperature, had no significant effect on photosynthesis, photosynthetic efficiency and calcification.”

- Lower seawater pH due to atmospheric CO₂ enrichment and increased temperature (but short of reaching the bleaching level) “will both enhance active biotic calcification” of *Agaricia agaricites* corals.
- “The immediate effects of rising seawater temperature and ocean acidification may be tolerable for some species,” possibly because the increased availability of CO_{2(aq)} under ocean acidification conditions may enhance algal productivity, especially in *Symbiodinium* phylotypes with less efficient carbon-concentrating mechanisms that rely to a greater extent on the passive, diffusive uptake of CO_{2(aq)} and its fertilization effect.

In a paper published in *Nature Climate Change*, McCulloch *et al.* (2012) describe how biogenic calcification occurs within an extracellular calcifying fluid located in the semi-isolated space between a coral's skeleton and its calicoblastic ectoderm, where during active calcification the pH of the calcifying fluid (pH_{cf}) is often increased relative to ambient seawater pH. At a typical seawater pH of ~8.1, for example, the pH of aragonitic corals shows a species-dependent range of 8.4 to 8.7, representing a systematic increase in pH_{cf} relative to ambient sea water (ΔpH) of ~0.3–0.6 units. They report *in situ* measurements of pH within the calcifying medium of live coral polyps using microelectrodes (Al-Horani *et al.*, 2003; Ries, 2011a) and pH-sensitive dyes (Venn *et al.*, 2011) have registered enhanced pH_{cf} values between 0.6 and 1.2—and sometimes up to 2—pH units above seawater during the day, when both net production and calcification are highest.

Using a model of pH regulation combined with abiotic calcification, McCulloch *et al.* show “the enhanced kinetics of calcification owing to higher temperatures has the potential to counter the effects of ocean acidification,” and “the extra energy required to up-regulate pH is minor, only <1% of that generated by photosynthesis,” which highlights the importance of maintaining the zooxanthellae-coral symbiosis for sustaining calcification. They further note their model predicts “a ~15% increase in calcification rates from the Last Glacial Maximum to the late Holocene,” an increase they describe as being “consistent with the expansion of tropical habitats that occurred during

this time despite P_{CO_2} increasing.”

Projecting into the future with their experimentally verified model, the four researchers assess the response of coral reefs “to both global warming, with mean tropical sea surface temperatures $\sim 2^\circ\text{C}$ higher, and with P_{CO_2} increasing from present-day levels to $\sim 1,000$ ppm by the year 2100.” For this scenario, they report their model predicts “either unchanged or only minimal effects on calcification rates.” Thus, from a strictly chemical and kinetic perspective, their model indicates “ocean acidification combined with rising ocean temperatures should have only minimal effects on coral calcification,” which they describe as “a direct outcome” of corals’ ability to up-regulate pH at the site of calcification.

Rodolfo-Metalpa *et al.* (2010) collected three live colonies of the Mediterranean zooxanthellate coral *Cladocora caespitosa* in the Bay of Villefranche (Ligurian Sea, France) at about 25 meters depth in July 2006, plus three other colonies in February 2007. They divided the colonies into fragments and removed single polyps they attached to PVC plates and randomly assigned to aquariums continuously supplied with unfiltered seawater maintained at ambient or elevated water temperature (T or $T + 3^\circ\text{C}$) in equilibrium with air of ambient or elevated CO_2 concentration (400 or 700 ppm). They subjected the polyps to “(1) mid-term perturbations (1 month) in summer and winter conditions of irradiance and temperature, and (2) a long-term perturbation (1 year), mimicking the seasonal changes in temperature and irradiance.”

They found “an increase in CO_2 , in the range predicted for 2100, does not reduce [the coral’s] calcification rate,” and “an increase in CO_2 , alone or in combination with elevated temperature, had no significant effect on photosynthesis, photosynthetic efficiency and calcification.” They report a 3°C rise in temperature in winter resulted in a 72% increase in gross photosynthesis and a significant increase in daytime calcification rate.

Rodolfo-Metalpa *et al.* conclude “the conventional belief that calcification rates will be affected by ocean acidification may not be widespread in temperate corals.” They note Ries *et al.* (2009) have reported the calcification rate of the temperate coral *Oculina arbuscula* is also unaffected by an increase in atmospheric CO_2 concentration of up to 840 ppm, and a large decrease in calcification was found only at a CO_2 concentration in excess of 2,200 ppm. In addition, they write, “some marine invertebrates may be able to calcify in the face of ocean acidification or, contrary to what is generally

expected, may increase their calcification rates as reported on the ophiourid brittlestar *Amphiura filiformis* (Wood *et al.*, 2008), the seastar *Pisaster ochraceus* (Gooding *et al.*, 2009) exposed to lower pH (7.8–7.3), the Caribbean coral *Madracis mirabilis* at pH 7.6 (Jury *et al.*, 2010), and shown for coralline red algae, calcareous green algae, temperate urchins, limpets, crabs, lobsters and shrimp (Ries *et al.*, 2009).” They note there are many cases where “rates of photosynthesis are either not affected (e.g. Langdon *et al.*, 2003; Reynaud *et al.*, 2003; Schneider and Erez, 2006; Marubini *et al.*, 2008) or slightly increased (e.g. Langdon and Atkinson, 2005) at the level of CO_2 expected in 2100.”

In a study designed to explore what controls calcification in corals, Sandeman (2012) suspended—by means of a torsion microbalance (as per Kesling and Crafts, 1962)—small pieces of coral he carefully removed from the edges of thin plates of *Agaricia agaricites* corals and lowered into gently stirred temperature-controlled seawater, after which he used the microbalance to measure coral net calcification rates over a range of seawater temperature and pH. He reported calcification rates of live *A. agaricites* coral increased by 15–17.7% per $^\circ\text{C}$ as seawater temperature rose from 27 to 29.5°C , and in his experiments in which the pH of the seawater was reduced from an average of 8.2 to 7.6, he observed calcification in living corals increased significantly. Similar experiments conducted with small portions of dead coral skeleton revealed “when the average pH was reduced from 8.2 to 7.5, calcification rate decreased.” He determined the difference between calcification rates in going from seawater of pH 8.2 to seawater of pH 7.8 ranged from +30% for coral with no dead areas to –21.5% for coral with 30% dead exposed surface area.

The Trent University researcher from Peterborough, Ontario (Canada) says his findings suggest lower seawater pH due to atmospheric CO_2 enrichment and increased temperature (but short of reaching the bleaching level) “will both enhance active biotic calcification.” He states the wide range of results between his and other scientists’ studies of calcification rate and carbon dioxide “may be explainable in terms of the ratio of ‘live’ to ‘dead’ areas of coral,” as is also suggested by the work of Rodolfo-Metalpa *et al.* (2011) and Ries (2011b), all of which leads him to conclude coral species that typically have smaller areas of exposed dead surface “may have a better chance of survival as pH levels drop.”

Schoepf *et al.* (2013) note “since scleractinian corals are calcifying organisms that already live close

to their upper thermal tolerance limits, both ocean warming and acidification severely threaten their survival and role as reef ecosystem engineers.” They observe “no studies to date have measured energy reserve pools (i.e., lipid, protein, and carbohydrate) together with calcification under ocean acidification conditions under different temperature scenarios.” Schoepf *et al.* studied the single and interactive effects of $p\text{CO}_2$ (382, 607, and 741 ppm) and temperature (26.5 and 29.0°C) on coral calcification, energy reserves (i.e., lipid, protein, and carbohydrate), chlorophyll *a*, and endosymbiont concentrations in four species of Pacific coral having different growth morphologies (*Acropora millepora*, *Pocillopora damicornis*, *Montipora monasteriata*, and *Turbinaria reniformis*).

The 13 researchers found coral energy reserves were largely *not* metabolized “in order to sustain calcification under elevated $p\text{CO}_2$ and temperature,” as “maintenance of energy reserves has been shown to be associated with higher resistance to coral bleaching and to promote recovery from bleaching (Rodrigues and Grottoli, 2007; Anthony *et al.*, 2009).” They report lipid concentrations increased under lower ocean pH levels conditions in both *A. millepora* and *P. damicornis* and “were fully maintained in *M. monasteriata* and *T. reniformis*.” Protein, carbohydrate, and tissue biomass also were “overall maintained under ocean acidification conditions in all species.” Thus “only one of the four corals species studied [*Acropora millepora*] decreased calcification in response to average ocean acidification levels expected by the second half of this century (741 ppm), even when combined with elevated temperature (+2.5°C).”

Schoepf *et al.* conclude “some corals could be more resistant to combined ocean acidification and warming expected by the end of this century than previously thought,” so “the immediate effects of rising seawater temperature and ocean acidification may be tolerable for some species,” possibly because the increased availability of $\text{CO}_{2(\text{aq})}$ under lower ocean pH levels conditions may enhance algal productivity, especially in *Symbiodinium* phylotypes with less efficient carbon-concentrating mechanisms that rely to a greater extent on the passive, diffusive uptake of $\text{CO}_{2(\text{aq})}$ and its fertilization effect, citing Herfort *et al.* (2008) and Brading *et al.* (2011).

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Climate Change Reconsidered II: Biological Impacts

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6.5.2.1.4 Field Studies

Several field studies have focused on the combined effects of lower ocean pH levels and higher temperatures. The key findings of these studies are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- Over the period 1937–1996, *Montastraea faveolata* colonies located in the upper Florida Keys maintained rates of extension and calcification in spite of the combination of local environmental and climatic changes.
- A nearly three-century-long history of coral calcification in the South China Sea reveals an 11% increase between 1716 and 2005.
- Between 1900 and 2010, increases in *Porites* coral calcification on reefs in the southeast Indian Ocean ranged from small, non-significant positive trends, to increases as high as 23% per decade. In these regions, “the rate of change in the thermal environment of coral reefs is currently the primary driver of change in coral calcification rates,” and “the large-scale phenomenon of ocean acidification is not currently limiting calcification on coral reefs uniformly at a global scale.”
- Flexibility in community composition observed along latitudinal environmental gradients across the Great Barrier Reef “indicates that climate change is likely to result in a re-assortment of coral reef taxa rather than wholesale loss of entire reef ecosystems.”

According to Cantin *et al.* (2009), “zooxanthellae (symbiotic dinoflagellates of the genus *Symbiodinium*) are critical to the survival of reef-building corals, providing a major source of energy from photosynthesis for cell maintenance, growth and reproduction of their coral hosts,” and these services include the energetically expensive process of calcification (Idso *et al.*, 2000). Cantin *et al.* studied the amount of photosynthetic “rent” paid by two clades of *Symbiodinium* (C1 and D) to their coral hosts (juvenile *Acropora millepora*) for the privilege of living within the latter’s calcareous “houses.” This was done by measuring the “financial transfer” to nine-month-old corals developed “from crosses involving the same parent corals.” This “planned

parenthood” minimized any host genetic differences that otherwise might have influenced the physiology of the host-symbiont “lease agreement.”

They found “*Symbiodinium* C1 exhibited a 121% greater capacity for translocation of photosynthate to *A. millepora* juveniles along with 87% greater relative electron transport through photosystem II under identical environmental conditions.” In addition, the five researchers note “*A. tenuis* and *A. millepora* juveniles in a previous study exhibited 2 to 3 times faster growth rates when associated with *Symbiodinium* C1 compared to those associated with *Symbiodinium* D (Little *et al.*, 2004) at the same field site where juveniles were reared in the present study.”

Cantin *et al.* conclude “the differences in carbon-based energy transfer between symbiont types may provide a competitive advantage to corals associating with *Symbiodinium* C1, particularly during their early life histories, when greater energy investment into rapid tissue and skeletal growth can prevent overgrowth of juveniles by competitors and mortality from grazers.” They write, “as the community structure of coral reefs shift in response to global climate change and water quality impacts, opportunistic corals harboring symbionts that enable maximum rates of growth may similarly gain a competitive advantage.” Consequently, in the economy of nature ample provision evidently has been made for corals to weather all sorts of environmental challenges that may come their way, including those IPCC contends will be driven by rising atmospheric CO₂ concentrations.

In studying coral calcification rates on Australia’s Great Barrier Reef, De’ath *et al.* (2009) report there was a 14% drop in *Porites* calcification rate from 1990 to 2005 (although a graphical view of their data indicates the decline began around 1970) and this decline “is unprecedented in at least the past 400 years,” which is indeed what their data show. Such statements, however, do not reveal the full story.

If, for example, their calcification history is followed back in time a mere 33 more years, from 1605 to 1572—when the air’s CO₂ concentration was more than 100 ppm less than it is today and, therefore, was supposedly so much healthier for corals (according to the ocean “acidification” hypothesis)—it shows the coral calcification rate at that earlier time was approximately 21% lower than it was at its twentieth century peak.

Another way of looking at De’ath *et al.*’s data is to realize that from 1572 to 1970, *Porites* calcification rates on the Great Barrier Reef increased by about 27% as the atmospheric CO₂ concentration and air

temperature rose concurrently. After 1970, calcification rates declined, but by a much smaller 14%, even as air temperature and CO₂ concentrations continued to increase, further obscuring the issue. De’ath *et al.* note, “the causes for the [1990 to 2005] Great Barrier Reef-wide decline in coral calcification of massive *Porites* remain unknown.”

Three years later, the work of another research team provided a possible answer. Uthicke *et al.* (2012) state, “tropical coral reefs are currently under threat by a variety of regional and global stressors,” with examples of the former being “land runoff and overfishing (e.g., Pandolfi *et al.*, 2003; Fabricius, 2005),” and examples of the latter “sea temperature increase and ocean acidification (Hoegh-Guldberg *et al.*, 2007; Fabricius *et al.*, 2011).” To determine which set of stressors is the most significant threat, Uthicke *et al.* analyzed sediment cores collected from inshore fringing coral reefs in the Whitsunday area of the Great Barrier Reef (GBR) of Australia. They collected these cores from three locations: inner near-shore reefs with low coral cover and high macroalgal abundance, intermediate reefs, and reefs at outer islands with low algal and high coral cover. They chose these three locations because inner near-shore reefs are typically the first to produce evidence of regional human impacts; reefs at outer islands are the last to experience the negative effects of human influence, as well as the most likely to exhibit evidence of global stressors; and intermediate reefs often show evidence of both.

The three researchers report benthic foraminiferal assemblages found in the cores of outer-island reefs unaffected by increased land runoff have been “naturally highly persistent over long (>2000 years) timescales.” In both of the other zones, assemblages were also persistent, but only until 150 years ago, and assemblages less than 55 years old from inner near-shore and intermediate reefs were significantly different from older assemblages.

Uthicke *et al.* conclude they found support for the likelihood “increased land runoff since the start of land clearing and agriculture in the catchment of the Whitsunday Region of the GBR has left a signature in the foraminiferal assemblages of inner and intermediate areas of the study area,” when previously the assemblages of these areas had been “persistent for at least several thousand years.” In addition, and based on the fact “no changes were observed on outer reefs located away from land runoff,” they propose “changes observed on inner and intermediate reefs were mainly driven by enhanced agricultural runoff after European settlement.” And finally, they affirm

“the hypothesis that global forcing, such as sea temperature increase or ocean acidification, altered the foraminiferal community found little support.”

Browne (2012) writes “local stressors erode reef resilience, and therefore increase their vulnerability to global stressors that include ocean warming, [which is] predicted to increase the severity and intensity of coral bleaching events (Hoegh-Guldberg, 1999), ocean acidification, [which is] predicted to reduce calcification rates and reef growth (Kleypas *et al.*, 1999), and increased storm and cyclone activity, [which is] predicted to reduce coral framework complexity and stability (Puotinen, 2004).” In a study designed to assess the overall impact of these several reef stressors, Browne describes how “coral growth rates (linear extension, density, calcification rates) of three fast-growing corals (*Acropora*, *Montipora*, *Turbinaria*) were studied *in situ* on Middle Reef, an inshore reef located on the central Great Barrier Reef (GBR),” in order to “assess the influence of changing environmental conditions on coral condition and reef growth.”

Browne found “despite local anthropogenic pressures and global climate change, Middle Reef has a robust and resilient coral community,” and “*Acropora* linear extension rates were comparable with rates observed at similar depths and sea surface temperatures on mid to offshore reefs on the GBR, and in the Caribbean.” In addition, “*Montipora* and *Turbinaria* are abundant on inshore turbid reefs due to their adaptive capacities and are therefore an important source of carbonate for reef growth and development.” Browne writes, “*Montipora* linear extension was greater than current estimates available, and *Turbinaria*, although characterized by slow linear extension, had a dense skeleton and hence may be more resilient to physical damage as ocean pH falls.” Although both species “may be more susceptible during the warmer months due to multiple stressors, they were able to rapidly recover during the cooler months,” Browne writes. “In summary,” Browne concludes, “corals on Middle Reef are robust and resilient to their marginal environmental conditions.”

Helmle *et al.* (2011) collected coral cores in May 1997 and June 1998 from seven *Montastraea faveolata* colonies located in the upper Florida Keys (USA), where they “were drilled at the location of maximum vertical growth of the colony.” The scientists constructed chronologies from the annual density bands found in the cores and determined all of them had a 60-year common period from 1937 to 1996. For these cores the scientists obtained and

analyzed annual extension, density, and calcification rates, to see how they varied over this period of intensifying warming and acidification of the global ocean.

The five U.S. scientists report their data show “no evidence of significant age effects” over the 1937–1996 period for extension, density, or calcification. Helmle *et al.* say their findings demonstrate “the measured corals have historically been able to maintain rates of extension and calcification over the 60-year period from 1937 to 1996 under the combination of local environmental and climatic changes.” They also note calcification rates were positively related to sea surface temperature, “similar to results for *Porites* corals from Tahiti (Bessat and Buigues, 2001) and the Great Barrier Reef (Lough and Barnes, 1997),” but they say the Florida results explained only about 7% of the annual calcification variability as opposed to ~30% at the Pacific locations.

As for why the Florida Keys corals have fared so well, Helmle *et al.* suggest the answer could be “massive reef-building corals are not as susceptible to declines in Ω_{arag} [aragonite saturation state] as demonstrated by laboratory experiments; local processes, such as high seasonal variation in Ω_{arag} in the Florida Keys, may be temporarily enabling these corals to maintain their historical rates of calcification; the role of Ω_{arag} in controlling calcification is masked amidst considerable natural inter-annual variability; or the actual *in situ* reef-site carbonate chemistry is decoupled from the oceanic values, which could occur as a result of shifts in benthic community metabolism, mineral buffering and/or coastal biogeochemical processes.”

Shi *et al.* (2012) state “rising atmospheric CO₂ and global warming are regarded as fatal threats to coral reefs,” noting “IPCC has reported that by the end of this century, coral reefs will be the first ecological system that will become extinct,” citing Wilkinson (2004). They write, “others contend that rising seawater temperature is conducive to enhanced coral calcification, and increased calcification will be higher than the decline caused by rising CO₂,” so “coral calcification will increase by about 35% beyond pre-industrial levels by 2100, and no extinction of coral reefs will occur in the future,” citing McNeil *et al.* (2004).

In late May of 2004 and 2007 Shi *et al.* extracted core samples of coral skeletons from several massive live and dead *Porites lutea* colonies comprising part of the Meiji Reef in the southern South China Sea, after which they analyzed their skeletal calcification

rates by means of X-ray photography, which enabled them to construct a nearly three-century-long history of coral calcification rate for the period 1716–2005. The results of the six scientists' efforts are depicted in Figure 6.5.2.1.3.1.

As best as can be determined from the Chinese scientists' graph, over the period of time depicted—when IPCC claims the world warmed at a rate unprecedented over the past millennium or two, and when the atmosphere's CO₂ concentration rose to values not seen for millions of years—the two “fatal threats to coral reefs,” even acting together, did not prevent coral calcification rates on Meiji Reef from rising by about 11% over the past three centuries.

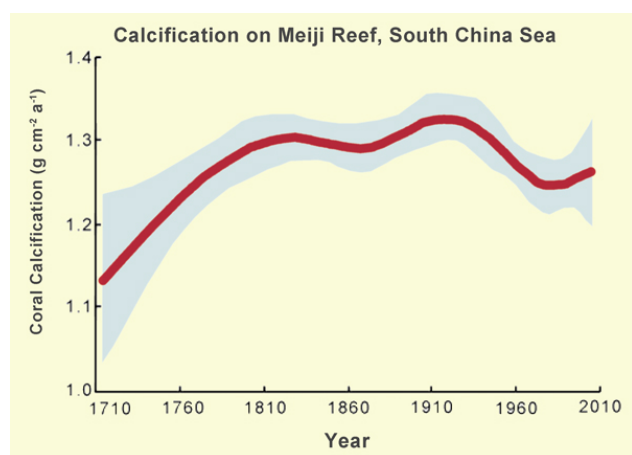


Figure 6.5.2.1.3.1. The long-term history of coral calcification rate on Meiji Reef. Adapted from Shi *et al.* (2012).

Cooper *et al.* (2012) studied coral reefs spanning an 11° latitudinal range in the southeast Indian Ocean, collecting 27 long cores from massive *Porites* coral colonies at six locations covering a north-south distance of about 1,000 km off the coast of Western Australia. From these cores they developed 1900–2010 histories of “annual extension (linear distance between adjacent density minima, cm/year), skeletal density (g/cm³), and calcification rate (the product of skeletal density and annual extension, g/cm²/year),” based on gamma densitometry data.

Cooper *et al.* report calcification rates at the Houtman Abrolhos Islands, where a relatively large sea surface temperature (SST) increase had occurred (0.10°C/decade), rose by 23.5%, and at Coral Bay and Tantabiddi, SST increases of 0.8 and 0.6°C/decade were associated with 8.7 and 4.9% increases in decadal calcification rates, respectively. They found smaller and non-significant positive trends in

calcification rates at Clerke and Imperieuse Reefs, where the increase in SST was only 0.2°C/decade.

The three Australian researchers say their latter non-significant findings are consistent with those of Helmle *et al.* (2011), who they say “found a similar non-correlation for the massive coral *Montastraea faveolata* in the Florida Keys between 1937 and 1996, when there was no significant SST warming.” Regarding the large increases in calcification rates they documented at the rapidly warming Houtman Abrolhos Islands, they write, “Lough and Barnes (2000) documented a similar positive correlation, suggesting that calcification rates may, at least initially, increase with global warming.” They conclude “the rate of change in the thermal environment of coral reefs is currently the primary driver of change in coral calcification rates,” driving them ever-higher as temperatures continue to rise, and “the large-scale phenomenon of ocean acidification is not currently limiting calcification on coral reefs uniformly at a global scale.”

Hughes *et al.* (2012) note, “contemporary research on how climate change affects coral reefs has matured beyond the simplistic ‘canary in the coal mine’ concept to a more nuanced recognition that climate-related pressures such as bleaching (due to the loss of symbiotic zooxanthellae) and ocean acidification do not affect all species equally.” And “in this context,” they note, “a critical issue for the future status of reefs will be their ability to maintain functional capacity in the face of the changes in species composition that are already underway due to multiple anthropogenic impacts.”

Hughes *et al.* applied a “rigorous quantitative approach to examine large-scale spatial variation in the species composition and abundance of corals on mid-shelf reefs along the length of Australia’s Great Barrier Reef, a biogeographic region where species richness is high and relatively homogeneous.” They used “a hierarchical, nested sampling design to quantify scale-dependent patterns of coral abundances [for] five regions of the Great Barrier Reef [they] sampled from north to south, each 250–500 km apart.” They thus identified and measured a total of 35,428 coral colonies on 33 reefs, categorizing each colony they encountered (including the majority of species that are too rare to analyze individually) into “ecologically relevant groups depending on their physiology, morphology and life history.”

The seven scientists report the diverse pool of species they examined along the latitudinal gradient of the Great Barrier Reef “can assemble in markedly different configurations across a wide range of

Climate Change Reconsidered II: Biological Impacts

contemporary environments.” Regarding temperature, for example, they indicate “the geographic ranges of 93% of the 416 coral species found on the Great Barrier Reef extend northwards toward the equator (e.g., to Papua New Guinea, the Solomon Islands, and/or the Indonesian archipelago),” whereas “46% are also found in colder conditions further to the south.” As for lower ocean pH levels, they write, “globally, ocean surface pH has decreased by 0.1 unit since 1750 due to the uptake of atmospheric CO₂, with a smaller 0.06 decline recorded for the tropics,” citing Kleypas *et al.* (2006). In contrast, they report contemporary variation in pH among various reef habitats on the Great Barrier Reef, as well as differences among short-term replicate measurements, span a range of 0.39 unit, from 8.37 to 7.98, citing Gagliano *et al.* (2010). And they note this short-term and habitat-scale variability literally swamps that of latitudinal trends.

Hughes *et al.* say their real-world observations “all point to a surprisingly resilient response by some elements of coral assemblages to spatial and temporal shifts in climatic conditions.” They conclude, “the flexibility in community composition that we document along latitudinal environmental gradients indicates that climate change is likely to result in a re-assortment of coral reef taxa rather than wholesale loss of entire reef ecosystems.” This clearly deflates the catastrophic prognostications put forth by IPCC with regard to the future of the planet’s corals.

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6.5.2.2 Echinoderms

This section examines what scientists have learned from studies focusing on the impacts of higher temperatures and lower seawater pH levels on echinoderms. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- The relative growth of juvenile sea stars increased linearly with temperature from 5°C to 21°C, while also responding positively to atmospheric CO₂ enrichment.

- Serpent starfish were able to successfully cope with the physiological changes brought about by a modest temperature increase and/or pH decline.
- The intertidal seastar *Parvulastra exigua* was shown to be resilient to elevated temperature and reduced pH, and “may possess scope for adaptation (evolutionary change) and/or acclimation via phenotypic plasticity” to withstand future changes in temperature and pH.
- The negative effects of a 0.35 to 0.55 CO₂-induced decline in seawater pH on the growth and calcification of the sea urchin *Triplaneustes gratilla* can be largely overcome by an accompanying 3°C increase in water temperature.
- No significant effect of ocean warming and lower seawater pH levels on the percentage of egg fertilization in four intertidal and shallow subtidal echinoids was found, possibly reflecting adaptation to the large temperature and pH fluctuations that characterize their shallow water coastal habitats.
- In a combined pH decline/temperature increase study on the sea urchin *Psammechinus miliaris*, it was determined “current ocean pH levels are suboptimal for *P. miliaris* sperm-swimming speed and that reproductive success for certain marine species may benefit from a reduced pH ocean.”
- Fertilization and embryonic development of the ecologically important sea urchin *Sterechinus neumayeri* to the blastula stage was “robust to levels of temperature and pH change predicted over coming decades.”
- The ecologically important sea urchin *Centrostephanus rodgersii* displays a genetic variation in tolerance affirming its ability to successfully adapt to ocean warming and falling ocean pH levels..

Gooding *et al.* (2009) measured growth and feeding rates of juvenile sea stars (*Pisaster ochraceus*) maintained in 246-liter aquaria filled with recirculating natural seawater maintained at temperatures ranging from 5 to 21°C and constantly bubbled with ambient air of 380 ppm CO₂ or CO₂-enriched air of 780 ppm CO₂. They found “the relative growth (change in wet mass/initial wet mass) of juvenile *P. ochraceus* increased linearly with temperature from

5°C to 21°C,” and it also responded positively to atmospheric CO₂ enrichment. The authors state “relative to control treatments, high CO₂ alone increased relative growth by ~67% over 10 weeks, while a 3°C increase in temperature alone increased relative growth by 110%.” They also state increased CO₂ “had a positive but non-significant effect on sea star feeding rates, suggesting CO₂ may be acting directly at the physiological level to increase growth rates.” Their data show the percentage of calcified mass in the sea stars dropped from approximately 12% to 11% in response to atmospheric CO₂ enrichment at 12°C, but it did not decline further in response to a subsequent 3°C warming at either ambient or elevated CO₂. The three Canadian researchers say their findings demonstrate “increased CO₂ will not have direct negative effects on all marine invertebrates, suggesting that predictions of biotic responses to climate should consider how different types of organisms will respond to changing climatic variables.” They state, “responses to anthropogenic climate change, including ocean acidification, will not always be negative.”

Wood *et al.* (2010) studied the serpent starfish (*Ophiura ophiura*), collecting 96 individuals with a disc diameter between 10 and 15 mm from Cawsand Bay, Plymouth Sound (50°09.77' N, 4°11.50' W). They exposed the brittlestars to three pH treatments (pH of 8.0, 7.7, or 7.3) and two temperature treatments (10.5°C or 15°C) for 40 days. They measured metabolism, calcification, mortality, motility, arm structure, and arm regeneration; the latter parameter was studied by removing either 10, 20, 30, or 40 mm of arm length on one of the animals' arms.

The researchers found survival was “100% at both temperatures and across all pH treatments”; metabolic rate increased as pH decreased in the low temperature treatment, but there was no significant difference across the different pH treatments in the high temperature regime; muscle appearance and density did not change over either the temperature or pH treatment ranges in established or regenerated arms; and a faster response time in movement (motility) was observed at low temperature and low pH. They also found brittlestars across “all treatments had the same net calcification throughout the experiment”; arm regeneration rate within the low temperature treatment was “unaffected by the length of arm lost and the rate was similar between all pH treatments”; and arm regeneration rate was significantly faster at higher temperatures than lower temperatures. Taken as a whole, the findings indicate the serpent starfish should be able to cope

successfully with the physiological changes brought about by any modest temperature increase and/or pH decline likely to occur in the future.

McElroy *et al.* (2012) measured the metabolic rates of adult specimens of the intertidal seastar *Parvulastra exigua* collected from Little Bay, Sydney (Australia) at conditions characteristic of high tide (ca. 18°C and pH 8.2), as well as at 3 and 6°C warmer conditions and at additional pH values of 7.8 and 7.6 “in all combinations.” The measurements revealed “the metabolic response of *P. exigua* to increased temperature (+3°C and +6°C) at control pH [8.2] indicates that this species is resilient to periods of warming as probably often currently experienced by this species in the field.” They also report they “did not observe a negative effect of acidification on rate of oxygen consumption at control temperature, a combination of stressors that this species currently experiences at night time low tide.”

Although the metabolic response of *P. exigua* is resilient to current levels of extreme temperature and pH stress—which are equivalent to mean conditions predicted for the end of the twenty-first century—it is possible the extreme seawater temperatures and pH levels at that future time (if IPCC predictions prove true) will be greater than the extreme levels of today, which could prove to be a real challenge for the seastars. McElroy *et al.* point out, in the concluding paragraph of their report, “species such as *P. exigua* with a broad distribution from warm to cold temperate latitudes may possess scope for adaptation (evolutionary change) and/or acclimation via phenotypic plasticity (Visser, 2008), as suggested for sympatric echinoid and ophiuroid species (Byrne *et al.*, 2011; Christensen *et al.*, 2011).”

Brennand *et al.* (2010) reared embryos of the sea urchin *Tripneustes gratilla* in flow-through chambers filled with filtered seawater maintained at all combinations of three temperatures (24, 27, and 30°C) and three pH values (8.15, 7.8, and 7.6), where the 24°C/pH 8.15 combination represented normal control conditions. After five days of such exposure, they assessed the growth and development of the larvae.

Brennand *et al.* found “larvae reared at pH 7.6 and pH 7.8 had smaller post oral arms when compared with those reared at control pH.” However, they report, “a +3°C warming diminished the negative effects of low pH/high CO₂,” as was “seen in the similar post oral arm length of larvae treated at 27°C/pH 7.6 and 27°C/pH 7.8 and those reared in control temperature and pH.” In addition, “as total length of calcite rods is largely comprised of the post

oral arms, this measure [of calcification] followed a similar pattern.”

The results of this study suggest the negative effects of a 0.35 to 0.55 CO₂-induced decline in seawater pH on the growth and calcification of the sea urchin *Tripneustes gratilla* can be largely overcome by a 3°C increase in water temperature. And since the projected maximum decline in seawater pH is somewhere in the range of 0.1 to 0.18 in the vicinity of AD 2100, there is little reason for concern about any negative impact of rising atmospheric CO₂ concentrations on this particular species of sea urchin, which is widely distributed throughout the Indo-Pacific region and well suited for production by aquaculture (Lawrence and Agatsuma, 2007; Juinio-Menez *et al.*, 1998; Dworjanyn *et al.* 2007).

Byrne *et al.* (2009) investigated the effects of lower ocean pH levels (pH values of 8.2–7.6, corresponding to atmospheric CO₂ concentrations of 230–690 ppm) and seawater temperature (20–26°C, where 20°C represents the recent thermal history of indigenous adults) on the fertilization of sea urchin (*Heliocidaris erythrogramma*) eggs and their subsequent development in what they call “the eastern Australia climate change hot spot,” located near Sydney.

According to the authors, over the ranges of seawater pH and temperature they studied, there was “no effect of pH” and “no interaction between temperature and pH” on sea urchin egg fertilization. Seawater pH also had no effect on the longer-term development of fertilized sea urchin eggs; but the six scientists say warming led to “developmental failure at the upper warming (+4 to +6°C) level, regardless of pH.” Even here, however, they appear quite hopeful, stating “it is not known whether gametes from *H. erythrogramma* adults acclimated to 24°C would have successful development in a +4°C treatment,” noting their study “highlights the potentiality that adaptive phenotypic plasticity may help buffer the negative effects of warming, as suggested for corals.” They write, “single stressor studies of thermotolerance in a diverse suite of tropical and temperate sea urchins show that fertilization and early development are robust to temperature well above ambient and the increases expected from climate change,” citing Farmanfarmanian and Giese (1963), Chen and Chen (1992), and Roller and Stickle (1993).

Byrne *et al.* (2010a) examined the interactive effects of near-future (ca. AD 2070–2100) ocean warming (temperature increases of 2–6°C) and lower ocean pH levels (pH reductions of 0.2–0.6) on fertilization in four intertidal and shallow subtidal

echinoids (*Heliocidaris erythrogramma*, *Heliocidaris Tuberculata*, *Tripneustes gratilla*, *Centrostephanus rodgersii*), an asteroid (*Patiriella regularis*), and an abalone (*Haliotis cocciradiata*), working with batches of eggs they collected from multiple females fertilized by sperm obtained from multiple males, all of which species were maintained in all combinations of three temperature and three pH treatments.

The eight researchers found “no significant effect of warming and acidification on the percentage of fertilization.” Byrne *et al.* say their results indicate “fertilization in these species is robust to temperature and pH/PCO₂ fluctuation,” and their findings “may reflect adaptation to the marked fluctuation in temperature and pH that characterizes their shallow water coastal habitats.”

Byrne *et al.* (2010b) investigated the effects of projected near-future oceanic warming and acidification of the sea urchin *Heliocidaris erythrogramma* for conditions predicted for southeast Australia within the timeframe of 2070–2100: an increase in sea surface temperature of 2 to 4°C and a decline in pH of 0.2 to 0.4. Byrne *et al.* conducted multifactorial experiments that incorporated a titration of sperm density (10–10³ sperm per ml) across a range of sperm-to-egg ratios (10:1–1500:1). They found “across all treatments there was a highly significant effect of sperm density, but no significant effect of temperature or interaction between factors.” They state “low pH did not reduce the percentage of fertilization even at the lowest sperm densities used, and increased temperature did not enhance fertilization at any sperm density.” They write, “a number of ecotoxicology and climate change studies, where pH was manipulated with CO₂ gas, show that sea urchin fertilization is robust to a broad pH range with impairment only at extreme levels well below projections for ocean acidification by 2100 (pH 7.1–7.4, 2,000–10,000 ppm CO₂),” citing Bay *et al.* (1993), Carr *et al.* (2006), and Kurihara and Shirayama (2004). Because neither seawater warming nor seawater acidification (caused by contact with CO₂-enriched air) had either a positive or a negative effect on sea urchin fertilization, the five scientists conclude “sea urchin fertilization is robust to climate change stressors.”

According to Caldwell *et al.* (2011), “the reproductive processes and early life-stages of both calcifying and non-calcifying animals are believed to be particularly vulnerable to a reduced pH environment,” but “there is as yet no clear and reliable predictor for the impacts of ocean acidification on marine animal reproduction.” Caldwell *et al.* “investigated the combined effect of

pH (8.06–7.67) and temperature (14–20°C) on percent sperm motility and swimming speed in the sea urchin *Psammechinus miliaris* using computer assisted sperm analysis (CASA),” working with specimens they collected from the Isle of Cumbrae (Scotland). “Surprisingly,” the six scientists write, “sperm swimming performance benefited greatly from a reduced pH environment,” as “both percent motility and swimming speeds were significantly enhanced at pHs below current levels.” In light of the additional fact that sperm-activating peptides—which are believed to have evolved some 70 million years ago during a period of high atmospheric CO₂ concentration—are fully functional from pH 6.6 to 8.0 (Hirohashi and Vacquier, 2002), they state “the combined data on motility, swimming speed and SAP function at reduced pH indicates that sperm are sufficiently robust to allow functionality at pHs that would have been experienced in the paleo-ocean (ca pH 7.4–7.6) and which are within projections for near-future climate change scenarios.” The UK researchers conclude “current ocean pH levels are suboptimal for *P. miliaris* sperm-swimming speed and ... reproductive success for certain marine species may benefit from a reduced pH ocean.”

Ericson *et al.* (2012) “examined the interactive effects of warming and acidification on fertilization and embryonic development of the ecologically important sea urchin *Sterechinus neumayeri* reared from fertilization in elevated temperature (+1.5°C and 3°C) and decreased pH (–0.3 and –0.5 pH units).” They found “fertilization using gametes from multiple males and females, to represent populations of spawners, was resilient to acidification at ambient temperature (0°C),” and development to the blastula stage was “robust to levels of temperature and pH change predicted over coming decades.” The sea urchins the seven scientists studied thus appear well-equipped to deal with IPCC-predicted near-future increases in seawater temperature and acidification.

Ho *et al.* (2013) report, “the impact of increased temperature (2–4°C above ambient) and decreased pH (0.2–0.4 pH units below ambient) on fertilization in the Antarctic echinoid *Sterechinus neumayeri* across a range of sperm concentrations was investigated in cross-factorial experiments,” where “gametes from multiple males and females in replicate experiments were used to reflect the multiple spawner scenario in nature.” They examined this species because “polar marine organisms are among the most stenothermal in the world due to the stability of their environment over evolutionary time (Clarke, 1983),” which suggests they may be “sensitive to the slightest of

environmental perturbations, particularly [in] early life history stages (Barnes and Peck, 2008).”

The five researchers’ work confirmed “the importance of considering both ocean warming and acidification,” and they note “decreased pH did not affect fertilization.” Warming, however, “enhanced fertilization ... likely through stimulation of sperm motility and reduced water viscosity.” In the concluding sentence of their paper’s abstract, Ho *et al.* state their results indicate “fertilization in *S. neumayeri*, even at low sperm levels potentially found in nature, is resilient to near-future ocean warming and acidification.”

Foo *et al.* (2012) write, “selection by stressful conditions will only result in adaptation if [1] variation in stress tolerance exists within a population, if [2] tolerance of stressors is heritable, and if [3] changes in tolerance traits are not constrained by negative genetic correlations with other fitness traits,” citing references both old and recent: Darwin (1859) and Blows and Hoffmann (2005).

Foo *et al.* “quantified genetic variation in tolerance of early development of the ecologically important sea urchin *Centrostephanus rodgersii* to near-future (2100) ocean conditions projected for the southeast Australian global change hot spot,” in which “multiple dam-sire crosses were used to quantify the interactive effects of warming (+2–4°C) and acidification (–0.3–0.5 pH units) across twenty-seven family lines” of the species. The four Australian researchers report, “significant genotype by environment interactions for both stressors [warming and acidification] at gastrulation indicated the presence of heritable variation in thermal tolerance and the ability of embryos to respond to changing environments.” They say “positive genetic correlations for gastrulation indicated that genotypes that did well at lower pH also did well in higher temperatures.” Thus, Foo *et al.* conclude “the presence of tolerant genotypes, and the lack of a trade-off between tolerance to pH and tolerance to warming contribute to the potential of *C. rodgersii* to adapt to concurrent ocean warming and acidification, adding to the resilience of this ecologically important species in a changing ocean.”

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Climate Change Reconsidered II: Biological Impacts

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6.5.2.3 Other Marine Species

This section examines what scientists have learned in studies, focusing on the impacts of changing seawater temperature and pH levels on marine species not discussed in prior sections. The key findings are presented in the bullet points below, followed by an expanded discussion of those findings. (Citations for passages in quotation marks in the bullet points are included in the main body of the section.)

- A high tolerance to pH decline and rising temperature was observed during the larval growth stage of the Portuguese oyster.
- The often complex and severe spatial and temporal variability of environmental conditions in coastal ecosystems suggests organisms living there are preconditioned to be tolerant of lower ocean pH levels and warming.
- There is no evidence that predator-prey interactions among green crabs and periwinkles will change in the future under lower ocean pH levels and warming.
- Analyses of tube mineralogy, ultrastructure, and mechanical properties of the serpulid tubeworm *Hydroides elegans* reveal “predicted coastal warming may not hinder *H. elegans* ability to build normal tubes even in the face of projected near-future decreases in pH or salinity.”
- Norway lobster (*Nephrops norvegicus*) “would benefit from global warming and be able to withstand the predicted decrease in ocean pH in the next century during their earliest life stages.”
- Baltic cod (*Gadus morhua*), which live in sea waters naturally high in $p\text{CO}_2$ “may be adapted to conditions predicted in ocean acidification scenarios for centuries to come,” as “no effect on hatching, survival, development, and otolith size was found at any stage in the development of Baltic cod” under projected future ocean pH levels and temperature scenarios.
- Polyps of the moon jellyfish have been shown to be tolerant of low pH and warmer temperatures, surviving and reproducing asexually. Yet analyses of “all available long-term datasets on changes in jellyfish abundance across multiple coastal stations” reveal there is no compelling evidence to support the view that the global abundance of jellyfish is increasing as a result of lower ocean pH levels and warming.
- Lower ocean pH levels and temperature increases were found to negatively impact the growth and survival of juvenile anemone fish. The negative effects were absent or reversed when the parents of the juveniles also experienced lower ocean pH levels and warming, revealing “conditions experienced by adults can have significant carry-over effects on the performance of their offspring ... leading to improved capacity to cope with environmental stress.”
- In a study of copepods, “higher production temperature induced a positive maternal effect resulting in faster hatching and indicating that the mothers can invest more in their eggs, and therefore produce better quality eggs.”

Thiyagarajan and Ko (2012) conducted a number of laboratory studies designed to see how the larval growth stage of the Portuguese oyster responds to various “climate change stressors,” investigating the effects of low pH (7.9, 7.6, 7.4) at ambient salinity (34 ppt) and low salinity (27 ppt), while “the combined effect of pH (8.1, 7.6), salinity (24 and 34 ppt) and temperature (24°C and 30°C) was examined using factorial experimental design.” The two researchers write, “surprisingly, the early growth phase from hatching to 5-day-old veliger stage showed high tolerance to pH 7.9 and pH 7.6 at both 34 ppt and 27 ppt,” and “larval shell area was significantly smaller at pH 7.4 only in low-salinity.”

In the three-factor experiment (see Figure 6.5.2.3.1), they observed “shell area was affected by salinity and the interaction between salinity and temperature but not by other combinations.” They also discovered “larvae produced the largest shell at the elevated temperature in low-salinity, regardless of pH.”

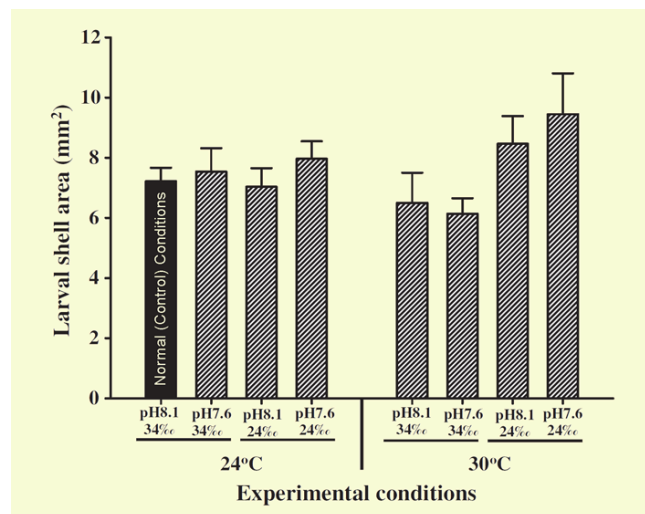


Figure 6.5.2.3.1. Mean shell area of the Portuguese oyster larvae exposed to a low-pH or elevated carbon dioxide treatment for five days at two levels of salinity (ambient and low-salinity) and temperature (ambient and elevated). Each bar represents the mean $\pm$ S.D. of four replicate cultures. Adapted from Thiyagarajan and Ko (2012).

Thiyagarajan and Ko conclude “the growth of the Portuguese oyster larvae appears to be robust to near-future pH level (>7.6) when combined with projected elevated temperature and low-salinity in the coastal aquaculture zones of [the] South China Sea.”

Pansch *et al.* (2012) note to date “most studies have focused on ocean acidification (OA) effects in fully marine environments, while little attention has been devoted to more variable coastal ecosystems, such as the Western Baltic Sea.” Since “natural spatial and temporal variability of environmental conditions such as salinity, temperature or CO_2 impose more complex stresses upon organisms inhabiting these habitats, species [living there] can be expected to be more tolerant to OA (or warming) than fully marine taxa.”

Pansch *et al.* acquired data on the variability of temperature and pH within the inner Kiel Fjord of Schleswig-Holstein, Germany, and on “the responses of the barnacle *Amphibalanus improvisus* from this habitat to simulated warming and OA during its early development.” They exposed *A. improvisus* nauplii

(the first larval stage of many crustaceans) and cyprids (the second larval stage of barnacles) to different temperatures (12, 20, and 27°C) and CO_2 (nominally 400, 1,250, and 3,250 ppm) treatments for eight and four weeks, respectively,” while “survival, larval duration and settlement success were monitored.”

The four researchers found a prolongation of the nauplius phase, which they acknowledge could “lead to a mismatch of the larvae with their phytoplankton prey.” However, they note the predicted increase in seawater temperature would likely “accelerate nauplii development and, thus, may buffer OA effects.” Such results, they write, have been observed “in sea urchin larvae and oysters, where higher temperatures mitigated negative effects of OA,” citing Brennand *et al.* (2010) and Waldbusser *et al.* (2011). In their own study, however, they found just the opposite, saying “warming negatively impacted cyprid survival” but “OA counteracted these negative effects.”

“It should also be stressed,” they continue, “that only the most severe OA level applied herein (3,250 ppm CO_2) had occasional effects, whereas the OA conditions as predicted by the end of this century (1,250 ppm CO_2) in most cases did not affect *A. improvisus* larvae.” In addition, and “interestingly,” they report, “the major release of larvae and thus, development, settlement and first intense calcification in *A. improvisus* occurs during early summer when pH is lowest.” They add, “*A. improvisus* is also found in stands of the brown macroalga *Fucus* spp. where 2,500 ppm CO_2 (pH 7.4) can be measured,” and they note “another barnacle species, *Chthamalus stellatus*, was shown to survive and grow at extremely low mean pH of 6.6 in the vicinity of volcanic CO_2 vents in Ischia, Italy (Hall-Spencer *et al.*, 2008).”

Pansch *et al.* write, “given their present wide tolerance and the possibility to adapt to shifting environmental conditions over many generations, barnacles (*A. improvisus*) from the Western Baltic Sea might be able to overcome OA as predicted by the end of this century.” And, “supporting this,” they note Parker *et al.* (2011) have shown “selectively bred lines of the estuarine oyster *Saccostrea glomerata* to be more resilient to OA than wild populations.”

Pansch *et al.* (2013) again collected juvenile barnacles (*Amphibalanus improvisus*) from Kiel Fjord in the western Baltic Sea and distributed them to different temperature and pH treatment combinations in a laboratory setting: seawater of two temperatures (20 and 24°C) and three pH levels (mean $p\text{CO}_2$ values of 700, 1,000, and 2,140 μatm). They fed the barnacles a mix of two marine diatoms every other

day until day 24, after which they added specified amounts of brine shrimp until the end of the experiment, on day 62. The four German scientists observed “reduced growth rates as well as weakening of barnacle shells only under very high $p\text{CO}_2$ ($>1930 \mu\text{atm}$).” They state “even under these highly acidified conditions, and corroborating other recent investigations on barnacles (e.g., McDonald *et al.*, 2009; Findlay *et al.*, 2010a,b), these impacts were subtle and sub-lethal.” And “furthermore,” they write, “ocean warming as expected to occur in the future (IPCC, 2007) has the potential to mitigate the negative effects of ocean acidification (Brennand *et al.*, 2010; Waldbusser, 2011; present study).” The findings of Pansch *et al.*, as well as those of the other researchers they cite, indicate juvenile barnacles of the species they studied are already equipped to meet the challenges of a significantly warmed and acidified ocean should such challenges occur.

Landes and Zimmer (2012) state, “both ocean warming and acidification have been demonstrated to affect the growth, performance and reproductive success of calcifying invertebrates.” However, they write, “relatively little is known regarding how such environmental change may affect interspecific interactions.” They separately treated green crabs (*Carcinus maenas*, the predators) and periwinkles (*Littorina littorea*, their prey) under conditions that mimicked either ambient conditions (control) or warming and acidification (both separately and in combination), for five months, after which they assessed the predators, their prey, and the predator-prey interaction for CO_2 - and warming-induced changes in response to the environmental perturbations imposed on them.

They found “acidification negatively affected the closer-muscle length of the crusher chela and correspondingly the claw-strength increment in *C. maenas*,” and “the effects of warming and/or acidification on *L. littorea* were less consistent but indicated weaker shells in response to acidification.” As might have been expected on the basis of these individual species responses to lower ocean pH levels and warming (weaker claw strength in the predator, but weaker shells in the prey), Landes and Zimmer say “on the community level,” they “found no evidence that predator-prey interactions will change in the future.”

Chan *et al.* (2013) write, “the majority of marine benthic invertebrates protect themselves from predators by producing calcareous tubes or shells that have remarkable mechanical strength,” but “an elevation of CO_2 or a decrease in pH in the

environment can reduce intracellular pH at the site of calcification and thus interfere with the animal’s ability to accrete CaCO_3 ,” which “may result in the animal producing severely damaged and mechanically weak tubes.” They investigated how the interaction of environmental drivers affects the production of calcareous tubes by the serpulid tubeworm, *Hydroides elegans*, in a factorial manipulative experiment in which they analyzed the effects of pH (8.1 and 7.8), salinity (34 and 27‰), and temperature (23 and 29°C) on the biomineral composition, ultrastructure, and mechanical properties of the tubeworm’s tubes.

The five researchers report, “at an elevated temperature of 29°C, the tube calcite/aragonite ratio and Mg/Ca ratio were both increased, the Sr/Ca ratio was decreased, and the amorphous CaCO_3 content was reduced.” And “notably,” they emphasize, at elevated temperature with decreased pH and reduced salinity, “the constructed tubes had a more compact ultrastructure with enhanced hardness and elasticity compared to decreased pH at ambient temperature.” Chan *et al.* conclude their “results from the analyses of tube mineralogy, ultrastructure and mechanical properties showed that predicted coastal warming may not hinder *H. elegans* ability to build normal tubes even in the face of projected near-future decreases in pH or salinity.”

The Norway lobster (*Nephrops norvegicus*) is a decapod crustacean found on the continental shelf and slope throughout the northeastern Atlantic Ocean and the Mediterranean Sea. Styf *et al.* (2013) exposed berried Norway lobsters (females carrying fertilized eggs on the undersides of their abdomens) to four months of “the combination of six ecologically relevant temperatures (5–18°C) and reduced pH (by 0.4 units),” studying embryonic development of the species “by quantifying proxies for development rate and fitness including: % yolk consumption, mean heart rate, rate of oxygen consumption, and oxidative stress.” The three Swedish scientists report “the rate of yolk consumption per day, as a measure of embryonic development rate, significantly increased with temperature,” and lower pH “had no effect on development rate.” They also found “pH had no effect on heart rate” and “there was no interaction between pH and temperature.” Further, “there was no significant effect of temperature on oxidative stress when analyzed independent of embryonic age,” but “there was a significantly higher level of oxidative stress in the control embryos compared with the embryos developed in low pH.” They “observed no mortality nor abnormalities.”

The three researchers conclude “this species

would benefit from global warming and be able to withstand the predicted decrease in ocean pH in the next century during their earliest life stages,” a significant expression of optimism regarding a species considered the most important crustacean in all Europe (Nofima, 2012).

Winans and Purcell (2010) tested the ability of jellyfish to respond to changes in water temperature and pH during the early life stages. Polyps produced by medusae collected from the moon jellyfish (*Aurelia labiata*) in Dyes Inlet, Washington (USA) were arbitrarily assigned (18 each) to one of six treatments comprised of all combinations of two water temperatures (9 and 15°C) and three pH levels (7.2, 7.5 and 7.9), where they were allowed to develop under controlled conditions for 122 days. The researchers found “polyp survival was 100% after 122 days in seawater in all six temperature and pH combinations,” and because few polyps strobilated at 9°C and “temperature effects on budding were consistent with published results,” they “did not analyze data from those three treatments further.” At 15°C, there were also no significant effects of pH on the numbers of ephyrae or buds produced per polyp or on the numbers of statoliths per statocyst.” However, they write, “statolith size was significantly smaller in ephyrae released from polyps reared at low pH.”

Winans and Purcell conclude “*A. labiata* polyps are quite tolerant of low pH, surviving and reproducing asexually even at the lowest tested pH.” Nevertheless, the authors note “the effects of small statoliths on ephyra fitness are unknown,” which means the phenomenon could bode poorly for jellyfish. Winans and Purcell acknowledge many organisms “may be able to acclimate or adapt to slowly changing pH conditions.” They report in Puget Sound “pH fluctuates from 7.2 to 9.6 in 2.4-meter deep water over the span of a couple of days,” and “with such large pH fluctuations due to plant photosynthesis during the day and respiration at night, many organisms may be exposed to low pH conditions routinely.”

That the findings of Winans and Purcell should not be considered as evidence of future jellyfish blooms is made clear by the study of Condon *et al.* (2013), who note there is “concern about the deterioration of the world’s oceans,” and that one line of evidence for this concern is “an increasing incidence of jellyfish blooms.” They say this “perception,” as they describe it, is “largely based on reports of increases in a few disparate regions (Condon *et al.*, 2012)” and on “an analysis of media reports and perceptions of scientific experts and

fishers (Brotz *et al.*, 2012).”

Condon *et al.* set out to analyze “all available long-term datasets on changes in jellyfish abundance across multiple coastal stations, using linear and logistic mixed models and effect-size analysis,” in order “to test the null hypothesis that jellyfish population sizes and the occurrence of blooms have not significantly increased in the world’s oceans.”

The 22 researchers, from Argentina, Australia, Canada, Japan, Norway, Peru, Slovenia, Spain, the United Kingdom, and the United States, found “no robust evidence for a global increase in jellyfish.” Although they acknowledge “there has been a small linear increase in jellyfish since the 1970s,” they say “this trend was unsubstantiated by effect-size analysis that showed no difference in the proportion of increasing vs. decreasing jellyfish populations over all time periods examined.” Instead, they report, “the strongest non-random trend indicated jellyfish populations undergo larger, worldwide oscillations with an approximate 20-year periodicity, including a rising phase during the 1990s that contributed to the perception of a global increase in jellyfish abundance.” They conclude their research points normal “recurrent phases of rise and fall in jellyfish populations that society should be prepared to face.”

Miller *et al.* (2012) note “a major limitation to predicting the effects of increasing [atmospheric] CO₂ concentrations on marine species and ecosystems is the lack of information on acclimation or adaptation to increased CO₂ over timescales relevant to climate change predictions,” and “there is increasing evidence that the capacity for acclimation to environmental stress may depend on the history of previous life stages (Marshall and Morgan, 2011; Parker *et al.*, 2012).”

Miller *et al.* conditioned adult anemone fish, *Amphiprion melanopus*, to present-day (430 ppm), moderate (581 ppm), and high (1,032 ppm) CO₂ treatments—“consistent with projections for CO₂ concentrations in the atmosphere and ocean over the next 50–100 years.” They allowed the fish to spawn naturally, after which juvenile fish from control parents were reared at either the control CO₂ or transferred to high CO₂ at each of three temperatures (28.5, 30.0, and 31.5°C), while “juveniles from parents in the moderate- and high-CO₂ treatments were reared in similar CO₂ conditions as their parents at each of the three temperatures.”

They found “ocean conditions projected for the end of the century (approximately 1,000 ppm CO₂ and a temperature rise of 1.5–3.0°C) cause an increase in metabolic rate and decreases in length,

weight, condition and survival of juvenile fish.” But the five Australian researchers found “these effects are absent or reversed when parents also experience high CO₂ concentrations,” indicating “conditions experienced by adults can have significant carry-over effects on the performance of their offspring (Bonduriansky and Day, 2009; Marshall and Morgan, 2011; Donelson *et al.*, 2012), often leading to improved capacity to cope with environmental stress (Bernardo, 1996; Donelson *et al.*, 2009).” Miller *et al.* conclude “parental effects prepare juveniles for similar conditions to those experienced in the parental generation,” and, therefore, they suggest “non-genetic parental effects can dramatically alter the response of marine organisms to increasing CO₂ and demonstrate that some species have more capacity to acclimate to ocean acidification than previously thought.”

Vehmaa *et al.* (2012) state “maternal effects are defined as cross-generation phenotypic plasticity, implying the capability of a mother to adjust the phenotype of her offspring [in] response to environmental cues that her offspring will encounter, in a manner that enhances offspring fitness (Parker and Begon, 1986; Lacey, 1998),” stating as an example, “Sydney rock oyster larvae are larger and develop faster in higher CO₂ conditions, if the adults also have been incubated in high CO₂ conditions (Parker *et al.*, 2012).”

Vehmaa *et al.* “tested the reproductive response of *Acartia* sp. calanoid copepods and the importance of maternal effects in determining the offspring quality in a changing environment according to a 2100 climate scenario of a pH decline by 0.4 unit and a temperature elevation of 3°C.” They monitored the egg production of copepods incubated in four pH and temperature conditions for five consecutive days, and on days one, three, and five they divided the eggs and allowed them to hatch in conditions either the same as or different from those in which they were produced.

The three Finnish researchers report, “higher production temperature induced a positive maternal effect resulting in faster hatching and indicating that the mothers can invest more in their eggs, and therefore produce better quality eggs.” They note the similar studies of Karell *et al.* (2008) and Jonasdottir *et al.* (2009) showed how “the egg quality in terms of maternal immunological or nutritional provisioning improved,” and they suggest this phenomenon may explain “the declining effect of pH difference on egg hatching.” Vehmaa *et al.* conclude maternal effects “are an important mechanism in the face of environmental change.”

Frommel *et al.* (2013) provide evidence for the

adaptive capacity of fish to overcome the potential threat of lower ocean pH levels as well. In spite of its predicted detrimental effects on calcifying organisms, studies of possible impacts of ocean acidification [OA] on fish “remain scarce,” the research team found. And although “adults will most likely remain relatively unaffected by changes in seawater pH,” they state the “early life-history stages are potentially more sensitive, due to the lack of gills with specialized ion-regulatory mechanisms.” They studied the egg and early larval stages of Baltic cod (*Gadus morhua*), which they describe as “the commercially most important fish stock in the Baltic Sea.” They examined the effects of lower ocean pH levels on a number of egg and larval properties of *G. morhua* “over the range of CO₂ concentrations predicted in future scenarios for the Baltic Sea (from current values of 380 µatm up to 3,200 µatm CO₂ water),” both “with and without the combination of increasing temperature.”

They report “no effect on hatching, survival, development, and otolith size was found at any stage in the development of Baltic cod,” where “in situ levels of pCO₂ are already at levels of 1,100 µatm with a pH of 7.2.” Their data showed “the eggs and early larval stages of Baltic cod seem to be robust to even higher levels of OA (3,200 µatm), indicating an adaptational response to CO₂.” Frommel *et al.* conclude, “since the Baltic Sea is naturally high in pCO₂, its fish stocks may be adapted to conditions predicted in ocean acidification scenarios for centuries to come.”

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Climate Change Reconsidered II: Biological Impacts

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7

Human Health

Key Findings**Introduction****7.1 Hot vs. Cold Weather**

- 7.1.1 Asia
- 7.1.2 Europe
- 7.1.3 North America
- 7.1.4 Other Regions
- 7.1.5 Multiple Regions

7.2 Cardiovascular Disease**7.3 Respiratory Disease****7.4 Stroke Occurrence****7.5 Malaria****7.6 Dengue Fever****7.7 Tick-Borne Diseases****7.8 Effects of CO₂**

- 7.8.1 Antioxidants
 - 7.8.2 Common Food Plants
 - 7.8.3 Medicinal Plants
 - 7.8.4 Health-Harming Substances
-

Key Findings

The following bulleted points summarize the main findings of this chapter:

- Warmer temperatures lead to a net 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.
- Some 4,600 deaths are delayed each year as people in the U.S. move from cold northeastern states to warm southwestern states. Between 3 and 7% of the gains in longevity experienced by the

U.S. population over the past three decades is 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 cardiovascular diseases associated with high temperatures and summer heat waves.
- The adverse health impacts of cold temperatures, especially with respect to respiratory health, are more significant than those of high temperatures in many parts of the world, including Spain, Canada, Shanghai, and Taiwan. In the subtropical island of Taiwan, for example, researchers found low minimum temperatures were the strongest risk

Climate Change Reconsidered II: Biological Impacts

factor associated with outpatient visits for respiratory diseases.

- A vast body of 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.
- While climatic factors largely determine the geographical distribution of ticks, temperature and climate change are not among the significant factors determining the incidence of tick-borne diseases.
- The ongoing rise in the air's CO₂ content 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.
- Atmospheric CO₂ enrichment 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 appears to be little reason to expect any significant CO₂-induced increases in human-health-harming substances produced by plants as the atmosphere's CO₂ concentration continues to rise.

Introduction

Carbon dioxide (CO₂) does not seriously affect human health until the CO₂ content of the air reaches approximately 15,000 ppm (Luft *et al.*, 1974; Schaefer, 1982), more than 37 times greater than the current concentration of atmospheric CO₂. 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 anthro-

pogenic 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. According to a draft from the Working Group II contribution to IPCC's *Fifth Assessment Report*,

The most important effect of climate change is that it will exacerbate current risks to health [*very high confidence*]. In recent decades, climate change has contributed to levels of ill-health (*likely*). If climate change continues as projected in scenarios in the next few decades, the major increases of ill-health compared to no climate change will occur through:

Greater incidence of injury, disease, and death due to more intense heat waves, storms, floods, and fires. [*very high confidence*]

Increased risk of under-nutrition resulting from diminished food production in poor regions. [*high confidence*]

Increased risks of food- and water-borne diseases and vector-borne infections. [*high confidence*]

... positive effects will be out-weighed, worldwide, by the magnitude and severity of the negative effects of climate change. [*high confidence*] (IPCC-II, 2013a, Chapter 11, Human Health, p. 3; italics in original, bold removed and formatting changed).

We should note before going on that IPCC's assignment of "confidence" levels to each of these claims is purely a rhetorical device and not based on any statistical tests. (Idso *et al.*, 2013) Placing these expressions of opinion in italics and brackets doesn't make any of these dubious or untrue statements any more credible or true.

In a draft Technical Summary of the same document, 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-II, 2013b, Technical Summary, p. 16; italics in original, bold removed).

As shown in the material presented in this chapter, however, 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 factors determining the transmission and prevalence of such diseases.

Finally, IPCC entirely overlooks several positive effects of rising levels of atmospheric CO₂ on human health. Carbon dioxide fertilization, for example, 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.

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7.1 Hot vs. Cold Weather

- Warmer temperatures lead to a net 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.

According to IPCC, rising atmospheric carbon dioxide concentrations cause global warming, and this temperature increase will lead to greater human mortality. However, examination of pertinent real-world data reveals warmer temperatures lead to a decrease in temperature-related deaths, and this phenomenon represents one of the many indirect benefits of atmospheric CO₂ enrichment that IPCC has long downplayed and ignored.

As illustrated in the research described below, it is abundantly clear unseasonable cold temperatures cause far more health-related maladies and deaths than do unseasonable warm temperatures.

7.1.1 Asia

Behar (2000) studied sudden cardiac death (SCD) and acute myocardial infarction (AMI) in Israel, concentrating on the role temperature may play in the incidence of these health problems. Behar notes "most of the recent papers on this topic have concluded that a peak of SCD, AMI and other cardiovascular conditions is usually observed in low temperature weather during winter." He cites an Israeli study by Green *et al.* (1994), which reported between 1976 and 1985 "mortality from cardiovascular disease was higher by 50% in mid-winter than in mid-summer, both in men and women and in different age groups," even though summer temperatures in the Negev, where much of the work was conducted, often exceed 30°C and winter temperatures typically do not drop below 10°C. Behar concludes these results "are reassuring for populations living in hot countries."

Several researchers have examined the relationship between temperature and human health in Shanghai, China. Kan *et al.* (2003), for example, investigated the association between temperature and daily mortality from 1 June 2000 to 31 December 2001, finding a V-like relationship between total mortality and temperature that had a minimum mortality risk at 26.7°C. Above this optimum temperature, they observe, "total mortality increased

by 0.73% for each degree Celsius increase; while for temperatures below the optimum value, total mortality decreased by 1.21% for each degree Celsius increase.” The net effect of a warming in Shanghai, China, therefore, would likely be reduced mortality on the order of 0.5% per degree Celsius increase in temperature, or perhaps more, since the warming of the past few decades has been primarily manifested in increases in daily minimum temperatures, with much smaller increases at the high end of the temperature spectrum. Hence, the recovery of Earth from the global chill of the Little Ice Age has had a positive effect on the health of the people of Shanghai that should continue into the foreseeable future if the planet continues to warm.

Tan *et al.* (2007) used a multivariate analysis “to investigate the relationships between mortality and heat wave intensity, duration, and timing within the summer season, along with levels of air pollution,” for the exceptional heat waves of 1998 and 2003. “For heat waves in both summers,” the researchers write, “mortality was strongly associated with the duration of the heat wave.” Whereas the heat wave of 2003 was of much greater duration than the heat wave of 1998 (19 days in 2003 vs. 11 days in 1998), the mortality experienced in 2003 was much less than that experienced in 1998 (6.3 deaths/heat day in 2003 vs. 13.3 deaths/heat day in 1998). Tan *et al.* write, “since the meteorological conditions and pollution levels for the two heat waves were alike, we conclude that improvements in living conditions in Shanghai, such as increased use of air conditioning [1.35/household in 2003 vs. 0.69/household in 1998], larger living areas [13.8 m²/person in 2003 vs. 9.7 m²/person in 1998], and increased urban green space, along with higher levels of heat awareness and the implementation of a heat warning system, were responsible for the lower levels of human mortality in 2003 compared to 1998.”

Kan *et al.* (2007) examined the association between Diurnal Temperature Range (DTR, defined as daily maximum temperature minus daily minimum temperature) and human mortality, using daily weather and mortality data from Shanghai over the period 1 January 2001 to 31 December 2004 via a semi-parametric generalized additive model after controlling for covariates including time trend, day of week, temperature, humidity, and outdoor air pollution levels. For cold days (below 23°C), “a 1°C increase of the 3-day moving average of DTR corresponded to 1.41%, 1.76% and 1.47% increases in total non-accidental, cardiovascular and respiratory mortality,” respectively, whereas for warm days

(above 23°C), “an increase of 1°C DTR corresponded to 1.13%, 1.91% and 0.54% increases in total non-accidental, cardiovascular and respiratory mortality.”

Kan *et al.* say their data suggest “even a slight increase in DTR is associated with a substantial increase in mortality.” In addition, they note over the past century global warming has been characterized by “the daily minimum temperature increasing at a faster rate ... than the daily maximum, resulting in a decrease in the DTR for many parts of the world.” Their results suggest that in addition to the reduction in human mortality typically provided by the increase in daily mean temperature, the accompanying decrease in DTR also should have been tending to reduce human mortality.

Ma *et al.* (2011) analyzed weather data from the Shanghai Meteorological Bureau to investigate the impact of heat waves and cold spells on hospital admissions in Shanghai, China. They defined a heat wave as a period of at least seven consecutive days with daily maximum temperature above 35.0°C and daily average temperatures above the 97th percentile during the study period. They defined a cold spell as a period of at least seven consecutive days with daily maximum temperature and daily average temperatures below the 3rd percentile during the study period. For one heat wave (24 July to 2 August, 2007) and one cold spell (28 January to 3 February, 2008), they obtained daily hospital admission data for these periods from the Shanghai Health Insurance Bureau.

The four researchers report the number of excess (above normal) hospital admissions during the eight-day heat wave was 352—driven by a 2% increase in all-cause admissions, an 8% increase in admissions due to cardiovascular problems, and a 6% increase in admissions related to respiratory problems. During the 10-day cold spell there were 3,725 excess admissions, driven by 38%, 33%, and 32% increases in admissions due to all-cause, cardiovascular, and respiratory problems, respectively. Ma *et al.* conclude “the cold spell seemed to have a larger impact on hospital admission than the heat wave in Shanghai.”

Cheng and Kan (2012) employed a generalized additive model with penalized splines to analyze mortality, air pollution, temperature, and covariate data over the period 1 January 2001 through 31 December 2004 in Shanghai, focusing on particulate matter of diameter 10 µm or less (commonly referred to as PM₁₀) and ozone (O₃). Cheng and Kan report they “did not find a significant interaction between air pollution and higher temperature [>85th percentile days],” but “the interaction between PM₁₀ and extreme low

temperature [<15 th percentile days] was statistically significant for both total and cause-specific mortality.” Compared to normal temperature days (15th–85th percentile), they found a $10\text{-}\mu\text{g}/\text{m}^3$ increase in PM_{10} on extreme low temperature days led to all-cause mortality rising from 0.17% to 0.40%. They add, “the interaction pattern of O_3 with low temperature was similar,” noting their finding of “a stronger association between air pollution and daily mortality on extremely cold days confirms those of three earlier seasonal analyses in Hong Kong, Shanghai and Athens,” citing Touloumi *et al.* (1996), Wong *et al.* (1999, 2001), and Zhang *et al.* (2006).

Wang *et al.* (2013) write, “a large change in temperature within one day may cause a sudden change in the heart rate and circulation of elderly people, which all may act to increase the risk of cardiopulmonary and other diseases, even leading to fatal consequences.” They further note, “it has been shown that a rise of the minimum temperature has occurred at a rate three times that of the maximum temperature during the twentieth century over most parts of the world, which has led to a decrease of the diurnal temperature range (Karl *et al.*, 1984, 1991).”

Wang *et al.* evaluated the short-term effect of diurnal temperature range (DTR) on emergency room (ER) admissions among elderly adults in Beijing. As they describe it, “after controlling the long-time and seasonal trend, weather, air pollution and other confounding factors, a semi-parametric generalized additive model (GAM) was used to analyze the exposure-effect relationship between DTR and ER admissions among elderly adults with different lag structures from 2009 to 2011 in Beijing,” where they “stratified groups by age and gender.”

The nine researchers report “significant associations were found between DTR and four major causes of daily ER admissions among elderly adults in Beijing.” They state “a 1°C increase in the 8-day moving average of DTR (lag 07) corresponded to an increase of 2.08% in respiratory ER admissions and 2.14% in digestive ER admissions,” and “a 1°C increase in the 3-day and 6-day moving average of DTR (lag 02 and lag 05) corresponded to a 0.76% increase in cardiovascular ER admissions, and a 1.81% increase in genitourinary ER admissions, respectively.” They add, “people aged 75 years and older were associated more strongly with DTR than the 65–74 age group.”

Guo *et al.* (2012) note knowledge of the health effects of extreme temperatures on mortality comes mainly from developed countries, particularly from regions with temperate climates, and they say “few

studies have been conducted in developing countries, particularly in tropical regions.” They used a Poisson regression model combined with a distributed lag non-linear model to examine the nonlinear and delayed effects of temperature on cause-specific and age-specific mortality, employing data from 1999 to 2008 for Chiang Mai, Thailand ($18^\circ47'\text{N}$, $98^\circ59'\text{E}$), with a population of 1.6 million people. Controlling for season, humidity, ozone, and particulate matter (PM_{10}) pollution, the three researchers found “both hot and cold temperatures resulted in immediate increase in all mortality types and age groups,” but “the hot effects on all mortality types and age groups were short-term, while the cold effects lasted longer.” The cold effects were greater, with more people dying from them than from the effects of heat.

Lindeboom *et al.* (2012) write, “while the association of weather and mortality has been well documented for moderate climate zones, little is known about sub-tropical zones, particularly Bangladesh.” They aimed “to assess the short-term relationship of temperature and rainfall on daily mortality after controlling for seasonality and time-trends.” Working with daily mortality and weather data for the period 1983–2009 pertaining to Matlab, Bangladesh, where a rigorous health and demographic surveillance system (HDSS) has been operational since 1966, Lindeboom *et al.* applied time series Poisson regression with cubic spline functions that allowed for lagged effects of weather on mortality, controlling for time trends and seasonal patterns.

The four researchers report “mortality in the Matlab surveillance area shows overall weak associations with rainfall, and stronger negative association with temperature.” They determined there was “a 1.4% increase in mortality with every 1°C decrease in mean temperature at temperatures below 29.2°C ,” but only “a 0.2% increase in mortality with every 1°C increase in mean temperature.” In addition, they note the “elderly, aged 60 years and above, seem to be most affected at lower temperatures, with a 5.4% increase in mortality with every 1°C decrease in temperature below 23°C .” Lindeboom *et al.* further report the Bangladesh Meteorological Department data on minimum and maximum temperatures observed in 1950–2010 “showed an increasing trend,” but they note the increase was faster for minimum temperature, as opposed to maximum temperature.

Wu *et al.* (2013) note “numerous studies have reported the association between ambient temperature and mortality,” but “few multi-city studies have been conducted in subtropical regions in developing countries.” They first assessed the health effects of

temperature on mortality in four subtropical cities of China (Changsha, Kunming, Guangzhou, and Zhuhai) by means of a “double threshold-natural cubic spline” distributed lag non-linear model at different temporal lags. They used the combined results to conduct a meta-analysis to estimate the overall cold and hot effects on mortality at different lag days. The 11 researchers report a U-shaped relationship between temperature and mortality was found in the four cities, indicating “mortality is usually lowest around a certain temperature and higher at lower or higher temperatures,” as they say also was found by Alberdi *et al.* (1998), Huynen *et al.* (2001), Curriero *et al.* (2002), O’Neill *et al.* (2003), Armstrong (2006), Laaidi *et al.* (2006), and Kan *et al.* (2007). In addition, “the hot effect peaked at the current day, and then diminished with lag days; whereas “the cumulative cold effect increased gradually with lag days, with the highest effect at lag 0–27.”

Although “both low and high temperatures were associated with increased mortality in the four subtropical Chinese cities,” Wu *et al.* state the “cold effect was more durable and pronounced than the hot effect.”

Yang *et al.* (2013) examined the effects of Diurnal Temperature Range (DTR) on human mortality rates, as well as whether the effects were different for different individual characteristics, such as gender, age, and education level. This was accomplished using daily meteorological data for the period 1 January 2003 through 31 December 2010 obtained from the China Meteorological Data Sharing System, which included daily mean temperature plus minimum and maximum temperatures collected from a single station located in the heart of the urban area of Guangzhou City (the largest metropolis in Southern China), along with individual data for all 189,379 registered deaths that occurred over the same time period, which they obtained from the Guangzhou Center for Disease Control and Prevention.

They found “a linear DTR-mortality relationship, with evidence of increasing mortality with DTR increase,” where “the effect of DTR occurred immediately and lasted for four days,” such that over that time period, a 1°C increase in DTR was associated with a 0.47% increase in non-accidental mortality. They also found “the elderly, females and residents with less education have been identified as more vulnerable to rapid temperature change within a single day.” In addition, they report there was a joint adverse effect with temperature “when mean temperature was below 22°C, indicating that high DTR enhanced cold-related mortality.”

In light of their findings, the eight researchers speculate the expected “decrease in DTR in future climate scenarios might lead to two benefits: one from decreasing the adverse effects of DTR [which is reduced due to greater warming at night than during the day], and the other from decreasing the interaction effect with temperature [which is expected to rise with greenhouse warming].”

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7.1.2 Europe

The early studies of Bull (1973) and Bull and Morton (1975a, b) in England and Wales demonstrate even normal changes in temperature are typically associated with inverse changes in death rates, especially in older people. That is, when temperatures rise, death rates fall, whereas when temperatures fall, death rates rise. In addition, at the lower end of the temperature range, Bull and Morton (1978) report, “there are more deaths the longer the ‘run of days,’ while at the higher end of the temperature range the reverse is true”; i.e., “the longer the ‘run’ the fewer the deaths,” suggesting people adapt more readily to extreme heat than to extreme cold. Such findings have been echoed in many studies across Europe.

Keatinge and Donaldson (2001) analyzed the effects of temperature, wind, rain, humidity, and sunshine during high pollution days in the greater London area over the period 1976–1995 to determine which weather and/or pollution factors have the biggest influence on human mortality. They observed simple plots of mortality rate versus daily air temperature revealed a linear increase as temperatures fell from 15°C to near 0°C. Mortality rates at temperatures above 15°C, however, were “grossly alinear,” as they describe it, showing no trend. Days with high SO₂, CO, or PM₁₀ (particulate matter of diameter less than 10µm) concentrations were colder than average, but a multiple regression analysis revealed none of these pollutants was associated with a significant increase in mortality among people 50 years of age or older. Only low temperatures were found to have a significant effect on immediate mortality (one day after a temperature perturbation) and long-term mortality (up to 24 days after a temperature perturbation), with the net increase in

mortality over the 24 days following a one-day fall in temperature amounting to 2.77 daily deaths per million people per degree Celsius temperature drop. Keatinge and Donaldson conclude “the large, delayed increase in mortality after low temperature is specifically associated with cold and is not due to associated patterns of wind, rain, humidity, sunshine, SO₂, CO, or smoke.”

How does cold kill? The two scientists say “cold causes mortality mainly from arterial thrombosis and respiratory disease, attributable in turn to cold-induced hemoconcentration and hypertension [in the first case] and respiratory infections [in the second case].” McGregor (2005) notes “anomalous cold stress can increase blood viscosity and blood pressure due to the activation of the sympathetic nervous system which accelerates the heart rate and increases vascular resistance (Collins *et al.*, 1985; Jehn *et al.*, 2002; Healy, 2003; Keatinge *et al.*, 1984; Mercer, 2003; Woodhouse *et al.*, 1993),” adding, “anomalously cold winters may also increase other risk factors for heart disease such as blood clotting or fibrinogen concentration, red blood cell count per volume and plasma cholesterol.” Keatinge and Donaldson conclude although “increases in mortality due to cold weather are large in many temperate regions ... effective protection against personal cold exposure virtually prevents excess winter mortality,” even in places as cold as Siberia.

In a study explicitly considering personal cold exposure, Gemmell (2001) analyzed the answers of 858 respondents to pertinent health and housing questions put to them in the second sweep of the “West of Scotland Twenty-07 Study” conducted in 1991. This effort indicated “over and above socioeconomic factors and house conditions, inadequate home heating is associated with poor health in those aged 55–60.” Gemmell notes, for example, “respondents who reported feeling cold in winter ‘most of the time’ were over three times more likely to suffer from a limiting condition and almost five times as likely to report ‘fair’ or ‘poor’ self assessed health,” leading him to conclude “living in a cold house will almost certainly exacerbate existing conditions and may lead to early mortality.” Gemmell suggests “affordable efficient methods of home heating could help reduce the number of people living in homes that are detrimental to their health.”

Carson *et al.* (2006) analyzed London mortality and meteorological data for four periods of the twentieth century they “selected to avoid times of war and influenza pandemics: 1900–1910, 1927–1937, 1954–1964, and 1986–1996.” They found “an

increase in risk at low temperatures in each period, but the strength of association gradually declined over the century ... from a 2.5% increase in mortality for each degree-C fall in temperature below 15°C in 1900–1910 to approximately a 1.2% increase in mortality per degree-C fall in temperature in 1986–1996.” At the other end of the temperature spectrum, their analyses “also provided some indication of heat-related mortality in the earlier periods of analysis, but not in 1954–1964 or 1986–1996.”

These results suggest cold is a more effective killer than heat. In addition, they suggest the deadly effects of both extreme cold and extreme heat have been muted with the passage of time, “despite the aging of the population and a progressive increase in the prevalence of cardiorespiratory disease, as Carson *et al.* add, “which would otherwise tend to increase susceptibility” to temperature-induced death.

Another implication of their study results, Carson *et al.* write, is “the decline in vulnerability to cold and heat is most readily explained by beneficial changes relating to increasing wealth.” Some of the items they mention are improvements in health care, nutrition, and housing; increased car ownership; climate-controlled transportation and shopping facilities; and improved clothing fabrics, although they say, “we cannot quantify or even identify all of the modifying factors that have contributed to this reduced susceptibility.” Finally, they say “it is reasonable to conclude that a similar modification of risk will occur among populations in other settings, particularly in low- and middle-income countries, as they grow richer.”

According to Christidis *et al.* (2010), “the IPCC AR4 states with very high confidence that climate change contributes to the global burden of disease and to increased mortality,” citing the contribution of Confalonieri *et al.* (2007) to that document. In an effort to evaluate this *very-high-confidence* contention of IPCC, Christidis *et al.* extracted the numbers of daily deaths from all causes from death registration data supplied by the UK Office of National Statistics for men and women 50 years of age or older in England and Wales for the period 1976–2005, which they divided by daily estimates of population “obtained by fitting a fifth order polynomial to mid-year population estimates, to give mortality as deaths per million people.” They then compared the death results with surface air temperature data that showed a warming trend during the same three-decade period of 0.47°C per decade. In addition, they employed a technique called optimal detection, which they describe as “a formal statistical methodology” that

can be used to estimate the role played by human adaptation in the temperature-related changes in mortality they observed.

As expected, during the hottest portion of the year, warming led to increases in death rates, whereas during the coldest portion of the year warming led to decreases in death rates. The three scientists report if no adaptation had taken place, there would have been 1.6 additional deaths per million people per year due to warming in the hottest part of the year over the period 1976–2005, but there would have been 47 fewer deaths per million people per year due to warming in the coldest part of the year, for a lives-saved to life-lost ratio of 29.4, representing a huge net benefit of the warming experienced in England and Wales over the three-decade period of warming. When adaptation was included in the analysis, as was the case in the data they analyzed, they found there were only 0.7 death per million people per year due to warming in the hottest part of the year, but a decrease of fully 85 deaths per million people per year due to warming in the coldest part of the year, for a phenomenal lives-saved to life-lost ratio of 121.4. Such observations indicate IPCC's "very-high-confidence" conclusion is woefully wrong. Warming is highly beneficial to human health, even without any overt adaptation to it. And when adaptations are made, warming is incredibly beneficial in terms of lengthening the human lifespan.

In France, Laaidi *et al.* (2006) conducted an observational population study in six regions between 1991 and 1995 to assess the relationship between temperature and mortality in areas of widely varying climatic conditions and lifestyles, including urban (Paris), oceanic (Finistere), semi-continental (Cote-d'Or), or mountain (the Hautes-Alpes) climates and two types of Mediterranean climate, one relatively mild and sheltered (the Alpes-Maritimes) and the other more extreme and windy (the Herault). Daily death and cause-of-death data were provided by the Epidemiological Centre on the Medical Causes of Death, part of the country's National Institute for Health and Medical Research.

Laaidi *et al.* report "mean daily counts of deaths showed an asymmetrical V-like or U-like pattern with higher mortality rates at the time of the lowest temperatures experienced in the area than at the time of the highest temperatures," noting "between these two peaks, there is a critical temperature threshold, referred to as the thermal optimum, where mortality rates are minimal." This relationship varied somewhat between the two sexes and among different age groups and causes of death. In all cases, however,

they found "more evidence was collected showing that cold weather was more deadly than hot weather." These findings, the researchers say, are "broadly consistent with those found in earlier studies conducted elsewhere in Europe (Kunst *et al.*, 1993; Ballester *et al.*, 1997; Eurowinter Group, 1997; Keatinge *et al.*, 2000a,b; Beniston, 2002; Muggeo and Vigotti, 2002), the United States (Curriero *et al.*, 2002) and South America (Gouveia *et al.*, 2003)." They also say their findings "give grounds for confidence in the near future," stating even a 2°C warming over the next half century "would not increase annual mortality rates."

Diaz *et al.* (2005) examined the effect of extreme winter temperature on mortality in Madrid, Spain for people older than 65, using data from 1,815 winter days over the period 1986–1997, during which time 133,000 deaths occurred. They found daily $T_{\max}$ was more closely correlated with mortality than was daily $T_{\min}$, because, as they describe it, "very low $T_{\min}$ occur mostly during stagnation episodes, characterized by very cold nights and sunny days, with a typical temperature range of between 15°C and 20°C," while "most of the days with very low $T_{\max}$ occur under cloudy conditions, with very limited temperature ranges of around 5°C," so "human exposure to low temperatures during these days is longer than that occurring during the stagnation days associated with a very low $T_{\min}$." In addition, they note, " $T_{\min}$ is usually recorded around 7 a.m., when very little human activity occurs outdoors, while $T_{\max}$ is usually recorded at around 4 p.m."

Diaz *et al.* determined that as $T_{\max}$ dropped below 6°C, which they describe as an unusually cold day (UCD), "the impact on mortality also increased significantly." They also found the impact of UCDs increased as the winter progressed, with the first UCD of the season producing an average of 102 deaths/day at a lag of eight days and the sixth UCD producing an average of 123 deaths/day at a lag of eight days. This behavior suggests, in their words, "acclimatisation does not occur, with every cold spell enhancing the pathologies produced in previous spells." Consequently, whereas they report "the impact of heat waves is reduced as they occur during a certain season, suggesting an acclimatisation to heat," just the opposite occurs in the case of recurring cold, which becomes ever more deadly with each new occurrence.

Fernandez-Raga *et al.* (2010) obtained from Spain's National Meteorological Institute data from weather stations situated in eight of the provincial capitals in the Castile-Leon region—a plateau in the northwestern part of the country that includes nine

provinces “with a low population density that can be considered as ageing.” The data covered the period 1980–1998, and they obtained contemporary mortality data from the country’s National Institute for Statistics for deaths associated with cardiovascular, respiratory, and digestive system diseases.

Analyses of the monthly averaged data revealed a number of interesting results. First, for all three of the disease types studied, Fernandez-Raga *et al.* found “the death rate is about 15% higher on a winter’s day than on a summer’s day,” which they describe as “a result often found in previous studies,” citing Fleming *et al.* (2000), Verlato *et al.* (2002), Grech *et al.* (2002), Law *et al.* (2002), and Eccles (2002). Second, in a finding that helps explain the first, the three researchers discovered when monthly averaged human death rates were plotted against monthly averages of daily mean, maximum, and minimum air temperature, the results nearly always took the form of a U-shaped concave parabola. And for all three disease types, they found all three temperatures (daily mean, maximum, and minimum) at which minimum death rates occurred—which they refer to as ideal or comfort temperatures—were within about 1–7°C of the maximum values typically reached by those three types of temperature, and they were anywhere from 14–24°C away from their minimum values. Consequently, the ideal or comfort temperatures always were very close to (and sometimes nearly identical to) the maximum values reached by the mean, maximum, and minimum temperatures experienced in the region, and they were much more removed from the minimum values of those three temperature parameters, as illustrated in Figure 7.1.2.1, which relates death rates due to cardiovascular diseases to mean air temperature.

The data of Figure 7.1.2.1 clearly demonstrate the people of the Castile-Leon region of Spain are much more likely to die from a cardiovascular disease in the extreme cold of winter than in the extreme heat of summer. The same holds true with respect to dying from respiratory and digestive system diseases.

Referencing the *Fourth Assessment Report* of

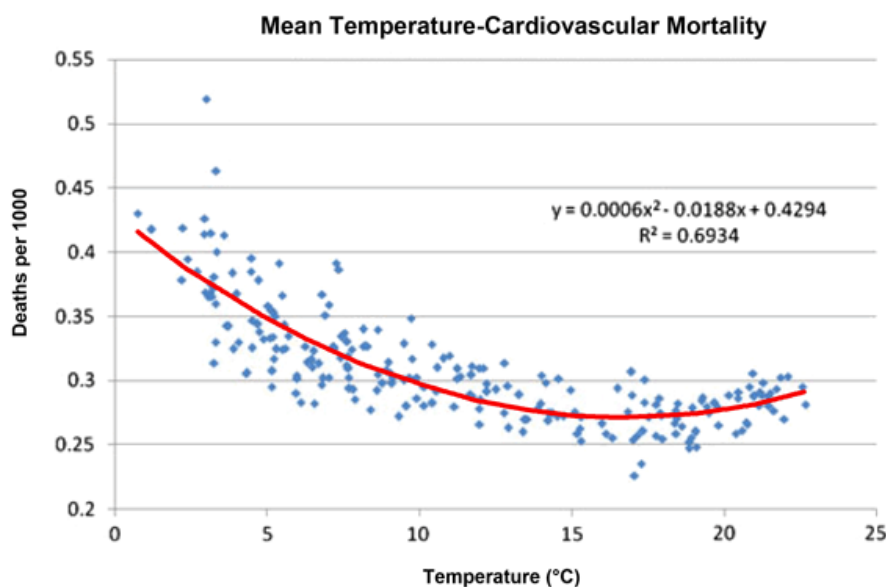


Figure 7.1.2.1. Monthly deaths in the Castile-Leon region of Spain attributable to cardiovascular disease. Adapted from Fernandez-Raga *et al.* (2010).

IPCC, Wichmann *et al.* (2011) write “temperature, a key climate change indicator, is expected to increase substantially in the Northern Hemisphere, with potentially grave implications for human health.” Concerned about what that might mean for their homeland, the five Danish researchers investigated the association between the daily three-hour maximum apparent temperature (which reflects the physiological experience of combined exposure to humidity and temperature) and deaths due to cardiovascular disease (CVD), cerebrovascular disease (CBD), and respiratory disease (RD) in the nation’s capital, Copenhagen, over the period 1999–2006.

During the warm half of the year (April–September), Wichmann *et al.* found a rise in temperature had an inverse or protective effect with respect to CVD mortality (a 1% decrease in death in response to a 1°C increase in apparent temperature). This finding is unusual but also has been observed in Dublin, Ireland, as reported by Baccini *et al.* (2008, 2011). Wichmann *et al.* found no association with RD and CBD mortality. At the other end of the thermal spectrum, during the cold half of the year, all three associations were inverse or protective. This finding, according to the researchers, is “consistent with other studies (Eurowinter Group, 1997; Nafstad *et al.*, 2001; Braga *et al.*, 2002; O’Neill *et al.*, 2003; Analitis *et al.*, 2008).”

Whereas many observers (including IPCC) continue to emphasize the primarily negative impact

of summer heat waves on human death rates in low- and mid-latitude regions of Earth, essentially neglecting to report what happens there during winter cold spells, Wichmann *et al.*'s summer results tell a dramatically different story that is likely typical of higher latitudes. They also portray what tends to happen nearly everywhere in winter, noting during that cold part of the year "only protective effects [of warming] were observed."

Matzarakis *et al.* (2011) developed a relationship between heat stress and all-cause mortality in the densely populated city of Vienna (Austria), using a human biometeorological index known as the physiologically equivalent temperature or PET, which "describes the thermal situation by the air temperature of a reference environment, in which the core and the skin temperature is the same as in the complex outdoor environment." This reference environment is defined as "a room with a wind velocity < 0.1 m/sec, a vapor pressure of 12 hPa and a mean radiation temperature that equals the air temperature," as described in more detail by Mayer and Hoppe (1987).

Based on data from 1970–2007, and after adjusting the long-term mortality rate to account for temporal variations in the size of the population of Vienna, temporal changes in life expectancy, and the changing age structure of Vienna's population, the three researchers found a significant relationship between heat stress and mortality. Over this 38-year period, "some significant decreases of the sensitivity were found, especially in the medium heat stress levels," they report.

With respect to the cause of this decrease in heat stress sensitivity, Matzarakis *et al.* state in the final sentence of their abstract, these decreases in sensitivity "could indicate active processes of long-term adaptation to the increasing heat stress." In the discussion section of their paper, they write such sensitivity changes "were also found for other regions," citing Davis *et al.* (2003), Koppe (2005), Tan *et al.* (2007), and Donaldson and Keatinge (2008). In the conclusion of their paper, they refer to these changes as "positive developments."

Vocks *et al.* (2001) statistically evaluated the influence of various meteorological variables on the intensity of clinical symptoms (itching) caused by the skin disease atopic eczema in the high-mountain area of Davos, Switzerland for the period 1983–1989. Itching intensity was found to be inversely correlated with air temperature, air pressure, and water vapor pressure, such that an increase in any of these variables decreased the severity of itching. Examination of the three variables during periods of

abrupt and/or prolonged change, on the order of several weeks to months, substantially improved the correlations. Such findings suggest future warming, whether local, regional, or global, will bring a measure of relief from itching to sufferers of atopic eczema.

In Germany, Laschewski and Jendritzky (2002) analyzed daily mortality rates in Baden-Wurttemberg (10.5 million inhabitants) over the 30-year period 1958–1997 to determine the sensitivity of the population of this moderate climatic zone to long- and short-term episodes of heat and cold. Their research indicates mortality shows "a marked seasonal pattern with a minimum in summer and a maximum in winter." With respect to short-term exposure to heat and cold, they found "cold spells lead to excess mortality to a relatively small degree, which lasts for weeks," and "the mortality increase during heat waves is more pronounced, but is followed by lower than average values in subsequent weeks." The authors say the latter observation suggests people who died from short-term exposure to heat possibly "would have died in the short term anyway."

With respect to this short-term mortality displacement in the case of heat-related deaths, it is worth noting Laschewski and Jendritzky's data demonstrate it is merely a displacement of deaths and not an overall increase. They found, for example, the mean duration of above-normal mortality for the 51 heat episodes that occurred from 1968 to 1997 was 10 days, with a mean increase in mortality of 3.9%, after which there was a mean decrease in mortality of 2.3% for 19 days. Hence, the net effect of the two perturbations was an overall decrease in mortality of 0.2% over the full 29-day period. This is additional evidence cold spells are more deadly than heat waves. Hence, global warming should be expected to confer significant benefits upon mankind in both the short- and long-term, for in both situations, cold kills but heat heals, especially in the long term, which is what global warming projections are all about.

Focusing on the Czech Republic, Kysely and Huth (2004) calculated deviations of the observed number of deaths from the expected number of deaths for each day of the year for the period 1992–2000. They found "the distribution of days with the highest excess mortality in a year is clearly bimodal, showing a main peak in late winter and a secondary one in summer." Regarding the smaller number of summer heat-wave-induced deaths, they also found "a large portion of the mortality increase is associated with the harvesting effect, which consists in short-term shifts in mortality and leads to a decline in the number of

deaths after hot periods (e.g. Rooney *et al.*, 1998; Braga *et al.*, 2002; Laschewski and Jendritzky, 2002).” For the Czech Republic, they report, “the mortality displacement effect in the severe 1994 heat waves can be estimated to account for about 50% of the total number of victims.” As they describe it, “people who would have died in the short term even in the absence of oppressive weather conditions made up about half of the total number of deaths.” Hence, not only is the overall number of deaths typically smaller in the warmest part of the year than in the coldest time of the year in the Czech Republic, approximately half of the heat-related excess deaths associated with the severe 1994 heat waves likely would have occurred even without the unseasonable heat, as they were merely normal deaths simply hastened by unseasonably warm temperatures.

Kysely and Plavcova (2012) write, “there is much concern that climate change may be associated with large increases in heat-related mortality,” but “growing evidence has been emerging that the relationships between temperature extremes and mortality impacts are nonstationary,” and “most of these studies point to declining heat-related mortality in developed countries, including the US, Australia, the UK, the Netherlands and France (Davis *et al.*, 2002, 2003a, 2003b; Bi and Walker, 2001; Donaldson *et al.*, 2003; Garssen *et al.*, 2005; Carson *et al.*, 2006; Fouillet *et al.*, 2008; Sheridan *et al.*, 2009).” This is true, they note, despite “aging populations and prevailing rising trends in temperature extremes.”

Most of the studies cited above were conducted in developed countries; the two Czech researchers note “much less is understood about temporal changes in the impacts of temperature extremes in developing (low- and middle-income) countries and in regions that have undergone (or are undergoing) a transition from the developing to the developed world,” They note “post-communist Central and Eastern Europe is one such region, where pronounced changes have occurred over the past 20 years.” They examined “temporal changes in mortality associated with spells of large positive temperature anomalies (hot spells) in extended summer season in the population of the Czech Republic (Central Europe) during 1986–2009.”

Kysely and Plavcova found declining mortality trends in spite of rising temperature trends, just the opposite of what IPCC claims will occur in response to global warming. The Czech scientists add, “the finding on reduced vulnerability of the population remains unchanged if possible confounding effects of within-season acclimatization and mortality displacement are taken into account,” and “neither

does it depend on the changing age structure of the population, since similar (and slightly more pronounced) declines in the mortality impacts are found in the elderly (age group 70+ years) when examined separately.”

Kysely and Plavcova write, “recent positive socioeconomic development following the collapse of communism in 1989 is the likely primary cause of the declining impacts of hot spells,” and “other important factors have been enhanced media coverage and better public awareness of heat-related risks.” They also note their key result “supports the idea that the adverse health effects of heat are largely preventable (e.g., Matthies and Menne, 2009),” ultimately concluding “climate change may have relatively little influence on heat-related deaths, particularly if the recent warming trend is viewed as an early manifestation of anthropogenic climate change.” They continue, “it appears that changes in other factors that influence vulnerability of a population are dominant instead of temperature trends and that the level of adaptability to high ambient temperatures may be large.”

Huynen *et al.* (2001) evaluated the impact of heat waves and cold spells on mortality rates of people of all ages throughout the Netherlands for the 19-year period 1 January 1979 through 31 December 1997. During heat waves they found a mean excess mortality of 39.8 deaths per day, whereas during cold spells they found a mean excess mortality of 46.6 deaths per day. These numbers indicate a typical cold-spell day kills at a rate 17% greater than a typical heat-wave day. They also report the heat waves of the period they studied ranged from six to 13 days in length, whereas the cold spells lasted from nine to 17 days, making the average cold spell approximately 37% longer than the average heat wave. Adjusting for this duration differential makes the number of deaths per cold spell in the Netherlands fully 60% greater than the number of deaths per heat wave. Also, excess mortality continued for the entire month after the cold spells, leading to even more deaths, whereas in the case of heat waves, there appeared to be mortality deficits in the following month, suggesting “some of the heat-induced increase in mortality can be attributed to those whose health was already compromised” or “who would have died in the short term anyway.” That conclusion also was reached by Kunst *et al.* (1993), Alberdi *et al.* (1998), Eng and Mercer (1998), and others mentioned in this section. It is highly likely, therefore, that the 60% greater death toll calculated for Dutch cold spells compared to Dutch heat waves is a vast underestimate of the

true differential killing power of these two temperature extremes.

In a letter to the editor of *Epidemiology*, the senior and second authors of the Huynen *et al.* paper discussed whether global climate change reduces thermal stress in the Netherlands (Martens and Huynen, 2001). Based on the predictions of nine GCMs for an atmospheric CO₂ concentration of 550 ppm in the year 2050—taken to imply a 50% increase in Dutch heat waves and a 67% drop in Dutch cold spells—they calculated a total mortality decrease of approximately 1,100 people per year for the country at that point in time.

In a multiregional study, Keatinge *et al.* (2000a) examined heat- and cold-related mortality in north Finland, south Finland, southwest Germany, the Netherlands, Greater London, north Italy, and Athens, Greece, in people aged 65–74. For each of these regions, they determined the 3°C temperature interval of lowest mortality and then evaluated mortality deviations from that base level as temperatures rose and fell by increments of 0.1°C. As they describe their findings, “all regions showed more annual cold related mortality than heat related mortality.” Over the seven regions studied, annual cold-related deaths were nearly 10 times greater than annual heat-related deaths. Moreover, Keatinge *et al.* note the very successful adjustment of the populations in their study to widely different summer temperatures “gives grounds for confidence that they would adjust successfully, with little increase in heat related mortality, to the global warming of around 2°C predicted to occur in the next half century.” They say their data suggest “any increases in mortality due to increased temperatures would be outweighed by much larger short term declines in cold related mortalities.” For the entire population of Europe, therefore, even a 2°C increase in temperature, if it were to occur, would be a climate change for the better.

In a major assessment of cold-weather effects on mortality in Europe, Analitis *et al.* (2008) state, “in recent years, the effects of meteorologic factors on health have attracted renewed interest because of the observed and predicted climate change, which is expected to result in a general rise in temperature.” This development, they write, has led to a “recent focus on heat-wave episodes,” which may have fostered the perception cold-related mortality is not as important a public health concern as heat-related mortality.

Analitis *et al.* analyzed short-term effects of cold weather on mortality in 15 European cities: Athens,

Greece; Barcelona, Spain; Budapest, Hungary; Dublin, Ireland; Helsinki, Finland; Ljubljana, Slovenia; London, United Kingdom; Milan, Italy; Paris, France; Prague, Czech Republic; Rome, Italy; Stockholm, Sweden; Turin, Italy; Valencia, Spain; and Zurich, Switzerland. They assessed the effects of minimum apparent temperature on cause- and age-specific daily mortality over the cold half of the year (October–March), using data from 1990–2000 they analyzed via “Poisson regression and distributed lag models, controlling for potential confounders.”

The international team of scientists—from Finland, Greece, Ireland, Italy, Slovenia, Spain, and Sweden—found “a 1°C decrease in temperature was associated with a 1.35% increase in the daily number of total natural deaths and a 1.72%, 3.30% and 1.25% increase in cardiovascular, respiratory, and cerebrovascular deaths, respectively.” In addition, they report “the increase was greater for the older age groups,” and the cold effect “persisted up to 23 days, with no evidence of mortality displacement.” Analitis *et al.* conclude their results “add evidence that cold-related mortality is an important public health problem across Europe and should not be overlooked by public health authorities because of the recent focus on heat-wave episodes.”

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7.1.3 North America

Goklany and Straja (2000) examined trends in United States death rates over the period 1979–1997 due to excessive hot and cold weather. They report there were no trends in deaths due to either extreme heat or cold in the entire population or, “more remarkably,” as they say, in the older, more-susceptible age groups, those aged 65 and over, 75 and over, and 85 and over. Deaths due to extreme cold in these older age groups exceeded those due to extreme heat by as much as 80% to 125%. With respect to the absence of trends in death rates attributable to either extreme heat or cold, Goklany and Straja say this “suggests that adaptation and technological change may be just as important determinants of such trends as more obvious meteorological and demographic factors.”

Davis *et al.* (2002) studied changes in the impact of high temperatures on daily mortality rates over a period of four decades in six major metropolitan areas along a north-south transect in the eastern United States. They found few significant weather-mortality relationships for any decade or demographic group in the three southernmost cities examined, where warmer weather is commonplace. In the three northernmost cities, however, there were statistically significant decreases in population-adjusted mortality rates during hot and humid weather between 1964 and 1994. The authors write, “these statistically significant reductions in hot-weather mortality rates suggest that the populace in cities that were weather-sensitive in the 1960s and 1970s have become less impacted by extreme conditions over time because of improved medical care, increased access to air conditioning, and biophysical and infrastructural adaptations.” They further note, “this analysis counters the paradigm of increased heat-related mortality rates in the eastern US predicted to result from future climate warming.”

Davis *et al.* (2003) evaluated “annual excess mortality on days when apparent temperatures—an index that combines air temperature and humidity—exceeded a threshold value for 28 major metropolitan areas in the United States from 1964 through 1998.” They found “for the 28-city average, there were 41.0 ± 4.8 excess heat-related deaths per year (per standard million) in the 1960s and 1970s, 17.3 ± 2.7 in the 1980s, and 10.5 ± 2.0 in the 1990s.” Analyzing these results together with various types of ancillary data, they conclude, “this systematic desensitization of the metropolitan populace to high heat and humidity over time can be attributed to a suite of technologic, infrastructural, and biophysical adaptations, including increased availability of air conditioning.” Consequently, because “all-causes mortality during heat stress events has declined despite increasingly stressful weather conditions in many urban and suburban areas ... heat-related mortality in the United States seems to be largely preventable at present.” The technology and infrastructure advancements made possible by the economic progress of the past few decades have more than compensated for the increasing heat stress during this period of what IPCC describes as “unprecedented” global warming.

Davis *et al.* (2004) examined the seasonality of mortality due to all causes, using monthly data for 28 major U.S. cities from 1964 to 1998, then calculated the consequences of a future 1°C warming of the conglomerate of those cities. At all locations studied, they report “warmer months have significantly lower

mortality rates than colder months.” They calculate “a uniform 1°C warming results in a net mortality decline of 2.65 deaths (per standard million) per metropolitan statistical area.” Since the annual death rate of about 9,500 deaths (per standard million) is so much larger, however, the “death benefits” of the warming are extremely small—a reduction in the annual number of deaths of less than 0.03%, which also pales in comparison to the nearly 20% reduction in annual mortality that has occurred as a consequence of technological advancements experienced between the 1960s–1970s and the 1990s.

The primary implication of Davis *et al.*’s findings, in their words, “is that the seasonal mortality pattern in US cities is largely independent of the climate and thus insensitive to climate fluctuations, including changes related to increasing greenhouse gases.”

O’Neill *et al.* (2005) assessed the influence of air pollution and respiratory epidemics on empirical associations between apparent temperature, which “represents an individual’s perceived air temperature,” and daily mortality in Mexico’s largest and third-largest cities: Mexico City and Monterrey, respectively. They report, “the effects of cold weather on all-age mortality were similar in Monterrey and Mexico City.” When considering the entire temperature spectrum, they found “in Mexico City, the 7-day temperature mortality association has a hockey stick shape with essentially no effect of higher temperatures,” whereas in Monterrey the function they fit to the data “shows a U-shape,” with “a higher mortality risk at both ends of the distribution,” although the effect is much weaker at the high-temperature end of the plot than at the low-temperature end, and the absolute value of the slope of the mortality vs. temperature relationship is smaller across the high-temperature range of the data.

Most interesting, perhaps, was the researchers’ finding that “failure to control for respiratory epidemics and air pollution resulted in an overestimate of the impact of hot days by 50%,” whereas “control for these factors had little impact on the estimates of effect of cold days.” They note “most previous assessments of effects of heat waves on hot days have not controlled for air pollution or epidemics.” In other words, the death-dealing effects of heat waves typically are not adjusted for concurrent effects of air pollution and respiratory epidemics, which often account for as much as half of the deaths attributed to hot temperatures; these two confounding factors do not appear to impact assessments of the effect of cold temperatures on

deaths.

A prime example of the failure to account for concurrent air pollution effects on mortality occurred in the aftermath of the European heat wave of 2003. In analyzing the impact of air pollutants present during that episode in the United Kingdom, Stedman (2004) found 21–38% of the total excess deaths claimed to be due to high temperatures were actually the result of elevated concentrations of ozone and PM₁₀ (particulate matter of diameter less than 10µm). Likewise, Fischer *et al.* (2004) determined 33–50% of the deaths attributed to the same heat wave in the Netherlands were caused by concurrent high ozone and PM₁₀ concentrations. This factor is often unaccounted for in mortality-related studies of heat waves.

Deschenes and Moretti (2009) analyzed the relationship between weather and mortality, based on “data that include the universe of deaths in the United States over the period 1972–1988,” in which they “match each death to weather conditions on the day of death and in the county of occurrence.” This “high-frequency data and the fine geographical detail,” they write, allow them “to estimate with precision the effect of cold and hot temperature shocks on mortality, as well as the dynamics of such effects.” Most notably, the data allowed them to detect the existence or absence of a “harvesting effect,” whereby the temperature-induced deaths are or are not subsequently followed by a drop in the normal death rate, which could compensate for the prior extreme temperature-induced deaths.

The two researchers say their results “point to widely different impacts of cold and hot temperatures on mortality.” They discovered “hot temperature shocks are indeed associated with a large and immediate spike in mortality in the days of the heat wave,” but “almost all of this excess mortality is explained by near-term displacement.” As a result, “in the weeks that follow a heat wave, we find a marked decline in mortality hazard, which completely offsets the increase during the days of the heat wave,” so “there is virtually no lasting impact of heat waves on mortality.”

In the case of cold temperature days, they also found “an immediate spike in mortality in the days of the cold wave,” but “there is no offsetting decline in the weeks that follow,” so “the cumulative effect of one day of extreme cold temperature during a thirty-day window is an increase in daily mortality by as much as 10%.” In addition, they write, “this impact of cold weather on mortality is significantly larger for females than for males,” but “for both genders, the

effect is mostly attributable to increased mortality due to cardiovascular and respiratory diseases.”

Deschenes and Moretti state “the aggregate magnitude of the impact of extreme cold on mortality in the United States is large,” noting it “roughly corresponds to 0.8% of average annual deaths in the United States during the sample period.” They estimate “the average person who died because of cold temperature exposure lost in excess of ten 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.

Interestingly, Deschenes and Moretti report many people in the United States have taken advantage of these evident facts by moving “from cold northeastern states to warm southwestern states.” Based on their findings, for example, they calculate “each year 4,600 deaths are delayed by the changing exposure to cold temperature due to mobility,” and “3% to 7% of the gains in longevity experienced by the U.S. population over the past three decades are due to the secular movement toward warmer states in the West and the South, away from the colder states in the North.”

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7.1.4 Other Regions

In Brazil, Gouveia *et al.* (2003) extracted daily counts of deaths from all causes except violent deaths and neonatal deaths up to one month of age, from Sao Paulo’s mortality information system for the period 1991–1994. They analyzed this data for the effects of temperature on the age groups of less than 15 years (children), 15–64 years (adults), and 65 years or older (elderly), determining “change points” at which heat and cold effects started.

Interestingly, the authors found the change points for both heat- and cold-induced deaths were identical: 20°C. For each 1°C increase above this value for a given and prior day’s mean temperature, they observed a 2.6% increase in deaths from all causes in children, a 1.5% increase in deaths from all causes in adults, and a 2.5% increase in deaths from all causes in the elderly. For each 1°C decrease below the 20°C change point, the effect was greater, with increases in deaths from all causes in children, adults, and the elderly registering 4.0%, 2.6%, and 5.5%, respectively. These cooling-induced death rates were 54%, 73%, and 120% greater than those attributable to warming.

Bi *et al.* (2008) used correlation and autoregressive integrated moving average regression analyses to derive relationships between various aspects of weather and mortality in the general population and elderly (65 years of age and older) of Brisbane, Australia, which they describe as having a subtropical climate, over the period 1986–1995. They found “death rates were around 50–80 per 100,000 in June, July, and August [winter], while they were around 30–50 per 100,000 in the rest of the year, including the summer,” and “this finding applied both to the general population and to the elderly population, and to deaths from various causes.”

In discussing their finding that “more deaths occurred in the winter than during other seasons of the year, although winter in Brisbane is very mild,” the researchers note “it is understandable that more deaths would occur in winters in cold or temperate regions, but even in a subtropical region, as indicated in this study, a decrease in temperatures (in winters) may increase human mortality.” The evidence continues to grow for extremes of cold leading to the deaths of many more people than extremes of heat, in

both cold and warm climates.

Xu *et al.* (2013) preface their work by stating, “previous studies have found that high and cold temperatures increase the risk of childhood diarrhea,” but much less is known about whether the within-day variation of temperature (i.e., the daily maximum minus minimum, or diurnal temperature range, DTR) has any effect on it. They write, “a Poisson generalized linear regression model combined with a distributed lag non-linear model was used to examine the relationship between diurnal temperature range and emergency department admissions for diarrhea among children under five years in Brisbane [Australia] from 1st January 2003 to 31st December 2009.”

The six scientists found “a statistically significant relationship between diurnal temperature range and childhood diarrhea,” such that “a 1°C increase in diurnal temperature range was associated with a 3% increase of Emergency Department Admissions for childhood diarrhea.” They conclude, “as climate change continues, DTRs are likely to become more variable,” and as a result, “the incidence of childhood diarrhea may increase.” Other research suggests this is likely *not* to be the case: Karl *et al.* (1984, 1991) have shown during most of twentieth century global warming, daily minimum temperatures rose at a rate fully three times greater than daily maximum temperature over most of the world. DTRs actually declined over this period and must have led to significant decreases in emergency department admissions for diarrhea among children under five years of age, representing yet another positive health benefit of global warming.

Mrema *et al.* (2012) state “weather and climate changes are associated with a number of immediate and long-term impacts on human health that occur directly or indirectly, through mediating variables,” but “few studies to date have established the empirical relationship between monthly weather and mortality in sub-Saharan Africa.” Working with mortality data obtained from the Rufiji (Tanzania) Health and Demographic Surveillance System (RHDS) for the period 1999 to 2010, Mrema *et al.* employed time-series Poisson regression models to estimate the association between monthly temperature—which ranges from 27.9 to 34.4°C in this tropical region—and mortality, adjusted for long-term trends, in three age groups (0–4, 5–59, 60+).

The four Tanzanian researchers report “mortality in all age groups peaked up at the mid of the year,” which is “the time when the temperature is relatively lower compared to other periods of the year in

Rufiji.” If the monthly average temperature drops to a value of 24°C from the threshold, they state, “mortality will increase by 80.7%, 65.7% and 74% in age groups 0–4, 5–59 and over 60, respectively.” Mrema *et al.* note “Rufiji’s population is accustomed to a tropical climate and, like any other population, is exposed to cold temperatures relative to its average climate.” Hence even in a warm, tropical region, relative cold kills far more people than relative heat.

Egondi *et al.* (2012) state, “many studies have established a link between weather (primarily temperature) and daily mortality in developed countries,” but “little is known about this relationship in urban populations in sub-Saharan Africa.” They employed mortality data from the Nairobi Urban Health and Demographic Surveillance System (NUHDSS) along with time-series models “to study the relationship between daily weather and mortality for a population of approximately 60,000 during the period 2003–2008.”

“Overall,” the six scientists report, “there are seasonal fluctuations in mortality, with the highest rates of death occurring during periods of relative cold.” They also note “mortality risk over the year rises from the lowest mortality risk by about 40% in the 0–4 age group and by about 20% for all ages” in response to a drop in temperature. In addition, “the effects of low temperatures on mortality can last for days,” and therefore, “although the world will get warmer in the future, the low temperature-related mortality is likely to remain an important concern.” Such findings further demonstrate a change in the weather or shifting of the seasons to cooler conditions, rather than an equivalent increase in warmth, is typically the more deadly of the two types of temperature evolution, even in relatively warm places.

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7.1.5 Multiple Regions

Studying North Carolina (USA); South Finland, comprising all of Finland except the northern provinces of Oulu and Lapland; and Southeast England, comprising Greater London, Essex, Kent, Sussex, Hampshire, Surrey, Berkshire, Oxfordshire, Buckinghamshire, and Bedfordshire, Donaldson *et al.* (2003) determined the mean daily May–August 3°C temperature band in which deaths of people aged 55 and above were at a minimum. They compared the numbers of heat- and cold-related deaths at temperatures above and below this optimum temperature interval for each region and determined how heat-related deaths in the three areas changed between 1971 and 1997 in response to the 1.0°C temperature rise experienced in North Carolina over this period, starting from an initial temperature of 23.5°C; the 2.1°C temperature rise experienced in Southeast England, starting from an initial temperature of 14.9°C; and the unchanging 13.5°C temperature of South Finland.

Donaldson *et al.* report the 3°C temperature band at which mortality was at its local minimum was lowest for the coldest region (South Finland), highest for the warmest region (North Carolina), and in between for the “in between” region (Southeast England), indicating the populations of these three regions are somewhat acclimated to their respective thermal climates. They also found cold-related mortality was greater than heat-related mortality in each region. With respect to changes in heat-related

mortality from 1971 to 1997, they determined for the coldest of the three regions (South Finland, where there was no change in temperature over the study period), heat-related deaths per million inhabitants in the 55-and-above age group declined from 382 to 99. In somewhat warmer Southeast England, where it warmed by 2.1°C over the study period, heat-related deaths per million of the at-risk age cohort declined, but only from 111 to 108. And in the warmest of the three regions (North Carolina, where mean daily May–August temperature rose by 1.0°C over the study period), corresponding heat-related deaths also fell from 228 to a mere 16 per million.

Such findings imply first that people can adapt to both warmer and cooler climates to some degree. Beyond that, local cooling tends to produce many more deaths than does local warming in all three of the areas studied. As for the dramatic decline in the number of heat-related deaths over a period of warming in the hottest area of the study (North Carolina), Donaldson *et al.* attribute this phenomenon to “the increase of air conditioning in the South Atlantic region of the U.S.A.,” where they note “the percentage of households with some form of air conditioning in that region rose from 57% in 1978 to 72% in 1997.” With respect to the declining heat-related deaths in the other two regions, they say, “the explanation is likely to lie in the fact that both regions shared with North Carolina an increase in prosperity, which could be expected to increase opportunities for avoiding heat stress.”

In a review article touching on multiple aspects of temperature-related deaths, Keatinge and Donaldson (2004) report “cold-related deaths are far more numerous than heat-related deaths in the United States, Europe, and almost all countries outside the tropics,” noting coronary and cerebral thrombosis account for about half of all cold-related mortality. In describing the mechanisms behind this cold temperature-death connection, they say cold stress causes an increase in arterial thrombosis “because the blood becomes more concentrated, and so more liable to clot during exposure to cold.” The sequence of events, as they describe it, is as follows: “the body’s first adjustment to cold stress is to shut down blood flow to the skin to conserve body heat,” which “produces an excess of blood in central parts of the body,” and to correct for this effect, “salt and water are moved out from the blood into tissue spaces,” leaving behind “increased levels of red cells, white cells, platelets and fibrinogen” that lead to increased viscosity of the blood and a greater risk of clotting. In addition, cold stress “tends to suppress immune

responses to infections,” and respiratory infections typically “increase the plasma level of fibrinogen,” which also “contributes to the rise in arterial thrombosis in winter.”

Keatinge and Donaldson note “cold spells are closely associated with sharp increases in mortality rates,” and “deaths continue for many days after a cold spell ends.” On the other hand, “increased deaths during a few days of hot weather are followed by a lower than normal mortality rate,” because “many of those dying in the heat are already seriously ill and even without heat stress would have died within the next 2 or 3 weeks.”

Keatinge and Donaldson state, “since heat-related deaths are generally much fewer than cold-related deaths, the overall effect of global warming on health can be expected to be a beneficial one.” As an example, and even including the heat-harvesting of naturally expected deaths, they report “the rise in temperature of 3.6°F expected over the next 50 years would increase heat-related deaths in Britain by about 2,000 but reduce cold-related deaths by about 20,000.” Keatinge and Donaldson conclude, “the overall effect of global warming on health can be expected to be a beneficial one.”

Hajat *et al.* (2005) analyzed the history of heat-wave-related deaths in three cities of contrasting wealth (defined as gross national income per capita)—Delhi (India), Sao Paulo (Brazil), and London (England)—based on daily numbers of nonviolent deaths derived from mortality registries for the four-year period January 1991 to December 1994, examining “time-series of daily mortality data in relation to daily ambient temperature using Poisson models and adjusting for season, relative humidity, rainfall, particulate air pollution, day of the week and public holidays,” and using “unconstrained distributed lag models to identify the extent to which heat-related [death] excesses were followed by deficits.” The latter phenomenon (mortality displacement) arises when people who die during heat waves would have died shortly thereafter even in the absence of the elevated warmth.

For each city, an increase in all-cause mortality was observed for same- and previous-day temperatures greater than 20°C, with excess deaths being greatest in Delhi and smallest in London. In Delhi, the excess of deaths persisted for three weeks, whereas in London it prevailed for only two days and was followed by deficits that led to the sum of the two effects being zero by day 11. In Sao Paulo, as might have been expected, the pattern of deaths was intermediate between these two extremes. Summed

over the course of 28 days, the risk of death associated with heat stress was 2.4% per degree greater than 20°C in Delhi, 0.8% in Sao Paulo, and negative 1.6% in London. These findings led Hajat *et al.* to conclude, “populations in low-income countries where life-threatening infections are still common may have the greatest vulnerability to the effects of heat,” and “those most susceptible to heat are likely to remain susceptible if there is not due attention paid to infectious disease, diarrheal illness, and other major causes of early mortality in these poor populations.”

Byremo *et al.* (2006) studied the effects of temperature on atopic eczema, “a chronic inflammatory skin disease characterized by itching, lesions and lichenification,” especially at “the flexure sites of the major joints of the upper and lower extremities.” The pain and itching associated with the disease, as they describe it, “may cause depressive symptoms, social isolation and reduced self-perception,” lowering the quality of life in children and their caretakers. They report epidemiological studies suggest climate influences the disease’s prevalence, noting “atopic eczema has been reported worldwide to be positively associated with latitude and negatively with temperature (Weiland *et al.*, 2004).”

Byremo *et al.* transported 30 children, 4 to 13 years of age with severe atopic eczema, from their homes in Norway to the Canary Islands, where they stayed for four weeks before returning, and 26 similarly infected children of the same age group stayed at home in Norway the entire time. All were evaluated for various disease characteristics at the start of the study, at the conclusion of the group-of-30’s four-week period of stay in the Canary Islands, and three months after the 30 children left the islands to return home to Norway. The specific disease parameters employed in the evaluation were the Scoring of Atopic Dermatitis, the Children’s Dermatology Life Quality Index, skin colonization by *Staphylococcus aureus*, and pharmacological skin treatment.

Noting temperatures during the children’s stay in the Canary Islands were much higher than those in Norway, Byremo *et al.* report the children’s time in the warmer climate significantly reduced the severity of atopic eczema, and the youths improved in severity of eczema, quality of life, and bacterial skin culture, which was reflected in a reduction in the use of topical steroids, antihistamines, and topical antibiotics. These positive changes were observed at the conclusion of the four-week stay in the Canary Islands as well as back home in Norway three months later. The researchers state the four weeks spent in the

Canary Islands “led to a lasting improvement for the children,” whereas “the control group did not show similar improvement.”

Although greater exposure to sunlight and the effect of regularly bathing in seawater, such as the children did at the Canary Islands, likely played positive roles in reducing the severity of their atopic eczema, the results of this study are harmonious with the worldwide negative correlation that prevails between eczema and temperature, suggesting global warming may prove beneficial to people unfortunate enough to suffer from it.

According to Young and Kakinen (2010), “Arctic populations, especially indigenous people, could be considered as ‘vulnerable,’ because their health status generally shows disparities when compared to the national or more southern populations,” and “it is not known if the harsh climate, and especially cold temperatures, could be a contributing or causative factor of the observed health inequalities.” To shed some light on this subject, they determined “mean January and July temperatures ... for 27 Arctic regions based on weather station data for the period 1961–1990 and their association with a variety of health outcomes assessed by correlation and multiple linear regression analyses.”

The two researchers report mean January temperature correlated negatively with several health outcomes, including infant mortality rate, age-standardized mortality rates (all causes, respiratory, cancer, injuries), perinatal mortality rate, and tuberculosis incidence rate, but it correlated positively with life expectancy. That is to say, as mean January temperature rose, life expectancy at birth rose as well, whereas the undesirable health metrics (such as mortality and disease incidence) declined. They report, “for every 10°C increase in mean January temperature, the life expectancy at birth among males increased by about six years,” whereas “infant mortality rate decreased by about four deaths per thousand live births.” Young and Kakinen conclude the cold climate of the Arctic is “significantly associated with higher mortality” and “should be recognized in public health planning,” noting “within a generally cold environment, colder climate results in worse health.”

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7.2 Cardiovascular Disease

- 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 cardiovascular diseases associated with high temperatures and summer heat waves.

According to IPCC, global warming will pose numerous challenges to human health, including premature death due to heat-induced cardiovascular problems. This section examines the results of studies that dealt with this important subject in the past decade or so.

Enquesselassie *et al.* (1993) investigated the effects of extremes of temperature and rainfall, as well as intermediate levels, on the number of coronary events, both fatal and nonfatal, reported in the Hunter Region of New South Wales, Australia, located on the east coast of the country about 150 km north of Sydney, for the five-year period 1 July 1985 to 30 June 1990. “Daily temperature and rainfall,” they write, “were taken as indicators of acute effects of weather and the month when an event occurred was used to indicate longer-term or seasonal effects.”

Regarding seasonal effects, Enquesselassie *et al.* report “fatal coronary events and non-fatal definite myocardial infarction were 20–40% more common in winter and spring than at other times of year.” As to daily temperature effects, they found “rate ratios for deaths were significantly higher for low tem-

peratures,” noting “on cold days coronary deaths were up to 40% more likely to occur than at moderate temperatures.” Effects of humidity and rainfall were negligible. The authors conclude their data “support the theory of increased risk of coronary mortality when temperatures are unusually low,” and “avoiding temperature extremes could contribute to reduction in annual peaks in coronary events,” which occur during the colder part of the year.

Thanks to Norwegian law, which requires all deaths be examined by a physician who diagnoses cause and reports it on the death certificate, Nafstad *et al.* (2001) were able to examine the effects of temperature on mortality due to all forms of cardiovascular disease for citizens of the country’s capital over the period 1990 to 1995. Their analysis showed the average daily number of cardiovascular-related deaths was 15% higher in the winter months (October–March) than in the summer months (April–September), leading them to conclude “a milder climate would lead to a substantial reduction in average daily number of deaths.”

Research in Israel conducted by Green *et al.* (1994) revealed that between 1976 and 1985, mortality from cardiovascular disease was higher by 50% in mid-winter than in mid-summer, both in men and in women, as well as in different age groups. Summer temperatures in the Negev, where much of the work was conducted, often exceeded 30°C, whereas winter temperatures typically did not drop below 10°C. These findings have been substantiated by several other Israeli studies, including those reviewed by Behar (2000), who wrote “most of the recent papers on this topic have concluded that a peak of sudden cardiac death, acute myocardial infarction and other cardiovascular conditions is usually observed in low temperature weather during winter.”

Evidence of a seasonal variation in cardiac-related mortality also has been noted in the relatively mild climate of southern California in the United States. In a study of all 222,265 death certificates issued by Los Angeles County for deaths caused by coronary artery disease from 1985 through 1996, Kloner *et al.* (1999) found death rates in December and January were 33% higher than those observed in June through September. Likewise, based on a study of the Hunter region of New South Wales, Australia, which covered 1 July 1985 to 30 June 1990, Enquselassie *et al.* (1993) determined “fatal coronary events and non-fatal definite myocardial infarction were 20–40% more common in winter and spring than at other times of year.” With respect to daily temperature effects, they found “rate ratios for deaths

were significantly higher for low temperatures,” noting “on cold days coronary deaths were up to 40% more likely to occur than at moderate temperatures.”

Hajat and Haines (2002) set out to determine whether the number of cardiovascular-related doctor visits by the elderly bore a similar relationship to cold temperatures. Based on data obtained between January 1992 and September 1995 for registered patients aged 65 and older from several practices in London, England, they found the number of general practitioner consultations was higher in the cool-season months (October–March) than in the warm-season months (April–September) for all cardiovascular diseases.

In a study of both “hot” and “cold” cities in the United States—where Atlanta, Georgia; Birmingham, Alabama; and Houston, Texas comprised the “hot” group, and Canton, Ohio; Chicago, Illinois; Colorado Springs, Colorado; Detroit, Michigan; Minneapolis-St. Paul, Minnesota; New Haven, Connecticut; Pittsburgh, Pennsylvania; and Seattle and Spokane, Washington comprised the “cold” group—Braga *et al.* (2002) determined both the acute effects and lagged influence of temperature on cardiovascular-related deaths. They found in the hot cities neither hot nor cold temperatures had much impact on mortality related to cardiovascular disease (CVD). In the cold cities, on the other hand, both high and low temperatures were associated with increased CVD deaths. The effect of cold temperatures persisted for days, whereas the effect of high temperatures was restricted to the day of the death or the day before. For all CVD deaths, the hot-day effect was five times smaller than the cold-day effect. In addition, the hot-day effect included some “harvesting,” where Braga *et al.* observed a deficit of deaths a few days later, which they did not observe for the cold-day effect.

Gouveia *et al.* (2003) determined the number of cardiovascular-related deaths in adults aged 15–64 years of age in Sao Paulo, Brazil over the period 1991–1994 increased by 2.6% for each 1°C decrease in temperature below 20°C, while they found no evidence for heat-induced deaths due to temperatures rising above 20°C. In the elderly (65 years of age and above), a 1°C warming above 20°C led to a 2% increase in deaths, but a 1°C cooling below 20°C led to a 6.3% increase in deaths, more than three times as many cardiovascular-related deaths due to cooling than to warming in the elderly.

For the period 1974–1999, McGregor *et al.* (2004) obtained data on ischaemic heart disease (IHD) and temperature for five English counties aligned on a north-south transect (Tyne and Wear,

West Yorkshire, Greater Manchester, West Midlands, and Hampshire) and analyzed them for relationships between the two parameters. They determined “the seasonal cycles of temperature and mortality are inversely related,” and “the first harmonic accounts for at least 85% (significant at the 0.01 level) of the variance of temperature and mortality at both the climatological and yearly time scales.” They also report “years with an exaggerated mortality peak are associated with years characterized by strong temperature seasonality,” and “the timing of the annual mortality peak is positively associated with the timing of the lowest temperatures.” McGregor *et al.* explain, “frequent exposure to cold causes a rise in IHD risk factors (Lloyd, 1991) through increasing blood pressure and viscosity, vasoconstriction, heart rate and angina (Morgan and Moran, 1997).”

Chang *et al.* (2004) analyzed data from the World Health Organization (WHO) Collaborative Study of Cardiovascular Disease and Steroid Hormone Contraception (WHO, 1995) to determine the effects of monthly mean temperature on rates of hospitalization for arterial stroke and acute myocardial infarction (AMI) among young women aged 15–49 from 17 countries in Africa, Asia, Europe, Latin America, and the Caribbean. These efforts revealed “among young women from 17 countries, the rate of hospitalized AMI, and to a lesser extent stroke, was higher with lower mean environmental air temperature.” They report, “on average, a 5°C reduction in mean air temperature was associated with a 7 and 12% increase in the expected hospitalization rates of stroke and AMI, respectively.” They also note “the findings of an inverse association between mean air temperature and hospitalization rate of AMI in this study are in agreement with several other studies,” citing Douglas *et al.* (1990), Douglas *et al.* (1991), Mackenbach *et al.* (1992), Douglas *et al.* (1995), Seto *et al.* (1998), Danet *et al.* (1999), and Crawford *et al.* (2003). Finally, they note, “lagging the effects of temperature suggested that these effects were relatively acute, within a period of a month.”

Bartzokas *et al.* (2004) “examined the relationship between hospital admissions for cardiovascular (cardiac in general including heart attacks) and/or respiratory diseases (asthma etc.) in a major hospital in Athens [Greece] and meteorological parameters for an 8-year period.” Over the year, “there was a dependence of admissions on temperature” and low temperatures were “responsible for a higher number of admissions,” they found. Specifically, “there was a decrease of cardiovascular or/and respiratory events from low to high values [of

temperature], except for the highest temperature class in which a slight increase was recorded.”

Nakaji *et al.* (2004) evaluated seasonal trends in deaths in Japan due to various diseases, using nationwide vital statistics from 1970 to 1999 and recorded weather data, specifically, mean monthly temperature. The nine researchers note Japan has “bitterly cold winters,” and their analysis indicates the numbers of deaths due to infectious and parasitic diseases including tuberculosis, respiratory diseases including pneumonia and influenza, diabetes, digestive diseases, and cerebrovascular and heart diseases rise to a maximum during that cold time of year. Of the latter two categories, they found peak mortality rates due to heart disease and stroke were one-and-a-half to two times greater in winter (January) than at the time of their yearly minimums (August and September). They conclude, in order “to reduce the overall mortality rate and to prolong life expectancy in Japan, measures must be taken to reduce those mortality rates associated with seasonal differences.” They also note, “it has long been recognized that cold temperature acts as a trigger for coronary events,” and “major infectious diseases are epidemic in winter.”

Hence, to achieve the scientists’ stated objectives, it is necessary to bring about a “reduction in exposure to cold environments,” as they put it, which is precisely what global warming does, and what it does best by warming more in winter than in summer, as Nakaji *et al.* demonstrate to be the case in Japan, where winter warming over the past 30 years was twice as great as it was during the rest of the year.

In Sao Paulo, Brazil, where 12,007 deaths were observed from 1996 to 1998, Sharovsky *et al.* (2004) investigated “associations between weather (temperature, humidity and barometric pressure), air pollution (sulfur dioxide, carbon monoxide, and inhalable particulates), and the daily death counts attributed to myocardial infarction.” Their efforts revealed “a significant association of daily temperature with deaths due to myocardial infarction ($p < 0.001$), with the lowest mortality being observed at temperatures between 21.6 and 22.6°C.” For all practical purposes, however, their data showed little variation in death rates from 18°C to just over 25°C, with the latter representing the typical upper limit of observed temperature in Sao Paulo, which is located on the Tropic of Capricorn at an altitude of 800 m. As mean daily temperature dropped below 18°C, however, death rates rose in essentially linear fashion to attain a value at 12°C (the typical lower limit of observed temperature in Sao Paulo) more than 35%

greater than the minimum baseline value registered between 21.6 and 22.6°C.

Sharovsky *et al.* say their findings “demonstrated a strong association between daily temperature and myocardial infarction in Sao Paulo, Brazil,” which suggests “an acclimatization of the population to the local climate occurs and that myocardial infarction deaths peak in winter not only because of absolute low temperature but possibly secondary to a decrease relative to the average annual temperature.” This indeed must be true, for deaths due to heart attacks are consistently greater in winter than in summer, as they write, “across many regions of the world (Marshall *et al.*, 1998; Douglas *et al.*, 1991; Seto *et al.*, 1998; Sheth *et al.*, 1999).”

Kovats *et al.* (2004) analyzed patterns of temperature-related hospital admissions and deaths in Greater London during the mid-1990s. For the three-year period 1994–1996, cardiovascular-related deaths were approximately 50% greater during the coldest part of the winter than during the peak warmth of summer, whereas respiratory-related deaths were nearly 150% greater in the depths of winter cold than at the height of summer warmth. Also, with respect to heat waves, the mortality impact of the notable heat wave of 29 July to 3 August 1995 was so tiny it could not be discerned among the random scatter of plots of three-year-average daily deaths from cardiovascular and respiratory problems versus day of year.

In a review article published in the *Southern Medical Journal*, Keatinge and Donaldson (2004) begin with a clear declaration of the relative dangers of heat and cold for human mortality, writing, “cold-related deaths are far more numerous than heat-related deaths in the United States, Europe, and almost all countries outside the tropics, and almost all of them are due to common illnesses that are increased by cold.”

Keatinge and Donaldson report coronary and cerebral thrombosis account for about half of all cold-related deaths, and respiratory diseases account for approximately half of the rest. They say cold stress causes an increase in arterial thrombosis “because the blood becomes more concentrated, and so more liable to clot during exposure to cold.” As they describe it, “the body’s first adjustment to cold stress is to shut down blood flow to the skin to conserve body heat,” which “produces an excess of blood in central parts of the body,” and to correct for this effect, “salt and water are moved out from the blood into tissue spaces,” leaving behind “increased levels of red cells, white cells, platelets and fibrinogen” that lead to increased viscosity of the blood and a greater risk of

clotting.

As to respiratory-related deaths, the British scientists report the infections that cause them spread more readily in cold weather because people “crowd together in poorly ventilated spaces when it is cold.” In addition, they say “breathing of cold air stimulates coughing and running of the nose, and this helps to spread respiratory viruses and bacteria.” The “train of events leading to respiratory deaths,” they continue, “often starts with a cold or some other minor infection of the upper airways,” which “spreads to the bronchi and to the lungs,” whereupon “secondary infection often follows and can lead to pneumonia.” They also note cold stress “tends to suppress immune responses to infections,” and respiratory infections typically “increase the plasma level of fibrinogen, and this contributes to the rise in arterial thrombosis in winter.”

Keatinge and Donaldson also note “cold spells are closely associated with sharp increases in mortality rates,” and “deaths continue for many days after a cold spell ends.” On the other hand, they report, “increased deaths during a few days of hot weather are followed by a lower than normal mortality rate,” because “many of those dying in the heat are already seriously ill and even without heat stress would have died within the next 2 or 3 weeks.”

With respect to the implications of global warming for human mortality, Keatinge and Donaldson state “since heat-related deaths are generally much fewer than cold-related deaths”—and, it should be noted, consist primarily of deaths that typically would have occurred shortly even without excess heat—“the overall effect of global warming on health can be expected to be a beneficial one.” They report, “the rise in temperature of 3.6°F expected over the next 50 years would increase heat-related deaths in Britain by about 2,000 but reduce cold-related deaths by about 20,000.”

Keatinge and Donaldson concluded, “even in climates as warm as southern Europe or North Carolina [USA], cold weather causes more deaths than hot weather.” They report “global warming will reduce this at first,” but “the improvement is not likely to continue without action to promote defenses against cold.” They report “people in regions with mild winters become careless about cold stress, protect themselves less effectively against cold, and generally have more winter deaths than people in colder regions,” noting “climatic warming therefore calls for action to control cold stress as well as heat stress,” and stating if appropriate precautions are taken, “rising temperatures could reduce overall

mortality rates.” Consequently, they conclude, “the overall effect of global warming on health can be expected to be a beneficial one.”

McGregor (2005) noted “anomalous cold stress can increase blood viscosity and blood pressure due to the activation of the sympathetic nervous system which accelerates the heart rate and increases vascular resistance (Collins *et al.*, 1985; Jehn *et al.*, 2002; Healy, 2003; Keatinge *et al.*, 1984; Mercer, 2003; Woodhouse *et al.*, 1993),” while further noting “anomalously cold winters may also increase other risk factors for heart disease such as blood clotting or fibrinogen concentration, red blood cell count per volume and plasma cholesterol.” He conducted an analysis to determine whether there was any association between the level of IHD mortality in three English counties (Hampshire, West Midlands, and West Yorkshire) and the winter-season North Atlantic Oscillation (NAO), which exerts a fundamental control on the nature of winter climate in Western Europe, focusing on the winters of 1974–1975 through 1998–1999.

McGregor found “generally below average monthly and all-winter IHD mortality is associated with strong positive values of the monthly or winter climate index which indicates the predominance of anomalously warm moist westerly flows of air over England associated with a positive phase of the NAO.” At the other extreme, he found “winters with elevated mortality levels ... have been shown to be clearly associated with a negative NAO phase and anomalously low temperatures,” adding “the occurrence of influenza ... helps elevate winter mortality above that of summer.”

Carder *et al.* (2005) used generalized linear Poisson regression models to investigate the relationship between outside air temperature and deaths due to all non-accident causes in the three largest cities of Scotland (Glasgow, Edinburgh, and Aberdeen) between January 1981 and December 2001. They observed “an overall increase in mortality as temperature decreases,” which “appears to be steeper at lower temperatures than at warmer temperatures,” while “there is little evidence of an increase in mortality at the hot end of the temperature range.” They also report “the observed relation between cold temperature and mortality was typically stronger among the elderly,” and “cold temperature effects on mortality persist with lag periods of beyond two weeks.” The seven scientists found, for temperatures below 11°C, a 1°C drop in the daytime mean temperature on any one day was associated with an increase in cardiovascular-caused mortality of

3.4% over the following month. At any season of the year a decline in air temperature in the major cities of Scotland leads to increases in deaths due to cardiovascular causes, whereas there is little or no such increase in mortality associated with heat waves.

Cagle and Hubbard (2005) examined the relationship between temperature and cardiac-related deaths in King County, Washington (USA) over the period 1980–2000 using Poisson regression analysis, based on information provided by the Washington State Department of Health on out-of-hospital deaths of all adults over the age of 54, plus historical meteorological data obtained from the National Climate Data Center for the Seattle-Tacoma International Airport. They determined there was an average of 2.86 cardiac-related deaths per day for all days when the maximum temperature fell within the broad range of 5–30°C. For days with maximum temperatures less than 5°C, the death rate rose by 15% to a mean value of 3.30, whereas on days with maximum temperatures greater than 30°C, death rates did not rise at all, actually dropping by 3% to a mean value of 2.78. In addition, “the observed association between temperature and death rate is not due to confounding by other meteorological variables,” and “temperature continues to be statistically significantly associated with death rate even at a 5-day time lag.”

Cagle and Hubbard describe a number of human haematological changes that occur upon exposure to cold, including a decrease in blood plasma volume (Bass and Henschel, 1956; Chen and Chien, 1977; Fregley, 1982; Collins *et al.*, 1985) that is accompanied by “a sympathetic nervous system reflex response to cold-induced stress (LeBlanc *et al.*, 1978; Collins *et al.*, 1985; LeBlanc, 1992)” and “an increase in packed cell volume due to increased numbers of red cells per unit volume (Keatinge *et al.*, 1984), increased platelet counts and platelet volume (Finkel and Cumming, 1965; Keatinge *et al.*, 1984), increased whole blood viscosity (Keatinge *et al.*, 1984), increased serum lipid levels (Keatinge *et al.*, 1984; Woodhouse *et al.*, 1993; Neild *et al.*, 1994), and increased plasma fibrinogen and factor VII clotting activity values (Keatinge *et al.*, 1984; Woodhouse *et al.*, 1994).” These haemodynamic and vasoconstrictive factors combine “to produce what Muller *et al.* (1994) refer to as ‘acute risk factors’ that may trigger a cardiac event.” Vasoconstriction and concomitant increases in central blood volume and systolic blood pressure, for example, “put additional workload on the heart which may lead to increased arrhythmias (Amsterdam *et al.*, 1987), decreased thresholds for angina and abnormal myocardial

contractions (De Lorenzo *et al.*, 1999), as well as increasing the risk of dislodging a vulnerable plaque which could lead to thrombosis (Muller *et al.*, 1994),” which “may occur through increased cardiac filling pressure and stroke volume which in turn increases cardiac oxygen requirements while lessening cardiac access to oxygen (Muza *et al.*, 1988; De Lorenzo *et al.*, 1999).” In addition, the Washington researchers report “greater blood viscosity also works to increase the load on the heart through greater resistance to flow (Frisancho, 1993) and increasing blood pressure (Keatinge *et al.*, 1984).”

Tam *et al.* (2009) employed daily mortality data for the years 1997 to 2002, obtained from the Hong Kong Census and Statistics Department, to examine the association between diurnal temperature range (DTR = daily maximum temperature minus daily minimum temperature) and cardiovascular disease among the elderly (people aged 65 and older). They report “a 1.7% increase in mortality for an increase of 1°C in DTR at lag days 0–3” and describe these results as being “similar to those reported in Shanghai.” The four researchers state “a large fluctuation in the daily temperature—even in a tropical city like Hong Kong—has a significant impact on cardiovascular mortality among the elderly population.” In addition, the DTR has declined significantly over many parts of the world as mean global temperature has risen over the past several decades (Easterling *et al.*, 1997), perhaps another reason why colder temperatures are a much greater risk to human life than are warmer temperatures.

Working in the nine urban districts of Shanghai, China, Cao *et al.* (2009) used time-series and case-crossover approaches to assess the relationship between DTR and coronary heart disease (CHD) deaths that occurred between 1 January 2001 and 31 December 2004, based on mortality data for elderly (66 years of age or older) people, obtained from the Shanghai Municipal Center of Disease Control and Prevention, and temperature data they obtained from a fixed-site station in the Xuhui District of Shanghai. They adjusted the data to account for the mortality impacts of long-term and seasonal trends in CHD mortality, day of week, temperature, relative humidity, and concomitant atmospheric concentrations of PM₁₀, SO₂, NO₂, and O₃, which they obtained from the Shanghai Environmental Monitoring Center. They found “a 1°C increase in DTR (lag = 2) corresponded to a 2.46% increase in CHD mortality on time-series analysis, a 3.21% increase on unidirectional case-crossover analysis, and a 2.13% increase on bidirectional case-crossover

analysis,” and “the estimated effects of DTR on CHD mortality were similar in the warm and cool seasons.” The seven scientists conclude their “data suggest that even a small increase in DTR is associated with a substantial increase in deaths due to CHD.”

Employing a generalized additive statistical model that blends the properties of generalized linear models with additive models, Bayentin *et al.* (2010) analyzed the standardized daily hospitalization rates for ischemic heart disease (IHD) and their relationship with climatic conditions up to two weeks prior to the day of admission—controlling for time trends, day of the season, and gender—to determine the short-term effects of climate conditions on the incidence of IHD over the 1989–2006 time period for 18 health regions of Quebec. The authors report, “a decline in the effects of meteorological variables on IHD daily admission rates was observed over the period of 1989–2006.” This observation, they write, “can partly be explained by the changes in surface air temperature,” which they describe as warming “over the last few decades,” as is further described by Bonsal *et al.* (2001) and Zhang *et al.* (2000) for the twentieth century portion of the study’s duration. In addition, they note, “winters have been steadily warmer” while “summers have yet to become hotter for most regions,” another beneficial characteristic of the warming experienced over most of the planet throughout the latter part of the twentieth century (Easterling *et al.*, 1997). The six scientists also report what they call their “counter-intuitive finding,” that “cold temperatures resulted in a protective effect for women except for most Northern regions.”

Toro *et al.* (2010) note “several studies have demonstrated that cardiovascular mortality has a seasonal distribution (Arntz *et al.*, 2000; Weerasinghe *et al.* 2002; Nakaji *et al.*, 2004; Kloner, 2006)” and “the relationship between cold weather and ischemic heart disease mortality is well established (Vuori, 1987; Gyllerup *et al.*, 1993; Gyllerup, 2000).” They state “cold temperature may be an important factor in bringing on the onset of life-threatening cardiac events, even in regions with relatively mild winters,” citing Cagle and Hubbard (2005).

Working with data on 7,450 cardiovascular-related deaths that occurred in Budapest, Hungary between 1995 and 2004, where the deceased were “medico-legally autopsied,” Toro *et al.* sought potential relationships between daily maximum, minimum, and mean temperature, air humidity, air pressure, wind speed, global radiation, and daily numbers of the heart-related deaths.

The six Hungarian scientists report and restate

their primary finding numerous times throughout their paper, writing, “both the maximum and the minimum daily temperatures tend to be lower when more death cases occur in a day,” “on the days with four or more death cases, the daily maximum and minimum temperatures tend to be lower than on days without any cardiovascular death events,” “the largest frequency of cardiovascular death cases was detected in cold and cooling weather conditions,” “we found a significant negative relationship between temperature and cardiovascular mortality,” “the analysis of 6-hour change of air pressure suggests that more acute or chronic vascular death cases occur during increasing air pressure conditions (implying cold weather fronts),” “we found a high frequency of cardiovascular death in cold weather,” “a significant negative relationship was detected between daily maximum [and] minimum temperature[s] and the number of sudden cardiovascular death cases,” and “a significant negative correlation was detected between daily mean temperature and cardiovascular mortality.” In a summary statement regarding their work, Toro *et al.* write, “with these analyses, we confirmed the results of other studies (Donaldson *et al.*, 1998; Gyllerup, 2000; Mercer, 2003) that mortality was in inverse relation to air temperature.”

Bhaskaran *et al.* (2010) explored the short-term relationship between ambient temperature and risk of heart attacks (myocardial infarction) in England and Wales by analyzing daily time series data from 15 metropolitan areas. The data covered 84,010 hospital admissions from 2003–2006. They found a broadly linear relationship between temperature and heart attacks that was well characterized by log-linear models without a temperature threshold, such that each 1°C reduction in daily mean temperature was associated with a 2.0% cumulative increase in risk of myocardial infarction over the current and following 28 days. They also report heat had no detrimental effect, as an increased risk of myocardial infarction at higher temperatures was not detected. They found adults aged 75–84 and those with previous coronary heart disease seemed more vulnerable to the effects of cold than other age groups (P for interaction 0.001 or less in each case), whereas those taking aspirin were less vulnerable (P for interaction 0.007).

Kysely *et al.* (2011) write, “in the Czech Republic, mortality associated with heat waves (Kysely, 2004; Kysely and Kriz, 2008) and cold spells (Kysely *et al.*, 2009) has been examined,” but they note, “previous studies were based on different definitions and approaches which did not allow for a comparative analysis.

Working with a nationwide database of daily mortality records that cover the 21-year period 1986–2006—which, in their words, “encompasses seasons with the hottest summers on record (1992, 1994, 2003) as well as several very cold winters (1986/87, 1995/96, 2005/06)” —Kysely *et al.* compared the effects of hot and cold periods on cardiovascular mortality using analogous definitions for heat waves and cold spells based on quantiles of daily average temperature anomalies and did not incorporate any location-specific threshold, while excluding periods characterized by epidemics of influenza and acute respiratory infections that occur primarily in winter and are also responsible for many deaths. The four Czech scientists report “both hot and cold spells are associated with significant excess cardiovascular mortality,” but “the effects of hot spells are more direct (unlagged) and typically concentrated in a few days of a hot spell, while cold spells are associated with indirect (lagged) mortality impacts persisting after a cold spell ends.” Although they report “the mortality peak is less pronounced for cold spells,” they determined “the cumulative magnitude of excess mortality is larger for cold than hot spells.”

With respect to gender differences, the researchers found a “much larger excess mortality of females in hot spells and more lagged effects in females than males associated with cold spells.” With respect to age, they report “effects of hot spells have a similar temporal pattern in all age groups but much larger magnitude in the elderly,” whereas in the case of cold spells, “relative excess mortality is largest in the middle-aged population (25–59 years).”

Kysely *et al.* (2011) conclude, “in the context of climate change, substantial reductions in cold-related mortality are very likely in mid-latitudinal regions, particularly if the increasing adaptability of societies to weather is taken into account (cf. Christidis *et al.*, 2010),” and “it is probable that reductions in cold-related mortality will be more important than possible increases in heat-related mortality.”

Lim *et al.* (2012) state, “with the increasing concern directed at climate change, temperature-related environment variables have been studied as risk factors for cardiovascular and respiratory diseases, especially in European, Australian, and US cities,” noting “in addition to heat or cold waves, diurnal temperature range (DTR) has been suggested as a predictor of mortality (Curriero *et al.*, 2002) and was, in fact, found to be a risk factor for human health.” Focusing on the four largest cities of Korea—the populations of which ranged from 2.5 to 9.8 million (Seoul, Incheon, Daegu, and Busan)—

Lim *et al.* obtained daily hospital admission information pertaining from the countrywide database of the Korea National Health Insurance Corporation, which covers 97% of Korea's population. They assessed the effects of increasing DTR on hospital admissions for the most common cardiovascular and respiratory diseases in those four cities for the period 2003–2006, employing two statistical approaches: “a Poisson generalized linear model (GLM) and a temperature-matched case-crossover (CC) design (Basu *et al.*, 2005).”

According to the three South Korean researchers, the data showed “the area-combined effects of DTR on cardiac failure and asthma were statistically significant,” and the DTR effects on asthma admissions were greater for the elderly (75 years or older) than for the non-elderly group. “In particular,” they write, “the effects on cardiac failure and asthma were significant with the percentage change of hospital admissions per 1°C increment of DTR at 3.0% and 1.1%, respectively.”

Because the global warming of the past several decades has been associated with a decrease in DTR (global warming is predominantly caused by an increase in daily minimum temperature), it likely has helped to significantly reduce hospital admissions for cardiac failure and asthma in the larger cities of Korea and around the world. Lim *et al.* note DTR effects on nonaccidental, cardiovascular, and respiratory mortality or emergency admissions have been studied in a number of Asian countries, citing Cao *et al.* (2009), Chen *et al.* (2007), Kan *et al.* (2007), Liang *et al.* (2008), Liang *et al.* (2009), Lim *et al.* (2012), Shinkawa *et al.* (1990), Song *et al.* (2008), and Tam *et al.* (2009). Each of these studies, Lim *et al.* note, “reported a 1 to 2% increase in mortality risk per 1°C increase of DTR.”

Wanitschek *et al.* (2013) note “previous studies reported an association of cold weather conditions with an excess incidence of acute coronary syndromes (ACS) according to hospital discharge reports (Eurowinter Group, 1997; Spencer *et al.*, 1998; Danet *et al.*, 1999; Kloner *et al.*, 1999; Dilaveris *et al.*, 2006).” However, they write, “whether these epidemiologic facts also translate into a significantly different rate of acute coronary angiographies between two consecutive winters characterized by a dramatic temperature increase is less clear.”

Noting the 2005/2006 winter was very cold, whereas the 2006/2007 winter was extraordinarily warm, Wanitschek *et al.* studied the cases of patients who were suffering acute myocardial infarctions and had been referred to the University Clinic of Internal

Medicine III (Cardiology) at Innsbruck Medical University, Tyrol, Austria, for coronary angiography (CA). They compared the patients' risk factors and in-hospital mortality rates between these two consecutive winters, the latter of which was 7.5°C warmer than the former. The two winters saw nearly identical CA cases (987 vs. 983). According to the six Austrian researchers, 12.9% of the CA cases in the colder winter were acute, while 10.4% of the cases in the warmer winter were acute. Diagnoses of STEMI (ST Elevation Myocardial Infarction) as an indication of acute CA were 74.1% in the colder winter 0 vs. 62.7% in the warmer. Wanitschek *et al.* conclude, “the average temperature increase of 7.5°C from the cold to the warm winter was associated with a decrease in acute coronary angiographies, in particular due to a lower incidence of STEMI referred for primary percutaneous intervention.”

Vasconcelos *et al.* (2013) studied the health-related effects of a daily human-biometeorological index known as the Physiologically Equivalent Temperature or PET, which is based on the input parameters of air temperature, humidity, mean radiant temperature, and wind speed, as employed by Burkart *et al.* (2011), Grigorieva and Matzarakis (2011), and Cohen *et al.* (2012), focusing their attention on Lisbon and Oporto Counties in Portugal over the period 2003–2007. The five Portuguese researchers report there was “a linear relationship between daily mean PET, during winter, and the risk of myocardial infarction, after adjustment for confounding factors,” thus confirming “the thermal environment, during winter, is inversely associated with acute myocardial infarction morbidity in Portugal.” They observed “an increase of 2.2% of daily hospitalizations per degree fall of PET, during winter, for all ages.” In Portugal and many other countries where low winter temperatures “are generally under-rated compared to high temperatures during summer periods,” Vasconcelos *et al.* conclude cold weather is “an important environmental hazard” that is much more deadly than the heat of summer.

These several studies clearly demonstrate global warming is beneficial to humanity, reducing the incidence of cardiovascular diseases related to low temperatures and wintry weather by a much greater degree than it increases the incidence of cardiovascular diseases associated with high temperatures and summer heat waves.

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Climate Change Reconsidered II: Biological Impacts

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7.3 Respiratory Disease

- The adverse health impacts of cold temperatures, especially with respect to respiratory health, are more significant than those of high temperatures in many parts of the world, including Spain, Canada,

Shanghai, and Taiwan. In the subtropical island of Taiwan, for example, researchers found low minimum temperatures were the strongest risk factor associated with outpatient visits for respiratory diseases.

According to IPCC, global warming will pose numerous challenges to human health, including the potential for an excess of deaths. This section examines the results of a number of studies conducted over the past decade or so that deal with this important subject as it applies to respiratory diseases. The studies show the excess death hypothesis from respiratory causes is 180 degrees out of phase with reality.

Hajat and Haines (2002) set out to determine whether the well-documented relationship between cold temperatures and respiratory mortality in the elderly extends to the number of visits by the elderly to general practitioners. They employed additive models to regress time-series of daily numbers of general practitioner consultations by the elderly against temperature. The consultation data they employed included visits to the doctor for asthma, lower respiratory diseases other than asthma, and upper respiratory diseases other than allergic rhinitis as obtained for registered patients aged 65 and older from several London practices between January 1992 and September 1995.

Hajat and Haines found the mean number of consultations was higher in cool-season months (October–March) than in warm-season months (April–September) for all respiratory diseases. At mean temperatures below 5°C, the relationship between respiratory disease consultations and temperature was linear, and stronger at a time lag of six to 15 days—a 1°C decrease in mean temperature below 5°C was associated with a 10.5% increase in all respiratory disease consultations.

Keatinge and Donaldson (2001) obtained similar results in their study of the effects of temperature on mortality in people over 50 years of age in the greater London area over the period 1976–1995. Simple plots of mortality rate versus daily air temperature revealed a linear increase in mortality as the air temperature fell from 15°C to near 0°C. Mortality rates at temperatures above 15°C, on the other hand, were, in their words, “grossly ailinear,” showing no trend. Low temperatures were shown to have a significant effect on both immediate (one day after the temperature perturbation) and long-term (up to 24 days after the temperature perturbation) mortality rates. Why are cold temperatures so deadly? Keatinge and

Donaldson say it is because “cold causes mortality mainly from arterial thrombosis and respiratory disease, attributable in turn to cold-induced hemo-concentration and hypertension and respiratory infections.”

Nafstad *et al.* (2001) studied the association between temperature and daily mortality in citizens of Oslo, Norway over the period 1990 to 1995. Because Norwegian law requires all deaths be examined by a physician, who diagnoses the cause of death and reports it on the death certificate, the authors were able to categorize and examine the effects of temperature on mortality specifically associated with respiratory diseases. The results showed the mean daily number of respiratory-related deaths was considerably higher in winter (October–March) than in summer (April–September). Winter deaths associated with respiratory diseases were 47% more numerous than summer deaths. Nafstad *et al.* conclude, “a milder climate would lead to a substantial reduction in average daily number of deaths.”

Braga *et al.* (2002) conducted a time-series analysis of both the acute and lagged influence of temperature and humidity on mortality rates in 12 U.S. cities, finding no clear evidence for a link between humidity and respiratory-related deaths. With respect to temperature, they found respiratory-related mortality increased in cities with more variable temperature. This phenomenon, they write, “suggests that increased temperature variability is the most relevant change in climate for the direct effects of weather on respiratory mortality.” This finding bodes well for a potentially warmer world, for Robeson (2002) has clearly demonstrated, based on a 50-year study of daily temperatures at more than 1,000 U.S. weather stations, that temperature variability declines with warming, and at a very substantial rate, so this aspect of a warmer world also would lead to a reduction in respiratory-related deaths.

Gouveia *et al.* (2003) extracted daily counts of deaths from all causes, except violent deaths and neonatal deaths (up to one month of age), from Sao Paulo, Brazil’s mortality information system for the period 1991–1994 and analyzed them for effects of temperature within three age groups: less than 15 years of age (children), 15–64 years old (adults), and more than 64 years old (elderly). This exercise revealed the change points (the temperatures above and below which temperature begins to impact mortality) for both heat- and cold-induced deaths were identical, at 20°C. For each 1°C increase above

this value for a given and prior day’s mean temperature, Gouveia *et al.* observed a 2.6% increase in deaths from all causes in children, a 1.5% increase in deaths from all causes in adults, and a 2.5% increase in deaths from all causes in the elderly. For each 1°C decrease below the 20°C change point, the cold effect was greater, with increases in deaths from all causes in children, adults, and the elderly registering 4.0%, 2.6%, and 5.5%, respectively. These cooling-induced death rates are 54%, 73%, and 120% greater than those due to warming.

Findings with respect to respiratory-induced deaths were similar. Death rates due to a 1°C cooling were twice as great as death rates due to a 1°C warming in adults, and 2.8 times greater in the elderly.

Nakaji *et al.* (2004) evaluated seasonal trends in deaths due to various diseases in Japan, using nationwide vital statistics from 1970 to 1999 and concurrent mean monthly air temperature data. They found the numbers of deaths due to diabetes, digestive diseases, cerebrovascular and heart diseases, infectious and parasitic diseases including tuberculosis, and respiratory diseases including pneumonia and influenza all rise to a maximum during the coldest time of the year. Hence, the team of nine scientists concludes, “to reduce the overall mortality rate and to prolong life expectancy in Japan, measures must be taken to reduce those mortality rates associated with seasonal differences.” Consequently, to achieve the scientists’ stated objectives, it is necessary to bring about a “reduction in exposure to cold environments,” as they put it.

Bartzokas *et al.* (2004) “examined the relationship between hospital admissions for cardiovascular (cardiac in general including heart attacks) and/or respiratory diseases (asthma etc.) in a major hospital in Athens [Greece] and meteorological parameters for an 8-year period.” Over the whole year, they found, “there was a dependence of admissions on temperature,” and low temperatures were “responsible for a higher number of admissions.” Specifically, “there was a decrease of cardiovascular or/and respiratory events from low to high values [of temperature], except for the highest temperature class in which a slight increase was recorded.”

Kovats *et al.* (2004) studied patterns of temperature-related hospital admissions and deaths in Greater London during the mid-1990s. For the three-year period 1994–1996, they found respiratory-related deaths were nearly 150% greater in the depth of winter cold than at the height of summer

warmth. They also found the mortality impact of the heat wave of 29 July to 3 August 1995 (which boosted daily mortality by just over 10%) was so tiny it could not be discerned among the random scatter of plots of three-year-average daily deaths from cardiovascular and respiratory problems versus day of year. Similarly, in a study of temperature effects on mortality in three English counties (Hampshire, West Midlands, and West Yorkshire), McGregor (2005) found “the occurrence of influenza ... helps elevate winter mortality above that of summer.”

Carder *et al.* (2005) used generalized linear Poisson regression models to investigate the relationship between outside air temperature and deaths due to all non-accident causes in the three largest cities of Scotland (Glasgow, Edinburgh, and Aberdeen) between January 1981 and December 2001. The authors observed “an overall increase in mortality as temperature decreases,” which “appears to be steeper at lower temperatures than at warmer temperatures,” and “there is little evidence of an increase in mortality at the hot end of the temperature range.” They also state “the observed relation between cold temperature and mortality was typically stronger among the elderly,” and “cold temperature effects on mortality persist with lag periods of beyond two weeks.” Specifically, “for temperatures below 11°C, a 1°C drop in the daytime mean temperature on any one day was associated with an increase in respiratory mortality of 4.8% over the following month.”

Noting “in temperate regions, respiratory disease adds greatly to the workload in general practice facilities and hospitals during the winter,” partly because of increases in cases of “bronchiolitis in young children caused by infection with respiratory syncytial virus (RSV),” Donaldson (2006) studied the effect of annual mean daily air temperature on the length of the yearly RSV season. He used weekly data on laboratory reports of RSV isolation by the Health Protection Agency and National Health Service hospital laboratories in England and Wales for 1981–2004, along with meteorological data from four surface stations (Ringway, Squires Gate, Malvern, and Rothamsted) that “are representative of a roughly triangular area of the United Kingdom enclosed by Preston, London, and Bristol.”

Reporting “climate change may be shortening the RSV season,” Donaldson found “the seasons associated with laboratory isolation of respiratory syncytial virus (for 1981–2004) and RSV-related emergency department admissions (for 1990–2004) ended 3.1 and 2.5 weeks earlier, respectively, per 1°C

increase in annual central England temperature ($P = 0.002$ and 0.043 , respectively).” Consequently, since “no relationship was observed between the start of each season and temperature,” he reports, “the RSV season has become shorter.” He concludes, “these findings imply a health benefit of global warming in England and Wales associated with a reduction in the duration of the RSV season and its consequent impact on the health service.”

According to Frei and Gassner (2008), from 1926 to 1991, hay fever prevalence in Switzerland rose from just under 1% of the country’s population to just over 14%, but from 1991 to 2000 it simply fluctuated about a mean value on the order of 15%. In addition, the authors write, “several studies show that no further increase in asthma, hay fever and atopic sensitization in adolescents and adults has been observed during the 1990s and the beginning of the new century,” citing Braun-Fahrlander *et al.* (2004) and Grize *et al.* (2006). To see what effect changes in pollen production might have had on this trend in respiratory ailments, Frei and Gassner analyzed daily average concentrations of birch and grass pollen monitored by the country’s National Pollen Network at Basel for the period 1969–2007, at Locarno for 1989–2007, and at Zurich for 1982–2007.

The two researchers report “the pollen exposure has been decreasing in Basel since the beginning of the 1990s,” and “in Locarno, most of the pollen species also show a decreasing trend,” while in Zurich, “most of the pollen types have been increasing,” although “some of the pollen counts of this station (grass, stinging nettle, mugwort and ragweed) have been decreasing in the period 1982–2007.” In addition, they state the length of the pollen season has recently tended “to get shorter.”

Frei and Gassner write, “parallel to the increasing hay fever rate, the pollen amounts of birch and grass were increasing from 1969 to 1990,” but “subsequently, the pollen of these plant species decreased from 1991 to 2007.” They say this finding “is more or less consistent with the changes of the hay fever rate that no longer increased during this period and even showed a tendency to decrease slightly.” Nearly identical findings were presented a year later (Frei, 2009). Although some have claimed rising temperatures and CO₂ concentrations will lead to more pollen and more hay fever (Wayne *et al.*, 2002), the analyses of Frei (2009) and Frei and Gassner (2008) suggest that is not true of Switzerland.

Jato *et al.* (2009) collected airborne samples of Poaceae pollen “using Hirst-type volumetric traps” in four cities in Galicia (Northwest Spain)—Lugo,

Santiago, Vigo, and Ourense—noting “the global climate change recorded over recent years may prompt changes in the atmospheric pollen season (APS). The subjected the data “to Spearman’s correlation test and regression models, in order to detect possible correlations between different parameters and trends.” They calculated the APS “using ten different methods, in order to assess the influence of each on survey results.” The Poaceae family (composed chiefly of herbaceous grasses), Jato *et al.* write, “is the most diverse and prolific herbaceous plant family in urban areas,” and “its pollen is considered a major aeroallergen, causing symptoms in over 80% of pollen allergy sufferers in Europe (D’Amato *et al.*, 2007).”

The four researchers report “all four cities displayed a trend towards lower annual total Poaceae pollen counts, lower peak values and a smaller number of days on which counts exceeded 30, 50 and 100 pollen grains/m³.” The percentage decline in annual pollen grain counts between 1993 and 2007 in Lugo was approximately 75%, and in Santiago the decline was 80%, as best as can be determined from the graphs of the researchers’ data. In addition, they write, “the survey noted a trend towards delayed onset and shorter duration of the APS.” Thus, even though there was a “significant trend towards increasing temperatures over the months prior to the onset of the pollen season,” according the Spanish scientists, Poaceae pollen became far less of a negative respiratory health factor in the four Galician cities over the decade and a half of their study.

Miller *et al.* (2012) say “there is concern that climate change may affect hay fever and other allergic conditions by impacting pollen amount, pollen allergenicity, pollen season, and plant and pollen distribution,” because “allergy and atopic disease rates are rising, and global warming has been implicated as a possible cause.” They note, “concomitant with climate change over the time course of many of these studies are changes in air pollution levels, economic factors, and lifestyle,” and they conducted a study to clarify the situation by separating these potentially confounding factors.

Miller *et al.* extracted annual prevalence data for frequent otitis media (defined as three or more ear infections per year), respiratory allergy, and non-respiratory seizures in children from the U.S. National Health Interview Survey for 1998 to 2006. They also obtained average annual temperatures for the same period from the U.S. Environmental Protection Agency. They performed “complex samples logistic regression analyses” to identify possible correlations

between annual temperature and each of the three disease conditions, while controlling for age and sex.

The three researchers—from the David Geffen School of Medicine at the University of California at Los Angeles, Harvard Medical School, and Brigham and Women’s Hospital in Boston—report the regression analysis found “annual temperature did not influence the prevalence of frequent otitis media,” “annual temperature did not influence prevalence of respiratory allergy,” and “annual temperature and sex did not influence seizure prevalence.” Miller *et al.* conclude their findings “may demonstrate that average temperature is not likely to be the dominant cause of the increase in allergy burden or that larger changes in temperatures over a longer period are needed to observe this association.” They conclude, “in the absence of more dramatic annual temperature changes, we do not expect prevalence of otitis media to change significantly as global warming may continue to affect our environment.”

Xu *et al.* (2013) state “childhood asthma is a major global health issue, affecting more than 300 million people worldwide (Baena-Cagnani and Badellino, 2011),” and it “is regarded as a national health priority in several countries,” citing Asher *et al.* (1995, 2006). They studied the relationship between diurnal temperature range (DTR) and the incidence of childhood asthma in Brisbane, Australia. For the study, “a Poisson generalized linear model combined with a distributed lag non-linear model was used to examine the relationship between DTR and emergency department admissions for childhood asthma in Brisbane from January 1st 2003 to December 31st 2009,” and daily maximum and minimum temperatures in Brisbane for the same time period were retrieved from the Australian Bureau of Meteorology. Each day’s DTR was calculated as the difference between its maximum and minimum temperatures.

The six scientists report “childhood asthma increased above a DTR of 10°C” and “was the greatest for lag 0–9 days, with a 31% increase in [hospital] emergency department admissions per 5°C increment of DTR,” further noting, “male children and children aged 5–9 years appeared to be more vulnerable to the DTR effect than others.” Since daily minimum temperatures have nearly always risen faster than have daily maximum temperatures in most locations around the globe whenever various regions have warmed, the study’s results indicate the decrease in DTR under global warming should lead to a decline in the number of cases of childhood asthma.

Ge *et al.* (2013) also investigated respiratory

health and DTR. They write, “respiratory tract infection (RTI) is among the most common acute diseases worldwide, leading to considerable morbidity, complications, and days lost from work and school,” citing Mourtzoukou and Falagas (2007). They report the DTR “has been identified as an independent risk factor for coronary heart disease (Cao *et al.*, 2009; Tam *et al.*, 2009), stroke (Shinkawa *et al.*, 1990; Kyobutungi *et al.*, 2005; Chen *et al.*, 2007), and chronic obstructive pulmonary disease (Song *et al.*, 2008).”

The researchers collected numbers of daily emergency-room visits for RTI at one of the largest medical establishments in Shanghai, China (Huashan Hospital) between 1 January 2008 and 30 June 2009, along with DTR data and data pertaining to possible confounding air pollutants (PM₁₀, SO₂, and NO₂). After making appropriate statistical analyses, the scientists determined increasing DTRs were closely associated with daily emergency-room visits for RTIs, such that “an increase of 1°C in the current-day and in the 2-day moving average DTR corresponded to a 0.94% and 2.08% increase in emergency-room visits for RTI, respectively.”

Lin *et al.* (2013) state “high temperatures have garnered considerable attention in Europe and the U.S. because of their short-term adverse health impacts.” However, they add, several studies have reported “the adverse health effects of cold temperatures may be more significant than those of high temperatures in Spain, Canada, Shanghai and Taiwan (Gomez-Acebo *et al.*, 2010; Lin *et al.*, 2011; Ma *et al.*, 2011; Martin *et al.*, 2012; Wang *et al.*, 2012),” and “mortality risk associated with low temperatures is likely underestimated when studies fail to address the prolonged effect of low temperature (Martin *et al.*, 2012; Mercer, 2003).” Working with data on daily area-specific deaths from all causes, circulatory diseases, and respiratory diseases, Lin *et al.* developed relationships between each of these cause-of-death categories and a number of cold-temperature related parameters for 2000–2008.

The five researchers discovered “mortality from [1] all causes and [2] circulatory diseases and [3] outpatient visits of respiratory diseases has a strong association with cold temperatures in the subtropical island, Taiwan.” In addition, they found “minimum temperature estimated the strongest risk associated with outpatient visits of respiratory diseases.”

The several studies described above clearly indicate a warmer world would be a much better world, especially with respect to the respiratory health of the world’s citizens.

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Climate Change Reconsidered II: Biological Impacts

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7.4 Stroke Occurrence

According to IPCC, global warming will pose numerous challenges to human health, including the potential for an excess of deaths. This section examines the results of a number of studies conducted over the past decade or so that deal with this subject as it applies to strokes.

Feigin *et al.* (2000) conducted what they call “the first truly population-based study on the relationship between stroke occurrence and weather parameters in Russia,” working within the city of Novosibirsk, Siberia, which has one of the highest stroke incidence rates in the world. Based on analyses of 2,208 patients with sex and age distributions similar to those of Russia as a whole, they found a statistically significant association between stroke occurrence and low ambient temperature over the period 1982–1993. In the case of ischemic stroke (IS), which accounted for 87% of all stroke types, they determined “the risk of IS occurrence on days with low ambient temperature [was] 32% higher than that on days with high ambient temperature.” Given what they describe as “the highly significant association observed between low ambient temperature ($< -2.0^{\circ}\text{C}$) and IS occurrence ($P = 0.02$), together with the proportion of days with such temperature in the region during a calendar year (41.3%),” they conclude the “very high stroke incidence in Novosibirsk, Russia may partially be explained by the highly prevalent cold factor there.” They suggest the implementation of “preventive measures in [the] region, such as avoiding low temperature.”

Hong *et al.* (2003) investigated the association

between the onset of ischemic stroke and prior episodic decreases in temperature in 545 patients who suffered strokes in Incheon, Korea from January 1998 to December 2000. They report “decreased ambient temperature was associated with risk of acute ischemic stroke,” with the strongest effect being seen on the day after exposure to cold weather, further noting “even a moderate decrease in temperature can increase the risk of ischemic stroke.” They also found “risk estimates associated with decreased temperature were greater in winter than in the summer,” which suggests “low temperatures as well as temperature changes are associated with the onset of ischemic stroke.” Finally, they explain the reason for the 24- to 48-hour lag between exposure to cold and the onset of stroke “might be that it takes some time for the decreasing temperature to affect blood viscosity or coagulation,” which is also suggested by the work of Keatinge *et al.* (1984), who found blood viscosity and the plasma fraction of platelets began to increase one hour after cold exposure and did not reach a peak until sometime beyond six hours later.

Nakaji *et al.* (2004) evaluated seasonal trends in deaths due to various diseases in Japan using nationwide vital statistics from 1970 to 1999 together with mean monthly temperature data. They note Japan has “bitterly cold winters,” and their analysis indicates the number of deaths due to cerebrovascular disease rises to a maximum during that cold time of year. They found the peak mortality rate due to stroke was two times greater in winter (January) than at the time of its yearly minimum (August and September). The team of nine scientists say it is necessary to bring about a “reduction in exposure to cold environments,” as they put it.

Chang *et al.* (2004) analyzed data from the World Health Organization (WHO) Collaborative Study of Cardiovascular Disease and Steroid Hormone Contraception (WHO, 1995) to determine the effects of monthly mean temperature on rates of hospitalization for arterial stroke and acute myocardial infarction among women aged 15–49 from 17 countries in Africa, Asia, Europe, Latin America, and the Caribbean. Among these women, a 5°C reduction in mean air temperature was associated with a 7% increase in the expected hospitalization rate due to stroke, and this effect was relatively acute, within a period of about a month, the scientists write.

Each spring, Asian dust storm (ADS) events originating in the deserts of Mongolia and China transport great quantities of fine particulate matter of $10\mu\text{m}$ diameter (PM_{10}) to populated cities of East Asia, including Taipei, Taiwan, where the tiny

particles have the potential to affect people's lives in a very big way. In an attempt to assess one aspect of this phenomenon, Yang *et al.* (2005) identified 54 ADS events that affected Taipei from 1996 to 2001, and they evaluated the impacts of these events on hospital admissions for primary intracerebral hemorrhagic stroke (PIH), ischemic stroke (IS), as well as the conglomerate of strokes of all types. The scientists found associations between dust storms and total stroke admissions and PIH and IS admissions were prominent three days after ADS events, with the relative risk for total stroke admissions being 1.05, that for IS admissions being 1.04, and that for PIH admissions being 1.15, with the latter finding being deemed statistically significant. For this particular stroke category, they additionally determined risk of stroke rose by 2.67% for each 10 $\mu\text{g}/\text{m}^3$ increase in PM_{10} concentration above the normal mean value of 55.43 $\mu\text{g}/\text{m}^3$.

With respect to how the ongoing rise in the air's CO_2 content might impact this phenomenon, Chapter 1 of this volume discusses the well-documented increase in plant water use efficiency that results from increases in atmospheric CO_2 concentration. This benefit should allow more plants to grow in the arid source regions of the Asian dust clouds, which will help to stabilize the soil and decrease its susceptibility to wind erosion, thereby reducing the severity of ADS events. Second, the propensity for elevated CO_2 concentrations to increase moisture contents of soils beneath plant canopies as a consequence of CO_2 -induced reductions in plant transpiration also should lead to greater ground cover and reduced wind erosion. Third, the ability of extra CO_2 in the atmosphere to enhance the growth of cryptobiotic soil crusts should stabilize the surface of the soil. And fourth, as noted by Zavaleta *et al.* (2003), global warming itself may increase soil moisture contents in water-limited regions by hastening plant senescence and thereby reducing the period of time over which transpiration-driven soil water losses occur.

If the air's CO_2 content continues to rise, even in the face of further warming, there should be a gradual reduction in the number of PM_{10} -induced strokes in the populace of Taipei, Taiwan, as well as in other places affected by Asian and other dust storms.

Gill *et al.* (2012) write, "in the past two decades, several studies reported that meteorologic changes are associated with monthly and seasonal spikes in the incidence of aneurysmal subarachnoid hemorrhage (aSAH)," and "analysis of data from large regional databases in both hemispheres has revealed increased seasonal risk for aSAH in the fall, winter and spring,"

citing Chyatte *et al.* (1994), Lejeune *et al.* (1994), Langmayr *et al.* (1995), Feigin *et al.* (2001), Abe *et al.* (2008), and Beseoglu *et al.* (2008). Gill *et al.* identified the medical records of 1,175 patients at the Johns Hopkins Hospital in Baltimore, Maryland (USA) who were admitted with a radiologically confirmed diagnosis of aSAH between 1 January 1991 and 1 March 2009. The researchers employed Poisson regression "to model the risk of a patient presenting with aSAH based on maximum ambient temperature (MAT), average relative humidity (ARH), and atmospheric pressure, clustering by season of the year to control for the previously reported relationship between season and aSAH presentation."

The six scientists report both "a one-day decrease in temperature and colder daily temperatures were associated with an increased risk of incident aSAH," and "these variables appeared to act synergistically" and were "particularly predominant in the fall, when the transition from warmer to colder temperatures occurred." Gill *et al.* add their study "is the first to report a direct relationship between a temperature decrease and an increased risk of aSAH," and "it also confirms the observations of several reports of an increased risk of aSAH in cold weather or winter," citing Lejeune *et al.* (1994), Jakovljevic *et al.* (1996), and Nyquist *et al.* (2001).

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7.5 Malaria

- A vast body of scientific examination and research contradict the claim that malaria will expand across the globe and intensify as a result of CO₂-induced warming.

According to IPCC, “‘If climate change continues as projected in scenarios in the next few decades, the major increases of ill-health compared to no climate change will occur through ...increased risks of food- and water-borne diseases and vector-borne infections. [*high confidence*]” (*IPCC-II, 2013*). Chapter 11, Human Health, Working Group II, *IPCC Fifth Assessment Report*, dated March 28, 2013, p. 3, italics in original, bold removed). This section investigates the reliability of IPCC’s claim with respect to malaria.. According to the results of a vast body of scientific examination and research on this topic, there is little support for IPCC’s claims. The next two sections will address the related claims regarding dengue fever and tick-borne diseases.

In a research report in *Science*, Rogers and Randolph (2000) note “predictions of global climate change have stimulated forecasts that vector-borne diseases will spread into regions that are at present too cool for their persistence.” There are, however, several problems with this scenario.

According to Reiter (2000), claims that malaria resurgence is the product of CO₂-induced global warming ignore other important factors and disregard known facts. A historical analysis of malaria trends, for example, reveals this disease was an important cause of illness and death in England during a period of colder-than-present temperatures throughout the Little Ice Age. Its transmission began to decline only in the nineteenth century, during a warming phase, when, according to Reiter, “temperatures were already much higher than in the Little Ice Age.” In short, malaria was prevalent in Europe during some of

the coldest centuries of the past millennium, and it has only recently undergone widespread decline, when temperatures have been warming. Clearly, there are other factors at work that are more important than temperature. Such factors include the quality of public health services, irrigation and agricultural activities, land use practices, civil strife, natural disasters, ecological change, population change, use of insecticides, and the movement of people (Reiter, 2000; Reiter, 2001; Hay *et al.*, 2002).

Nevertheless, concerns have lingered about the possibility of widespread future increases in malaria due to global warming. These concerns are generally rooted in climate models that typically use only one, or at most two, climate variables in making their predictions of the future distribution of the disease over Earth, and they generally do not include any of the non-climatic factors listed in the preceding paragraph. When more variables are included, a less-worrisome future is projected. In one modeling study, for example, Rogers and Randolph (2000) employed five climate variables and obtained very different results. Briefly, they used the present-day distribution of malaria to determine the specific climatic constraints that best define that distribution, after which the multivariate relationship they derived from this exercise was applied to future climate scenarios derived from state-of-the-art climate models, in order to map potential future geographical distributions of the disease.

Their study revealed very little change: a 0.84% increase in potential malaria exposure under the “medium-high” scenario of global warming and a 0.92% decrease under the “high” scenario. Rogers and Randolph explicitly state their quantitative model “contradicts prevailing forecasts of global malaria expansion” and “highlights the use of multivariate rather than univariate constraints in such applications.”

Hay *et al.* (2002) investigated long-term trends in meteorological data at four East African highland sites that experienced significant increases in malaria cases over the past couple of decades, reporting “temperature, rainfall, vapour pressure and the number of months suitable for *P. falciparum* transmission have not changed significantly during the past century or during the period of reported malaria resurgence.” Thus these factors could not be responsible for the observed increases in malaria cases. Likewise, Shanks *et al.* (2000) examined trends in temperature, precipitation, and malaria rates in western Kenya over the period 1965–1997, finding no linkages among the variables.

Small *et al.* (2003) examined trends in a climate-driven model of malaria transmission between 1911 and 1995, using a spatially and temporally extensive gridded climate dataset to identify locations in Africa where the malaria transmission climate suitability index had changed significantly over this time interval. After determining areas of change, they more closely examined the underlying climate forcing of malaria transmission suitability for those localities. They found malaria transmission suitability did indeed increase because of climate change in specific locations of limited extent, but in Southern Mozambique, the only region for which climatic suitability consistently increased, the cause of the increase was increased precipitation, not temperature. Small *et al.* state, “climate warming, expressed as a systematic temperature increase over the 85-year period, does not appear to be responsible for an increase in malaria suitability over any region in Africa.” They conclude “research on the links between climate change and the recent resurgence of malaria across Africa would be best served through refinements in maps and models of precipitation patterns and through closer examination of the role of nonclimatic influences,” the great significance of which also has been demonstrated by Reiter *et al.* (2003) for dengue fever, another important mosquito-borne disease.

Zhou *et al.* (2004) employed a nonlinear mixed-regression model study that focused on the numbers of monthly malaria outpatients of the past 10–20 years in seven East African highland sites and their relationships to the numbers of malaria outpatients during the previous time period, seasonality, and climate variability. They state, “for all seven study sites, we found highly significant nonlinear, synergistic effects of the interaction between rainfall and temperature on malaria incidence, indicating that the use of either temperature or rainfall alone is not sensitive enough for the detection of anomalies that are associated with malaria epidemics.” Githeko and Ndegwa (2001), Shanks *et al.* (2002), and Hay *et al.* (2002) reached the same conclusion. In addition, climate variability—not just temperature or not just warming—contributed less than 20% of the temporal variance in the number of malaria outpatients, and at only two out of the seven sites studied.

Zhou *et al.* conclude “malaria dynamics are largely driven by autoregression and/or seasonality in these sites,” and “the observed large among-site variation in the sensitivity to climate fluctuations may be governed by complex interactions between climate and biological and social factors.” The latter include

“land use, topography, *P. falciparum* genotypes, malaria vector species composition, availability of vector control and healthcare programs, drug resistance, and other socioeconomic factors,” including “failure to seek treatment or delayed treatment of malaria patients, and HIV infections in the human population,” which they say have “become increasingly prevalent.”

In a major review of the potential impacts of global warming on vector-borne diseases, Rogers and Randolph (2006) focus on recent upsurges of malaria in Africa, asking, “Has climate change already had an impact?” They demonstrate “evidence for increasing malaria in many parts of Africa is overwhelming, but the more likely causes for most of these changes to date include land-cover and land-use changes and, most importantly, drug resistance rather than any effect of climate,” noting “the recrudescence of malaria in the tea estates near Kericho, Kenya, in East Africa, where temperature has not changed significantly, shows all the signs of a disease that has escaped drug control following the evolution of chloroquine resistance by the malarial parasite.”

They explain, “malaria waxes and wanes to the beat of two rhythms: an annual one dominated by local, seasonal weather conditions and a *ca.* 3-yearly one dominated by herd immunity,” noting “effective drugs suppress both cycles before they can be expressed,” but “this produces a population which is mainly or entirely dependent on drug effectiveness, and which suffers the consequence of eventual drug failure, during which the rhythms reestablish themselves, as they appear to have done in Kericho.”

Two more review papers on the subject followed two years later. In the first, Zell *et al.* (2008) write, “it is assumed that global warming is forced by the anthropogenic release of ‘greenhouse gases,’” and a further “consistent assumption” has been a consequent “increased exposure of humans to tropical pathogens and their vectors.” They also note “there is dissent about this hypothesis (Taubes, 1997; Reiter, 2001; Hay *et al.*, 2002; Reiter *et al.*, 2003; Randolph, 2004; Zell, 2004; Halstead, 2008),” and they explore it in more detail, examining the pertinent literature and describing “those mechanisms that have led to an increase of virus activity in recent years.”

Based on their review, the three German researchers report “only very few examples point toward global warming as a cause of excess viral activity.” Instead, they determined “coupled ocean/atmosphere circulations and continuous anthropogenic disturbances (increased populations of humans and domestic animals, socioeconomic

instability, armed conflicts, displaced populations, unbalanced ecosystems, dispersal of resistant pathogens etc.) appear to be the major drivers of disease variability,” and “global warming at best contributes.”

In the second 2008 paper (Reiter, 2008), Paul Reiter—who works with the Insects and Infectious Disease Unit of the Institut Pasteur in Paris, France—writes, “man-made climate change has become a defining moral and political issue of our age,” noting “speculations on its potential impact often focus on infectious diseases, and on malaria in particular,” and “predictions are common that in the coming decades, tens—even hundreds—of millions more cases will occur in regions where the disease is already present, and that the vectors and the pathogens will move to higher latitudes and altitudes,” infecting even more people.

In analyzing these claims, Reiter first discusses the mathematical models employed in this endeavor, after which he discusses common misconceptions and the nature of malaria in temperate regions. In the latter discussions he mentions such items as ecological change, new farm crops, new rearing practices, urbanization and mechanization, human living conditions, and medical care. Then, in a discussion of malaria in the tropics, he considers stable endemic malaria, unstable endemic malaria, birth rate, forest clearance, agriculture, movement of people, urbanization, insecticide resistance, resistance to drugs, degradation of the health infrastructure, and war and civil strife. He then treats three additional topics: Highland malaria in the tropics, Kenya Highlands, and New Guinea Highlands.

Reiter concludes, “simplistic reasoning on the future prevalence of malaria is ill-founded; malaria is not limited by climate in most temperate regions, nor in the tropics, and in nearly all cases, ‘new’ malaria at high altitudes is well below the maximum altitudinal limits for transmission.” He further states, “future changes in climate may alter the prevalence and incidence of the disease, but obsessive emphasis on ‘global warming’ as a dominant parameter is indefensible; the principal determinants are linked to ecological and societal change, politics and economics.” Reiter’s conclusions have been borne out in additional studies of the subject.

Jackson *et al.* (2010) say “malaria is one of the most devastating vector-borne parasitic diseases in the tropical and subtropical regions of the world,” noting it affects more than 100 countries. According to the World Health Organization, Africa carries the highest infection burden of any continent, with nearly

200 million cases reported in 2006, and the Centers for Disease Control and Prevention estimates between 700,000 and 2.7 million people each year die from the dreaded disease (Suh *et al.*, 2004). In addition, Jackson *et al.* report “the African region bears 90% of these estimated worldwide deaths,” and “three-quarters of all malaria related deaths are among African children,” citing Breman (2001). They opine, “malaria could be greatly affected by the influence of climate change,” such as global warming.

The five U.S. researchers linked reported malaria cases and deaths from the years 1996 to 2006, obtained from the World Malaria Report (2008) for 10 countries in western Africa (Benin, Burkina Faso, Cote d’Ivoire, Gambia, Ghana, Liberia, Mali, Senegal, Sierra Leone, and Togo) with corresponding climate data from the U.S. National Oceanic and Atmospheric Administration’s National Climatic Data Center. They searched for transitive relationships between the weather variables and malaria rates via spatial regression analysis and tests for correlation. Jackson *et al.* report their analyses showed “very little correlation exists between rates of malaria prevalence and climate indicators in western Africa.” This result, as they describe it, “contradicts the prevailing theory that climate and malaria prevalence are closely linked and also negates the idea that climate change will increase malaria transmission in the region.”

Stern *et al.* (2011) examined trends in temperature and malaria for the Highlands of East Africa, which span Rwanda, Burundi, and parts of Kenya, Tanzania, and Uganda, to resolve controversies over whether the area has warmed and malaria has become more prevalent. For temperature, the authors used three time series obtained from the Climatic Research Unit (CRU) for four locations. Temperature data for Kericho extend through 2009, but only through 2006 for the Highlands. For malaria, the researchers used a data set on malaria cases through May 2010 at a hospital in Kericho, Kenya, and data from more than 5,200 surveys on the prevalence of malaria through 2009 in the Highlands. They report temperature has increased significantly in the region, yet “malaria in Kericho and many other areas of East Africa has decreased during periods of unambiguous warming.” Their paper does not attempt an explanation for the divergence in these trends.

In a model-based study, Nkurunziza and Pilz (2011) employed Bayesian generalized additive models (GAMs) to assess the impact of an increase in temperature on malaria transmission in Burundi. Overall, the two researchers write, “the results of the GAMs show that an increase in the maximum

temperature will cause an increase in minimum temperature,” and “the increase in the latter will result in a decreasing maximum humidity, leading to a decrease in rainfall.” These results, the writers continue, “suggest that an increased temperature will result in a shortening of the life span of mosquitoes (due to decreasing humidity) and decrease in the capacity of larva production and maturation (due to decreasing rainfall).” Thus, “the increase in temperature will not result in an increased malaria transmission in Burundi,” which is “in good agreement with some previous works on the topic,” citing as examples WHO, WMO, UNEP (2003), Lieshout *et al.* (2004), and Thomas (2004). In a final statement on the matter, Nkurunziza and Pilz note that in regions with endemic malaria transmission, such as Burundi, “the increase in temperature may lead to unsuitable climate conditions for mosquitoes survival and, hence, probably to a decreasing malaria transmission.”

In another model-based study, Béguin *et al.* (2011) quantified the independent effects of climate and socioeconomic factors on the historical and projected future global distribution of malaria. The authors also provide estimates of the factors’ separate and combined contributions to the populations at risk of malaria. Specifically, they estimated populations at risk of malaria (PAR) based on climatic variables, population growth, and GDP per capita (GDP_{pc}). GDP_{pc} is an approximation for per-capita income (“income” for short) for 1990, 2010, and 2050, based on sensitivity analyses for the following three scenarios: (1) a worst-case scenario, in which income declines to 50% of its 2010 values by 2050; (2) a “growth reduction” scenario, in which income declines by 25% in 2030 and 50% in 2050, relative to the A1B scenario; and (3) a scenario in which income stays constant at 2010 values.

The PAR was derived from information on the presence or absence of *P. vivax* malaria in 1990 based on a logistic model for malaria presence that used three parameters: the mean temperature of the coldest month, the mean precipitation of the wettest month during the period 1961–1990, and the square root of income. Accordingly, the PAR does not directly reflect the health impacts of malaria. Secular technological change was ignored in this study. The results are presented in Table 7.5.1.

The authors observe, “under the A1B climate scenario, climate change has much weaker effects than GDP_{pc} increase on the geographic distribution of malaria.” This result is consistent with the few studies that have considered the impact of climate change and

Model type	Population at Risk 2030 [billions]	Population at Risk 2050 [billions]
Socioeconomic changes only (no climate change)	3.52	1.74
Socioeconomic and climatic changes (A1B scenario)	3.58 [3.55–3.60]	1.95 [1.93–1.96]
Socioeconomic changes and CC (slower growth scenario)	3.82 [3.39–3.84]	3.42 [3.28–3.45]
No growth scenario , only CC	4.61 [4.54–4.67]	5.20 [5.11–5.25]
Pessimistic growth scenario and CC	5.18 [5.07–5.30]	6.27 [6.19–6.32]

Table 7.5.1. Effects of Climate and Socioeconomic Factors on the Projected Future Global Distribution of Malaria.
From Béguin *et al.* (2011).

socioeconomic factors on malaria. (See, e.g., Tol and Dowlatabadi, 2001; Bosello *et al.*, 2006). With respect to malaria, therefore, climate change is a relatively minor factor compared to economic development.

Kuhn *et al.* (2003) state, “there has been much recent speculation that global warming may allow the reestablishment of malaria transmission in previously endemic areas such as Europe and the United States.” In particular, they note “the British Chief Medical Officer’s recent report [*Getting Ahead of the Curve: A Strategy for Combating Infectious Diseases (Including Other Aspects of Health Protection)*, Department of Health (2002), London] asserted that ‘by 2050 the climate of the UK may be such that indigenous malaria could become re-established.’” To investigate the robustness of this hypothesis, they analyzed the determinants of temporal trends in malaria deaths within England and Wales in 1840–1910.

With respect to temperature changes over the period of study, Kuhn *et al.* report “a 1°C increase or decrease was responsible for an increase in malaria deaths of 8.3% or a decrease of 6.5%, respectively,” which explains “the malaria epidemics in the ‘unusually hot summers’ of 1848 and 1859.” Nevertheless, the long-term near-linear temporal decline in malaria deaths over the period of study, the researchers write, “was probably driven by nonclimatic factors,” among which they identify increasing livestock populations (which tend to divert mosquito biting from humans), decreasing acreages of marsh wetlands (where mosquitoes breed), as well as “improved housing, better access to health care and

medication, and improved nutrition, sanitation, and hygiene.” They also note the number of secondary cases arising from each primary imported case “is currently minuscule,” as demonstrated by the absence of any secondary malaria cases in the UK since 1953.

Although simplistic model simulations may suggest the increase in temperature predicted for Britain by 2050 is likely to cause an 8–14% increase in the potential for malaria transmission, Kuhn *et al.* say “the projected increase in proportional risk is clearly insufficient to lead to the reestablishment of endemicity.” They note “the national health system ensures that imported malaria infections are detected and effectively treated and that gametocytes are cleared from the blood in less than a week.” For Britain, therefore, they conclude “a 15% rise in risk might have been important in the 19th century, but such a rise is now highly unlikely to lead to the reestablishment of indigenous malaria,” because “socioeconomic and agricultural changes” have greatly altered the cause-and-effect relationships of the past.

Hulden and Hulden (2009) analyzed malaria statistics collected in Finland from 1750 to 2008 via correlation analyses between malaria frequency per million people and all variables that have been used in similar studies throughout other parts of Europe, including temperature data, animal husbandry, consolidation of land by redistribution, and household size. They report “malaria was a common endemic disease in Finland in the 18th and 19th centuries and prevalent in the whole country” and “mortality during malaria epidemics usually varied between 0.85 and 3%.” Thereafter, however, they found “malaria

declined slowly in Finland without any deliberate counter-measures,” such that “the last epidemic in Helsinki occurred in 1902” and “during the 1930s malaria was close to extinction.” Over the entire period, “malaria frequency decreased from about 20,000–50,000 per 1,000,000 people to less than 1 per 1,000,000 people,” they report.

When malaria was still common in the country, they did find “high peaks in malaria followed high temperatures in June–July,” but overriding this within-year temperature response over the long term, “both highs and lows in malaria frequency [were] declining independently of temperature trends.” The two Finnish researchers conclude, “indigenous malaria in Finland faded out evenly in the whole country during 200 years with limited or no counter measures or medication,” making that situation “one of the very few opportunities where natural malaria dynamics can be studied in detail.” Their study indicates “malaria in Finland basically was a sociological disease and that malaria trends were strongly linked to changes in the human household size and housing standard.”

Childs *et al.* (2006) present a detailed analysis of malaria incidence in northern Thailand based on a quarter-century monthly time series (January 1977 through January 2002) of total malaria cases in the country’s 13 northern provinces. Over this time period, when IPCC claims the world warmed at a rate and to a level unprecedented over the prior one to two millennia, Childs *et al.* report there was an approximately constant rate of decline in total malaria incidence (from a mean monthly incidence in 1977 of 41.5 cases per hundred thousand people to 6.72 cases per hundred thousand people in 2001). This decrease was due primarily to a reduction in cases positive for *Plasmodium falciparum* (mean monthly incidence in 1977 and 2001 of 28.6 and 3.22 cases per 100,000 people, respectively) and secondarily to a reduction in cases positive for *P. vivax* (mean monthly incidence in 1977 and 2001 of 12.8 and 3.5 cases per 100,000 people, respectively). Consequently, noting “there has been a steady reduction through time of total malaria incidence in northern Thailand, with an average decline of 6.45% per year,” they say this result “reflects changing agronomic practices and patterns of immigration, as well as the success of interventions such as vector control programs, improved availability of treatment and changing drug policies.”

Haque *et al.* (2010) analyzed monthly malaria case data for the malaria endemic district of Chittagong Hill Tracts in Bangladesh from January 1989 to December 2008, looking for potential

relationships between malaria incidence and various climatic parameters (rainfall, temperature, humidity, sea surface temperature, and the El Niño-Southern Oscillation), as well as the normalized difference vegetation index (NDVI), a satellite-derived measure of surface vegetation greenness. The six scientists report, “after adjusting for potential mutual confounding between climatic factors there was no evidence for any association between the number of malaria cases and temperature, rainfall and humidity,” and “there was no evidence of an association between malaria cases and sea surface temperatures in the Bay of Bengal and NINO3.” Instead, they found “the best leading indicator of the number of malaria cases was NDVI at a lag of 0–3 months, and that NDVI was negatively associated with malaria cases,” such that “each 0.1 increase in monthly NDVI was associated with a 30.4% decrease in malaria cases.” Haque *et al.* write, “it seems counterintuitive that a low NDVI, an indicator of low vegetation greenness, is associated with increases in malaria cases,” since the primary vectors of the disease in Bangladesh are associated with forests. In light of this surprising result, they state their study “draws attention again to the complex nature of the relationship between malaria and climate,” which in the case of the highlands of Bangladesh appears to be nonexistent.

Paaijmans *et al.* (2012) state “the development rate of parasites and pathogens within vectors typically increases with temperature,” and, therefore, “transmission intensity is generally assumed to be higher under warmer conditions.” However, they note, “development is only one component of parasite/pathogen life history,” adding, “there has been little research exploring the temperature sensitivity of other traits that contribute to transmission intensity.”

Paaijmans *et al.* examined prior “standard assumptions” and explored the resulting implications “for our understanding of the effects of temperature on disease transmission” on the rodent malaria *Plasmodium yoelii* and the Asian malaria vector *Anopheles stephensi*. The three U.S. researchers found “vector competence (the maximum proportion of infectious mosquitoes, which implicitly includes parasite survival across the incubation period) tails off at higher temperatures, even though parasite development rate increases.” Moreover, “the standard measure of the parasite incubation period (i.e., time until the first mosquitoes within a cohort become infectious following an infected blood-meal) is incomplete because parasite development follows a cumulative distribution, which itself varies with

temperature.” Finally, “including these effects in a simple model dramatically alters estimates of transmission intensity and reduces the optimum temperature for transmission.” Paaijmans *et al.* conclude their results “challenge current understanding of the effects of temperature on malaria transmission dynamics,” and they note their findings imply “control at higher temperatures might be more feasible than currently predicted.” Therefore, in regard to “the possible effects of climate warming,” they conclude “increases in temperature need not simply lead to increases in transmission.”

Russell (2009), a professor in the Department of Medicine of the University of Sydney (Australia) and founding director of its Department of Medical Entomology, reports, “during the past 10 years, there has been increasing concern for health impacts of global warming in Australia, and continuing projections and predictions for increasing mosquito-borne disease as a result of climate change.” He writes, these claims “are relatively simplistic, and do not take adequate account of the current or historic situations of the vectors and pathogens, and the complex ecologies that might be involved.” Russell reviewed the consequences of these several inadequacies for malaria, dengue fever, the arboviral arthritides (Ross River and Barmah Forest viruses), and the arboviral encephalitides (Murray Valley encephalitis and Kunjin viruses) within the context of predictions of climate change modeled by Australia’s Commonwealth Scientific and Industrial Research Organisation (CSIRO) and the Intergovernmental Panel on Climate Change (IPCC).

The abstract of Russell’s paper begins with a question: “Will warming climate increase the risk or prevalence of mosquito-borne disease in Australia, as has been projected in a number of scientific publications and governmental reports?” His conclusion provides the answer: “there might be some increases in mosquito-borne disease in Australia with a warming climate, but with which mosquitoes and which pathogens, and where and when, cannot be easily discerned.” He concludes, “of itself, climate change as currently projected, is not likely to provide great cause for public health concern with mosquito-borne disease in Australia.”

Tuchman *et al.* (2003) took leaf litter from *Populus tremuloides* (Michaux) trees that had been grown out-of-doors in open-bottom root boxes located within open-top aboveground chambers maintained at atmospheric CO₂ concentrations of either 360 or 720 ppm for an entire growing season, incubated the leaf litter for 14 days in a nearby

stream, and fed the incubated litter to four species of detritivorous mosquito larvae to assess its effect on their development rates and survivorship. They report larval mortality was 2.2 times higher for *Aedes albopictus* (Skuse) mosquitoes that were fed leaf litter that had been produced in the high-CO₂ chambers than it was for those fed litter that had been produced in the ambient-air chambers. In addition, they found larval development rates of *Aedes triseriatus* (Say), *Aedes aegypti* (L.), and *Armigeres subalbatus* (Coquillett) were slowed by 78%, 25%, and 27%, respectively, when fed litter produced in the high-CO₂ as opposed to the ambient-CO₂ chambers, so mosquitoes of these species spent 20, 11, and 9 days longer in their respective larval stages when feeding on litter produced in the CO₂-enriched as compared to the ambient-CO₂ chambers. The researchers suggest “increases in lignin coupled with decreases in leaf nitrogen induced by elevated CO₂ and subsequent lower bacterial productivity [on the leaf litter in the water] were probably responsible for [the] decreases in survivorship and/or development rate of the four species of mosquitoes.”

Concerning the significance of these findings, Tuchman *et al.* write, “the indirect impacts of an elevated CO₂ atmosphere on mosquito larval survivorship and development time could potentially be great,” because longer larval development times could result in fewer cohorts of mosquitoes surviving to adulthood. With fewer mosquitoes, there should be lower levels of mosquito-borne diseases.

Zell (2004) states many people “assume a correlation between increasing disease incidence and global warming.” However, he concludes after studying the issue in considerable depth, “the factors responsible for the emergence/reemergence of vector-borne diseases are complex and mutually influence each other.” As an example of this complexity, he notes, “the incidence and spread of parasites and arboviruses are affected by insecticide and drug resistance, deforestation, irrigation systems and dams, changes in public health policy (decreased resources of surveillance, prevention and vector control), demographic changes (population growth, migration, urbanization), and societal changes (inadequate housing conditions, water deterioration, sewage, waste management).” Therefore, he continues, “it may be over-simplistic to attribute emergent/re-emergent diseases to climate change and sketch the menace of devastating epidemics in a warmer world.” Zell states, “variations in public health practices and lifestyle can easily outweigh changes in disease biology,” especially those that might be caused by

global warming.

Nabi and Qader (2009) considered the climatic conditions that impact the spread of malaria—temperature, rainfall, and humidity—and the host of pertinent nonclimatic factors that play important roles in its epidemiology: the presence or absence of mosquito control programs, the availability or non-availability of malaria-fighting drugs, changing resistances to drugs, the quality of vector control, changes in land use, the availability of good health services, human population growth, human migrations, international travel, and standard of living. The two researchers report “global warming alone will not be of a great significance in the upsurge of malaria unless it is accompanied by a deterioration in other parameters like public health facilities, resistance to anti-malarial drugs, decreased mosquito control measures,” etc. They say “no accurate prediction about malaria can truly be made,” because “it is very difficult to estimate what the other factors will be like in the future.” They do note, however, mosquito-borne diseases were a major public health problem in the United States from the 1600s to the mid-1900s, “with occasional epidemics.” By the middle of the twentieth century, however, “malaria disappeared from the country along with the other mosquito borne diseases like Dengue and Yellow fever,” and “this decline was attributed to overall improvements in living conditions and better public health measures.” These factors have kept these diseases at bay throughout the latter half of the twentieth century as well, even though that period included what climate alarmists describe as “unprecedented global warming.”

Nabi and Qader conclude “as public health workers, it would be more justifiable for us to exert our efforts on these other [non-climatic] parameters for the eradication and control of malaria.”

Gething *et al.* (2010) observe, based on “model predictions” it is “reported widely in global climate policy debates that climate change is adding to the present-day burden of malaria and will increase both the future range and intensity of the disease,” citing IPCC (2007) and the U.S. Environmental Protection Agency (2010). Noting “it has long been known that the range of malaria has contracted through a century of economic development and disease control (Hay *et al.*, 2009),” when “global temperature increases have been unequivocal,” Gething *et al.* explore this seeming incongruity by comparing “an evidence-based map of contemporary malaria endemicity (Hay *et al.*, 2009)” with “the most reliable equivalent for the pre-intervention era, around 1900 (Lysenko *et al.*,

1968),” when malaria was “at its assumed historical peak,” thereby providing a comparison of “the magnitude of observed changes in range and endemicity to those proposed to occur in response to climate change.”

The six scientists—from the Spatial Ecology and Epidemiology Group, the Malaria Public Health and Epidemiology Group, and the Centre for Tropical Medicine of the UK’s University of Oxford, plus the Departments of Biology and Geography and the Emerging Pathogens Institute of the United States’ University of Florida—report “comparison of the historical and contemporary maps revealed that endemic/stable malaria is likely to have covered 58% of the world’s land surface around 1900 but only 30% by 2007.” They report, “even more marked has been the decrease in prevalence within this greatly reduced range, with endemicity falling by one or more classes in over two-thirds of the current range of stable transmission.” They write, “widespread claims that rising mean temperatures have already led to increases in worldwide malaria morbidity and mortality are largely at odds with observed decreasing global trends in both its endemicity and geographic extent.” Rather, “the combined natural and anthropogenic forces acting on the disease throughout the twentieth century have resulted in the great majority of locations undergoing a net reduction in transmission between one and three orders of magnitude larger than the maximum future increases proposed under temperature-based climate change scenarios.”

Gething *et al.* conclude there has been “a decoupling of the geographical climate-malaria relationship over the twentieth century, indicating that non-climatic factors have profoundly confounded this relationship over time.” They note “non-climatic factors, primarily direct disease control and the indirect effects of a century of urbanization and economic development, although spatially and temporally variable, have exerted a substantially greater influence on the geographic extent and intensity of malaria worldwide during the twentieth century than have climatic factors.” As for the future, they conclude climate-induced effects “can be offset by moderate increases in coverage levels of currently available interventions.”

The many findings described above make it clear a vast body of scientific examination and research contradict the claim that malaria will expand across the globe and intensify as a result of CO₂-induced warming.

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Climate Change Reconsidered II: Biological Impacts

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7.6 Dengue Fever

- 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.

According to Ooi and Gubler (2009), “dengue/dengue hemorrhagic fever is the most important vector-borne viral disease globally,” with more than half the world’s population living in areas deemed to be at risk of infection. Also, they note, “many voices have raised concern that global warming is likely to increase the geographic distribution of the dengue mosquito vectors and the frequency and magnitude of dengue epidemics.” Such concerns, as evidenced by the papers discussed below, are ill-founded.

In a major review of mosquito-borne diseases by one of the world’s premier authorities on the subject, Reiter (2001) analyzed the history of malaria and dengue fever in an attempt to determine whether the incidence and range of influence of these diseases would indeed increase in response to CO₂-induced global warming. This review indicates the natural history of these vector-borne diseases is highly complex, and the interplay of climate, ecology, vector biology, and a number of other factors defies definition by the simplistic analyses utilized in models that generate predictions of future geographical changes in these diseases under various global warming scenarios.

That there has in fact been a resurgence of these diseases in parts of the world is true; but, as Reiter notes, it is “facile to attribute this resurgence to climate change.” This he shows via a number of independent analyses that clearly demonstrate factors associated with politics, economics, and human activity are the principal determinants of the spread of these diseases. He describes these factors as being “much more significant” than climate in promoting

disease expansion.

Two years later, Reiter took up the subject again, this time with 19 other scientists as coauthors (Reiter *et al.*, 2003). They began by noting “it has frequently been stated that dengue, malaria, and other mosquito-borne diseases will become common in the United States as a result of global warming (Watson *et al.*, 1996; Jetten and Focks, 1997; Patz *et al.*, 1998; Watson *et al.*, 1998).” The Intergovernmental Panel on Climate Change had played a key role in promoting this claim, but Reiter and his colleagues had acquired solid evidence to prove IPCC was simply wrong on this point.

In the summer of 1999, toward the end of a significant dengue outbreak in “los dos Laredos”—Laredo, Texas, USA (population 200,000) and Nuevo Laredo, Tamaulipas, Mexico (population 290,000)—the team of scientists conducted a seroepidemiologic survey to examine factors affecting dengue transmission in the two cities, located adjacent to each other on opposite sides of the Rio Grande and experience, according to the team, “massive cross-border traffic across three multi-lane bridges.” They report “the incidence of recent cases, indicated by immunoglobulin M antibody serosurvey, was higher in Nuevo Laredo [16.0% vs. 1.3%], although the vector, *Aedes aegypti*, was more abundant in Laredo [91% vs. 37%].” Reiter *et al.* determined “environmental factors that affect contact with mosquitoes, such as air-conditioning and human behavior, appear to account for this paradox.”

They found, for example, “the proportion of dengue infections attributable to lack of air-conditioning in Nuevo Laredo [where only 2% of the homes had central air-conditioning compared to 36% of the homes in Laredo] was 55%,” which means 55% of the cases of dengue in Nuevo Laredo would not have occurred if all households there had had air-conditioning. Reiter *et al.* conclude, therefore, “if the current warming trend in world climates continues, air-conditioning may become even more prevalent in the United States, in which case, the probability of dengue transmission [there] will likely decrease.” Likewise, if the economy of Mexico continues to grow, the use of air-conditioners likely will increase there as well, which likely would lead to even greater decreases in the occurrence of dengue fever in that country.

In a major review of the general subject of infectious diseases in a warming world, Roland Zell (2004) of the Institute for Virology and Antiviral Therapy at the Friedrich Schiller University in Jena, Germany, reviewed what was known about the

putative link some scientists were postulating—and a host of climate alarmists were championing—between global warming and the spread of infectious diseases. Noting many people “assume a correlation between increasing disease incidence and global warming,” he states that after studying the issue in considerable depth, he must conclude “the factors responsible for the emergence/reemergence of vector-borne diseases are complex and mutually influence each other.” He notes “the incidence and spread of parasites and arboviruses are affected by insecticide and drug resistance, deforestation, irrigation systems and dams, changes in public health policy (decreased resources of surveillance, prevention and vector control), demographic changes (population growth, migration, urbanization), and societal changes (inadequate housing conditions, water deterioration, sewage, waste management).” Therefore, he continues, “it may be over-simplistic to attribute emergent/re-emergent diseases to climate change and sketch the menace of devastating epidemics in a warmer world.” He reiterates “variations in public health practices and lifestyle can easily outweigh changes in disease biology.”

Kyle and Harris (2008) note “dengue is a spectrum of disease caused by four serotypes of the most prevalent arthropod-borne virus affecting humans today,” and “its incidence has increased dramatically in the past 50 years,” to where “tens of millions of cases of dengue fever are estimated to occur annually, including up to 500,000 cases of the life-threatening dengue hemorrhagic fever/dengue shock syndrome.” In an effort to better understand this increase, they conducted a thorough review of the pertinent scientific literature, exploring “the human, mosquito, and viral factors that contribute to the global spread and persistence of dengue, as well as the interaction between the three spheres, in the context of ecological and climate change.”

With respect to the status of dengue fever within the context of global warming, they found “there has been a great deal of debate on the implications of global warming for human health,” but “at the moment, there is no consensus.” However, “in the case of dengue,” they report, “it is important to note that even if global warming does not cause the mosquito vectors to expand their geographic range, there could still be a significant impact on transmission in endemic regions,” because “a 2°C increase in temperature would simultaneously lengthen the lifespan of the mosquito and shorten the extrinsic incubation period of the dengue virus, resulting in more infected mosquitoes for a longer

period of time.” Nevertheless, they state there are “infrastructure and socioeconomic differences that exist today and already prevent the transmission of vector-borne diseases, including dengue, even in the continued presence of their vectors,” citing Reiter (2001). It thus appears whatever advantages rising temperatures may confer upon the dengue virus vector, they can be more than overcome by proper implementation of modern vector control techniques.

In another review of the scientific literature, Wilder-Smith and Gubler (2008) note “the past two decades saw an unprecedented geographic expansion of dengue,” reporting “each year an estimated 50 to 100 million dengue infections occur, with several hundred thousand cases of dengue hemorrhagic fever and about twenty thousand deaths.” They too state, “global climate change is commonly blamed for the resurgence of dengue,” but they add, “there are no good scientific data to support this conclusion.” Wilder-Smith and Gubler reviewed what was known about the problem and pieced together a logical conclusion.

With respect to the occurrence of dengue infections, the two researchers report, “climate has rarely been the principal determinant of [their] prevalence or range,” and “human activities and their impact on local ecology have generally been much more significant.” They cite as contributing factors “urbanization, deforestation, new dams and irrigation systems, poor housing, sewage and waste management systems, and lack of reliable water systems that make it necessary to collect and store water,” further noting “disruption of vector control programs, be it for reasons of political and social unrest or scientific reservations about the safety of DDT, has contributed to the resurgence of dengue around the world.” In addition, they write “large populations in which viruses circulate may also allow more co-infection of mosquitoes and humans with more than one serotype of virus,” which would appear to be borne out by the fact that “the number of dengue lineages has been increasing roughly in parallel with the size of the human population over the last two centuries.” Most important, perhaps, is “the impact of international travel,” of which they say “humans, whether troops, migrant workers, tourists, business travelers, refugees, or others, carry the virus into new geographic areas,” and these movements “can lead to epidemic waves.” The two researchers conclude, “population dynamics and viral evolution offer the most parsimonious explanation for the observed epidemic cycles of the disease, far more than climatic factors.”

Russell (2009)—a professor in the Department of Medicine of the University of Sydney and founding director of its Department of Medical Entomology—reports, “during the past 10 years, there has been increasing concern for health impacts of global warming in Australia, and continuing projections and predictions for increasing mosquito-borne disease as a result of climate change.” He notes these claims “are relatively simplistic, and do not take adequate account of the current or historic situations of the vectors and pathogens, and the complex ecologies that might be involved.” He reviewed the consequences of these inadequacies for malaria, dengue fever, the arboviral arthritides (Ross River and Barmah Forest viruses) and the arboviral encephalitides (Murray Valley encephalitis and Kunjin viruses) within the context of predictions of climate changes modeled by Australia’s Commonwealth Scientific and Industrial Research Organisation (CSIRO) and the Intergovernmental Panel on Climate Change (IPCC).

The abstract of Russell’s paper begins with a question: “Will warming climate increase the risk or prevalence of mosquito-borne disease in Australia, as has been projected in a number of scientific publications and governmental reports?” His conclusion provides the answer: “there might be some increases in mosquito-borne disease in Australia with a warming climate, but with which mosquitoes and which pathogens, and where and when, cannot be easily discerned.” He concludes, “of itself, climate change as currently projected, is not likely to provide great cause for public health concern with mosquito-borne disease in Australia.”

Russell *et al.* (2009) report similar findings. The team of scientists note “dengue has emerged as a leading cause of morbidity in many parts of the tropics,” and “Australia has had dengue outbreaks in northern Queensland.” In addition, they report, “substantial increases in distribution and incidence of the disease in Australia are projected with climate change,” or, more specifically, “with increasing temperatures.” Russell *et al.* explored the soundness of these projections by reviewing the history of dengue in Australia.

This work showed the dengue vector (the *Aedes aegypti* mosquito) “was previously common in parts of Queensland, the Northern Territory, Western Australia and New South Wales,” and it had, “in the past, covered most of the climatic range theoretically available to it,” adding “the distribution of local dengue transmission has [historically] nearly matched the geographic limits of the vector.” This being the case, they conclude the vector’s current absence from

much of Australia “is not because of a lack of a favorable climate.” Thus, they reason “a temperature rise of a few degrees is not alone likely to be responsible for substantial increases in the southern distribution of *A. aegypti* or dengue, as has been recently proposed.” Instead, they note, “dengue activity is increasing in many parts of the tropical and subtropical world as a result of rapid urbanization in developing countries and increased international travel, which distributes the viruses between countries.” Instead of futile attempts to limit dengue transmission by controlling the world’s climate, therefore, the medical researchers recommend “well resourced and functioning surveillance programs, and effective public health intervention capabilities, are essential to counter threats from dengue and other mosquito-borne diseases.”

Johansson *et al.* (2009) write, “the mosquito-borne dengue viruses are a major public health problem throughout the tropical and subtropical regions of the world,” and “changes in temperature and precipitation have well-defined roles in the transmission cycle and may thus play a role in changing incidence levels.” Since “the El Niño Southern Oscillation (ENSO) is a multiyear climate driver of local temperature and precipitation world wide,” and “previous studies have reported varying degrees of association between ENSO and dengue incidence,” they looked for relationships between ENSO, local weather, and dengue incidence in Puerto Rico (1986–2006), Mexico (1985–2006), and Thailand (1983–2006) using wavelet analysis as a tool to identify time- and frequency-specific associations.

The three researchers report they “did not find evidence of a strong, consistent relationship in any of the study areas,” and Rohani (2009), who wrote a Perspective piece on their study, states the three researchers found “no systematic association between multi-annual dengue outbreaks and El Niño Southern Oscillation.” Thus, as stated in the “Editors’ Summary” of Johansson *et al.*’s paper, their findings “provide little evidence for any relationship between ENSO, climate, and dengue incidence.”

Shang *et al.* (2010) used logistic and Poisson regression models to analyze biweekly, laboratory-confirmed dengue cases in Taiwan at their onset dates of illness from 1998 to 2007, in order to “identify correlations between indigenous dengue and imported dengue cases (in the context of local meteorological factors) across different time lags.” The researchers write, “the occurrence of indigenous dengue was significantly correlated with temporally-lagged cases

of imported dengue (2–14 weeks), higher temperatures (6–14 weeks), and lower relative humidity (6–20 weeks),” and “imported and indigenous dengue cases had a significant quantitative relationship in the onset of local epidemics.” The six Taiwanese researchers conclude, “imported dengue cases are able to initiate indigenous epidemics when appropriate weather conditions are present,” or as they state in another place, “imported dengue are able to serve as an initial facilitator, or spark, for domestic epidemics.” They suggest “early detection and case management of imported cases through timely surveillance and rapid laboratory-diagnosis may avert large scale epidemics of dengue/dengue hemorrhagic fever,” while noting “meteorology alone does not initiate an epidemic.” Finally, they state, “an increase in viremic international travelers has caused global dengue hemorrhagic fever case numbers to surge in the past several decades.”

Ooi and Gubler (2009a) examined “the history of dengue emergence” in order to determine “the major drivers for the spread of both the viruses and mosquito vectors to new geographic regions.” The two researchers note “frequent and cyclical epidemics are reported throughout the tropical world, with regular importation of the virus via viremic travelers into both endemic and non-endemic countries.” They state, “there is no good evidence to suggest that the current geographic expansion of the dengue virus and its vectors has been or will be due to global warming.” Instead, they conclude, “the magnitude of movement of the human population and trade materials, uncontrolled and poorly planned expansion of urban centers and the lack of effective disease prevention in dengue-endemic regions have served to produce conditions ideal for dengue virus transmission and have been the principal drivers of epidemic dengue for the past three decades,” citing Gubler (1998, 2004), Gubler *et al.* (2001), and Ooi and Gubler (2009b).

In another review paper, Dr. Paul Reiter of the Insects and Infectious Disease Unit of the Institut Pasteur in Paris writes, “it is widely stated that the incidence of vector-borne diseases will increase if global temperatures increase” (Reiter, 2010a); and while admitting temperature and rainfall do indeed “play a role” in the transmission of such diseases, he states, “many other factors are involved,” citing a paper he wrote at the turn of the century (Reiter, 2001). In revisiting this subject, Reiter (2010a) reviewed the scientific literature, distilling the essence of the then-current state of knowledge pertaining to the potential for yellow fever and dengue trans-

mission throughout modern-day Europe.

The review revealed “the introduction and rapidly expanding range of *Aedes albopictus* in Europe is an iconic example of the growing risk of the globalization of vectors and vector-borne diseases,” and “the history of yellow fever and dengue in temperate regions confirms that transmission of both diseases could recur, particularly if *Aedes aegypti*, a more effective vector, were to be re-introduced.” He states “conditions are already suitable for transmission.”

In light of Reiter’s findings, can we expect to face the problem of the two deadly diseases suddenly reappearing and racing across Europe, especially if the climate begins to warm again? Actually, it would not be incredibly surprising if that were to happen even if the climate were to cool, for Reiter concludes, “a more urgent emerging problem is the quantum leap in the mobility of vectors and pathogens that has taken place in the past four decades, a direct result of the revolution of transport technologies and global travel,” as described in his recently published article (Reiter, 2010b).

Carbajo *et al.* (2012) report “dengue cases have increased during the last decades, particularly in non-endemic areas, and Argentina was no exception in the southern transmission fringe.” Although temperature rise has been blamed for this geographical expansion of the disease, they write, “human population growth, increased travel and inefficient vector control may also be implicated.” Thus, they evaluated the relative contributions of geographic, demographic, and climatic variables to the recent spread of the disease.

Carbajo *et al.* divided their study into two halves—a first decade that included the reemergence of the disease, and a second decade that included several epidemics—in which “annual dengue risk was modelled by a temperature-based mechanistic model as annual days of possible transmission,” and “the spatial distribution of dengue occurrence was modelled as a function of the output of the mechanistic model, climatic, geographic and demographic variables for both decades.”

They found dengue spatial occurrence “was positively associated with days of possible transmission, human population number, population fall and distance to water bodies.” When considered separately, the researchers write, “the classification performance of demographic variables was higher than that of climatic and geographic variables.” Thus, although useful in estimating annual transmission risk, Carbajo *et al.* conclude temperature “does not fully describe the distribution of dengue occurrence at the country scale,” and “when taken separately,

climatic variables performed worse than geographic or demographic variables,” while acknowledging “a combination of the three types was best for this task.”

These several observations indicate 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.

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7.7 Tick-Borne Diseases

- While climatic factors largely determine the geographical distribution of ticks, temperature and climate change are not among the significant factors determining the incidence of tick-borne diseases.

Randolph and Rogers (2000) state tick-borne encephalitis (TBE) “is the most significant vector-borne disease in Europe and Eurasia,” having “a case morbidity rate of 10–30% and a case mortality rate of typically 1–2% but as high as 24% in the Far East.” The disease is caused by a flavivirus (TBEV), which is maintained in natural rodent-tick cycles; humans may be infected with it if bitten by an infected tick or by drinking untreated milk from infected sheep or goats.

Early discussions on the relationship of TBE to global warming predicted the disease would expand its range and become more of a threat to humans in a warmer world. However, Randolph and Rogers note, “like many vector-borne pathogen cycles that depend on the interaction of so many biotic agents with each other and with their abiotic environment, enzootic cycles of TBEV have an inherent fragility,” so “their continuing survival or expansion cannot be predicted from simple univariate correlations.”

Confining their analysis to Europe, Randolph and Rogers first matched the present-day distribution of TBEV to the present-day distributions of five climatic variables: monthly mean, maximum, and minimum temperatures, plus rainfall and saturation vapor pressure, “to provide a multivariate description of present-day areas of disease risk.” They applied this understanding to outputs of a general circulation model of the atmosphere that predicted how these five climatic variables may change in the future.

The results indicate the distribution of TBEV might expand both north and west of Stockholm, Sweden in a warming world. For most other parts of Europe, however, the two researchers say “fears for increased extent of risk from TBEV caused by global climate change appear to be unfounded.” They report, “the precise conditions required for enzootic cycles of TBEV are predicted to be disrupted” in response to global warming, and the new climatic state “appears to be lethal for TBEV.” This finding, they write, “gives the lie to the common perception that a warmer world will necessarily be a world under greater threat from vector-borne diseases.” In the case of TBEV, they report the predicted change “appears to be to our advantage.”

Noting “it is often suggested that one of the most important societal consequences of climate change may be an increase in the geographic distribution and transmission intensity of vector-borne disease,” Estrada-Peña (2003) evaluated the effects of various abiotic factors on the habitat suitability of four tick species that are major vectors of livestock pathogens in South Africa. They report “year-to-year variations in the forecasted habitat suitability over the period 1983–2000 show a clear decrease in habitat availability, which is attributed primarily to increasing temperature in the region over this period.” In addition, when climate variables were projected to the year 2015, Estrada-Peña found “the simulations show a trend toward the destruction of the habitats of the four tick species,” just the opposite of what is often predicted about this disease.

Zell (2004) also has noted many people “assume a correlation between increasing disease incidence and global warming.” He reviewed the scientific literature pertaining to the subject and determined “the factors responsible for the emergence/reemergence of vector-borne diseases are complex and mutually influence each other.” He cites as an example of this complexity, “the incidence and spread of parasites and arboviruses are affected by insecticide and drug resistance, deforestation, irrigation systems and dams, changes in public health policy (decreased resources of surveillance, prevention and vector control), demographic changes (population growth, migration, urbanization), and societal changes (inadequate housing conditions, water deterioration, sewage, waste management).”

Zell says “it may be over-simplistic to attribute emergent/re-emergent diseases to climate change and sketch the menace of devastating epidemics in a warmer world.” Indeed, he concludes, “variations in public health practices and lifestyle can easily outweigh changes in disease biology.”

Sarah Randolph (2010) of the University of Oxford’s Department of Zoology in the United Kingdom examined the roles played by various factors that may influence the spread of tick-borne diseases. She begins by noting many vector-borne diseases “have shown marked increases in both distribution and incidence during the past few decades, just as human-induced climate change is thought to have exceeded random fluctuations.” She adds, “this coincidence has led to the general perception that climate change has driven disease emergence.” However, she notes, “climate change is the inevitable backdrop for all recent events,” most of which no one would otherwise consider attributing to

changes in the planet’s temperature.

After describing some of the outbreaks of tick-borne disease in Europe over the past couple of decades, Randolph states “the inescapable conclusion is that the observed climate change alone cannot explain the full heterogeneity in the epidemiological change, either within the Baltic States or amongst Central and Eastern European countries,” citing Sumilo *et al.* (2007). Instead, she writes, “a nexus of interrelated causal factors—abiotic, biotic and human—has been identified,” and “each factor appears to operate synergistically, but with differential force in space and time, which would inevitably generate the observed epidemiological heterogeneity.”

Many of these factors, she continues, “were the unintended consequences of the fall of Soviet rule and the subsequent socio-economic transition (Sumilo *et al.*, 2008b),” among which she cites “agricultural reforms resulting in changed land cover and land use, and an increased reliance on subsistence farming; reduction in the use of pesticides, and also in the emission of atmospheric pollution as industries collapsed; increased unemployment and poverty, but also wealth and leisure time in other sectors of the population as market forces took hold.”

Randolph concludes “there is increasing evidence from detailed analyses that rapid changes in the incidence of tick-borne diseases are driven as much, if not more, by human behavior that determines exposure to infected ticks than by tick population biology that determines the abundance of infected ticks,” as per Sumilo *et al.* (2008a) and Randolph *et al.* (2008). She ends her analysis by stating, “while nobody would deny the sensitivity of ticks and tick-borne disease systems to climatic factors that largely determine their geographical distributions, the evidence is that climate change has not been the most significant factor driving the recent temporal patterns in the epidemiology of tick-borne diseases.”

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7.8 Effects of CO₂

Among the lesser-known findings about CO₂ enrichment of the air is that several health-promoting substances are often enhanced in plants growing at higher CO₂ concentrations. As discussed in the subsections below, these enhancements portend great benefits for human health, and they represent an important reality the IPCC assessment reports ignore.

7.8.1 Antioxidants

Oxidation is a chemical process that occurs naturally in plants, animals, and humans. Although the process is vital for life, it also 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 following subsections examine the impact of rising atmospheric CO₂ on antioxidant compounds and enzymes found in plants, illustrating major benefits it provides for both plants and humans. With respect to plants, 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, and these compounds are known to provide health benefits to animals and humans.

7.8.1.1 Benefits to Plants

Environmental stresses induced by exposure to pollutants, drought, intense solar radiation, and high air or water temperatures generate highly reactive oxygenated compounds that damage plants. Ameliorating these stresses typically involves the production of antioxidant enzymes that scavenge and detoxify the highly reactive oxygenated compounds. When stresses are present, concentrations and/or activities of antioxidants in plants are generally observed to be high so as to counter the effects of the stress. A number of researchers have examined the impact of atmospheric CO₂ enrichment on this relationship, the results of which are discussed below.

In a study of two soybean genotypes, Pritchard *et al.* (2000) report three months' exposure to twice-ambient CO₂ concentrations reduced the activities of superoxide dismutase and catalase by an average of 23 and 39%, respectively. Likewise, Polle *et al.* (1997) show two years of atmospheric CO₂ enrichment reduced the activities of several key antioxidative enzymes, including catalase and superoxide dismutase, in beech seedlings. And Schwanz and Polle (1998) demonstrate this phenomenon can persist indefinitely, for they discovered similar reductions in these same enzymes

in mature oak trees that had been growing near natural CO₂-emitting springs for 30 to 50 years.

The standard interpretation of these results is the observed reductions in the activities of antioxidative enzymes under CO₂-enriched conditions imply plants exposed to higher-than-current atmospheric CO₂ concentrations experience less oxidative stress and thus have a reduced need for antioxidant protection. This conclusion further suggests “CO₂-advantaged” plants will be able to funnel more of their limited resources into the production of other plant tissues or processes essential to their continued growth and development.

On the other hand, when oxidative stresses do occur under high CO₂ conditions, the enhanced rates of photosynthesis and carbohydrate production resulting from atmospheric CO₂ enrichment generally enable plants to better deal with such stresses by providing more of the raw materials needed for antioxidant enzyme synthesis. Thus, when CO₂-enriched sugar maple seedlings were subjected to an additional 200 ppb of ozone, Niewiadomska *et al.* (1999) report ascorbate peroxidase, which is the first line of enzymatic defense against ozone, significantly increased. Likewise, Schwanz and Polle (2001) note poplar clones grown at 700 ppm CO₂ exhibited a much greater increase in superoxide dismutase activity upon chilling induction than clones grown in ambient air. In addition, Lin and Wang (2002) found activities of superoxide dismutase and catalase were much higher in CO₂-enriched wheat than in ambiently grown wheat following the induction of water stress.

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, a number of physiological and biochemical parameters were measured on the plants’ third fully expanded leaves. Among their many findings, the researchers note, “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 discovered enrichment of the 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.

Lumping these positive effects of elevated CO₂ together, the two scientists conclude, “the increase in atmospheric CO₂ concentration seems to be one of the protective factors for maize grown in cold temperate regions.”

In a study focusing solely on temperature, Yu *et al.* (2004a) investigated how global warming might affect crop reactive oxygen species (ROS) scavenging activities and chelating capacities, the latter of which may inhibit radical-mediated oxidative chain reactions by stabilizing transition metals required to catalyze the formation of the first few radicals needed to initiate the radical reactions (Nawar, 1996). In one of the few studies to broach this subject, Wang and Zheng (2001) examined the effects of a group of day/night temperature combinations on the antioxidant activities of the juice of two strawberry varieties, finding, in the words of Yu *et al.*, “the highest day/night temperature resulted in fruits with the greatest phenolic content as well as antioxidant activities.” Encouraged by this finding, Yu *et al.* (2004a) decided to explore the subject further in a study of winter wheat.

Yu *et al.* examined and compared flour extracts of three hard winter wheat varieties grown at five locations in Colorado for their radical scavenging properties, chelating capacities, and total phenolic contents. Although they found no statistically significant correlations, the scientists report “a correlation coefficient of 0.890 (P = 0.110) was detected for the chelating activity of Akron flour and the total hours of the growth location exceeding 32°C during the 6-week grain-filling period.” Thus, although no firm conclusions could be drawn from the results of their study, in contrast to the study of Wang and Zheng (2001), Yu *et al.*’s findings are intriguing enough to lead them to state, “more research is needed to clarify how varieties and growing conditions alter the antioxidant properties of wheat, wheat flour and bran.”

A different set of authors, Yu *et al.* (2004b), note “oxidative stress is potentially experienced by all aerobic life when exposed to UV-B radiation,” and “elevated CO₂ can enhance the capacity of plants to resist stress-induced oxidative damage,” citing Ren *et al.* (2001), who worked with terrestrial plants. Yu *et al.* set out to see whether this was also true of marine plants, focusing their attention on phytoplankton, which they describe as “the single most important ecosystem on our planet.”

They grew the marine microalgae *Platymonas subcordiformis* (Wille) Hazen in the laboratory at ambient levels of atmospheric CO₂ concentration and

UV-B radiation flux density, and at elevated levels of 5,000 ppm CO₂ and UV-B radiation characteristic of that anticipated to result from a 25% stratospheric ozone depletion under clear sky conditions in summer. By itself, and by these means, the five researchers determined the elevated UV-B treatment significantly decreased microalgal dry weight, photosynthetic rate, chlorophyll *a* and carotenoid contents. The elevated CO₂ treatment by itself enhanced dry weight and photosynthetic rate, and chlorophyll *a* content and carotenoid content exhibited no major differences compared with those of ambient UV-B and ambient CO₂. They also report elevated UV-B by itself significantly increased the production of the toxic superoxide anion and hydrogen peroxide, as well as malonyldialdehyde, an end product of lipid peroxidation, whereas elevated CO₂ by itself did just the opposite. In addition, in the treatment consisting of both elevated UV-B and elevated CO₂, the concentrations of these three substances were lower than those observed in the elevated UV-B and ambient CO₂ treatment. Finally, they note elevated CO₂ decreased the levels of several antioxidative enzymes found in the microalgae, reflecting their reduced need for detoxification of reactive oxygen species in the elevated CO₂ treatment.

Yu *et al.* write their results suggest “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*.” They also state, “CO₂ enrichment showed a protective effect against the oxidative damage of UV-B-induced stress,” and therefore, “elevated CO₂ can be [in] favor of enhancing the capacity of stress resistance.” Put more simply, they conclude, “we have shown that algae grown under high CO₂ would better overcome the adverse impact of environmental stress factor[s] that act via generation of activated oxygen species.”

Plants cultured *in vitro* are known to typically suffer from a number of physiological and biochemical impairments, such that upon transfer to *ex vitro* conditions they often experience severe oxidative stress. Carvalho *et al.* (2005) conducted an analysis of the extent to which this stress might be alleviated by a nominal doubling of the air’s CO₂ content. They evaluated the damage done to the large subunit of rubisco in grapevine (*Vitis vinifera* L.) plantlets while exposed to *in vitro* conditions and the degree to which that damage was ameliorated by atmospheric CO₂ enrichment during subsequent exposure to *ex vitro* conditions.

The *in vitro* plantlet cultures were maintained in a growth chamber at a photon flux density (PFD) of 45 $\mu\text{mol m}^{-2} \text{s}^{-1}$, after which they were transferred to *ex vitro* conditions having a PFD of either 150 (low light) or 300 (high light) $\mu\text{mol m}^{-2} \text{s}^{-1}$ and an air CO₂ concentration of either 350 (low CO₂) or 700 (high CO₂) ppm. A number of physiological and biochemical measurements were made on the plantlets at seven-day intervals over a period of 28 days.

Carvalho *et al.* found rubisco degradation products were present in the leaves of plantlets in both *in vitro* and *ex vitro* conditions. However, “under low CO₂ they were maintained for almost all of the 28 days of the acclimatization period, while becoming scarcely detected after 14 days under high CO₂ and after 7 days when high CO₂ was associated with high light.” In addition, “patterns of soluble sugars in acclimatizing leaves under high light and high CO₂ also gave an indication of a faster acquisition of autotrophic characteristics.” Carvalho *et al.*’s results thus demonstrate the beneficial impact of high CO₂ concentrations in reducing the oxidative stress induced by the transfer of *in vitro*-produced plantlets to *ex vitro* conditions, as “a net benefit from high CO₂ treatments was clearly visible, contributing to an increased stability of Rubisco.” Also, “the disappearance of Rubisco large subunit degradation products in persistent leaves subjected to the *ex vitro* treatments may be considered an indicator of recovery from stress,” they write.

Levine *et al.* (2008) grew well-watered and 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”—which were housed in Plexiglas chambers maintained at atmospheric CO₂ concentrations of either 400, 1,500, or 10,000 ppm for periods of 14, 21, and 28 days. The scientists measured a number of plant metabolic properties along with the leaf concentrations of several flavonoids that are capable of scavenging ROS. The 13 researchers report “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% at 14, 21, and 28 days after planting, respectively, whereas 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. They report “both elevated CO₂ levels resulted in an overall 25% increase in biomass over the control plants.”

The U.S., Japanese, and German scientists write, “the increased accumulation of secondary metabolites in plants grown under elevated CO₂ may have implications regarding plant-herbivore interactions, decomposition rates for inedible biomass, and potential beneficial effects on plant tolerance to water stress (Idso, 1988) and cold stress (Solecka and Kacperska, 2003) due to their potentials for the scavenging of reactive oxygen species (ROS).”

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 say “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), so increases in the atmosphere’s CO₂ concentration may increase various plant antioxidant enzymes and thereby reduce the negative effects of various abiotic stresses.

Varga *et al.* grew two varieties of winter wheat within 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, when drought was induced in three phases—at first node appearance, heading, and grain filling—by completely withholding water for seven days, which dropped the volumetric soil water content in the pots from 20–25% to 3–5%. The four researchers—all of whom were associated with the Agricultural Research Institute of the Hungarian Academy of Sciences—report they observed “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.” Varga *et al.* 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,” which may help society’s crops better cope with whatever extremes of moisture insufficiency might be lurking in the future.

Perez-Lopez *et al.* (2009) noted soil salinity “is one of the major environmental constraints limiting plant productivity and distribution,” affecting, as it does, “19.5% of the world’s irrigated area” as well as “non-irrigated croplands and rangelands.” They grew two barley (*Hordeum vulgare* L.) cultivars, Alpha and Iranis, within 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 a salinity treatment was administered 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, Perez-Lopez *et al.* report. “On the other hand,” they 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.”

Perez-Lopez *et al.* write, “it is concluded that 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, 2001b).” Thus it would appear the ongoing rise in the air’s CO₂ content may help a wide variety of Earth’s plants better cope with the many serious problems caused by high soil salinity.

Farfan-Vignolo and Asard (2012) note “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).” The pair of Belgian researchers 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 where $ET = AT + 3^{\circ}C$.

“Not surprisingly,” they write, “drought caused significant increases in oxidative damage, i.e., in protein oxidation and lipid peroxidation levels.” But they found “in both species the impact of drought on protein oxidation was reduced in future climate conditions [ECO_2 and ET].” And speaking of the stress-reducing effect of ECO_2 , they say “this ‘ CO_2 -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). The scientists conclude they “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*.”

These observations make it clear plants exposed to higher-than-current atmospheric CO_2 concentrations are better equipped to deal with oxidative stress than plants growing at lower CO_2 concentrations. IPCC currently ignores these benefits.

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7.8.1.2 Benefits to Humans

As discussed in the prior section, various environmental stresses generate highly reactive oxygenated compounds that damage plants. Ameliorating these stresses typically involves the production of antioxidant enzymes that scavenge and detoxify the highly reactive oxygenated compounds. When stresses are present, concentrations and/or activities of antioxidants in plants are generally observed to be high so as to counter the effects of the stress. However, plants exposed to higher-than-current atmospheric CO₂ concentrations experience less oxidative stress and thus have a reduced need for antioxidant protection, allowing them to funnel 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, and these compounds are known to provide health benefits to animals and humans that ingest these plants. The material in this section examines this CO₂-induced stimulation of antioxidant compounds, revealing another important benefit of atmospheric CO₂ enrichment that remains unreported by IPCC.

It is well-known that reactive oxygen species (ROS) generated during cellular metabolism or peroxidation of lipids and proteins play a causative role in the pathogenesis of cancer and coronary heart disease (CHD), as demonstrated by Slaga *et al.* (1987), Frenkel (1992), Marnett (2000), and Zhao *et al.* (2000). Wilcox *et al.* (2004), for example, note oxidative stress “has been related to cardiovascular disease, cancer, and other chronic diseases that account for a major portion of deaths today.” Yu *et al.* (2004) note “antioxidant treatments may terminate ROS attacks and reduce the risks of CHD and cancer,

as well as other ROS-related diseases such as Parkinson's disease (Neff, 1997; Chung *et al.*, 1999; Wong *et al.*, 1999; Espin *et al.*, 2000; Merken and Beecher, 2000),” and “developing functional foods rich in natural antioxidants may improve human nutrition and reduce the risks of ROS-associated health problems.”

Willcox *et al.* (2004) investigated the role of exogenous antioxidants in controlling oxidation and reviewed the evidence for their roles in preventing disease. The three nutrition experts state, “diet plays a vital role in the production of the antioxidant defense system by providing essential nutrient antioxidants such as vitamin E, C, and β -carotene, other antioxidant plant phenols including flavonoids, and essential minerals that form important antioxidant enzymes.” In addition, they note, “epidemiological data generally indicate a benefit of consuming diets that are higher in antioxidant nutrients, specifically diets high in fruits and vegetables.”

While it may be much easier to obtain these antioxidants by simply popping a pill or two (or even three or four), and millions of people do so daily, that approach is probably not as effective as obtaining needed antioxidants via the food one eats.

Willcox *et al.* report, for example, that in many studies of antioxidant health benefits “it is not clear whether the benefit is derived from the specific nutrients under study or another food component having health benefits yet to be discovered,” or perhaps “there is a particular combination of antioxidant nutrients that provide protection.” Although some epidemiological studies “appear to demonstrate clear associations, direct tests of the relationships with clinical trials have not yielded similar results.” They say “the most convincing evidence of antioxidant effect on cancer prevention involves feeding fruits and vegetables rather than individual antioxidants.” But what role might atmospheric CO₂ play in the matter?

Wang *et al.* (2003) evaluated the effects of elevated CO₂ on the antioxidant activity and flavonoid content of strawberry fruit they grew out-of-doors in six clear-acrylic open-top chambers, two of which they maintained at the ambient atmospheric CO₂ concentration, two of which were maintained at ambient + 300 ppm CO₂, and two of which they maintained at ambient + 600 ppm CO₂ for a period of 28 months (from early spring of 1998 through June 2000). The fruits of their labor were harvested twice—“at the commercially ripe stage” in both 1999 and 2000—after which they had them analyzed for a number of antioxidant properties and flavonol

contents.

Wang *et al.* note “strawberries are good sources of natural antioxidants (Heinonen *et al.*, 1998).” They further report, “in addition to the usual nutrients, such as vitamins and minerals, strawberries are also rich in anthocyanins, flavonoids, and phenolic acids,” and “strawberries have shown a remarkably high scavenging activity toward chemically-generated radicals, thus making them effective in inhibiting oxidation of human low-density lipoproteins (Heinonen *et al.*, 1998).” They note previous studies (Wang and Jiao, 2000; Wang and Lin, 2000) have shown “strawberries have high oxygen radical absorbance activity against peroxyl radicals, superoxide radicals, hydrogen peroxide, hydroxyl radicals, and singlet oxygen.”

They found strawberries had higher concentrations of ascorbic acid (AsA) and glutathione (GSH) when grown under enriched CO₂ conditions. In going from ambient to +300 ppm and +600 ppm CO₂, for example, AsA concentrations rose by 10 and 13%, respectively, and GSH concentrations increased by 3 and 171%, respectively. They also learned “an enriched CO₂ environment resulted in an increase in phenolic acid, flavonol, and anthocyanin contents of fruit.” For nine flavonoids, for example, there was a mean concentration increase of $55 \pm 23\%$ in going from the ambient atmospheric CO₂ concentration to +300 ppm CO₂, and a mean concentration increase of $112 \pm 35\%$ in going from ambient to +600 ppm CO₂. In addition, the “high flavonol content was associated with high antioxidant activity.”

Wang *et al.* note “anthocyanins have been reported to help reduce damage caused by free radical activity, such as low-density lipoprotein oxidation, platelet aggregation, and endothelium-dependent vasodilation of arteries (Heinonen *et al.*, 1998; Rice-Evans and Miller, 1996).” In summarizing their findings, they write, “strawberry fruit contain flavonoids with potent antioxidant properties, and under CO₂ enrichment conditions, increased the[ir] AsA, GSH, phenolic acid, flavonol, and anthocyanin concentrations,” further noting, “plants grown under CO₂ enrichment conditions also had higher oxygen radical absorbance activity against [many types of oxygen] radicals in the fruit.”

Caldwell *et al.* (2005) note “the beneficial effects of isoflavone-rich foods have been the subject of numerous studies,” specifically citing Messina (1999) and Birt *et al.* (2001), adding, “foods derived from soybeans are generally considered to provide both specific and general health benefits.” They investigated how the isoflavone content of soybean

seeds might be affected by the ongoing rise in the air's CO₂ content.

They grew well-watered and fertilized soybean plants from seed to maturity in pots within two controlled-environment chambers, one maintained at an atmospheric CO₂ concentration of 400 ppm and one at 700 ppm. The chambers were initially kept at a constant air temperature of 25°C. At the onset of seed fill, air temperature was reduced to 18°C until seed development was complete, in order to simulate average outdoor temperatures at this stage of plant development. In a second experiment, this protocol was repeated, except that the temperature during seed fill was maintained at 23°C, with and without drought (a third treatment). In a third experiment, seed-fill temperature was maintained at 28°C, with or without drought.

In the first experiment, where air temperature during seed fill was 18°C, the elevated CO₂ treatment increased the total isoflavone content of the soybean seeds by 8%. In the second experiment, where air temperature during seed fill was 23°C, the extra CO₂ increased total seed isoflavone content by 104%. In the third experiment, where air temperature during seed fill was 28°C, the CO₂-induced isoflavone increase was 101%. When drought stress was added as a third environmental variable, the extra CO₂ boosted total seed isoflavone content by 186% when seed-fill air temperature was 23°C, and at a seed-fill temperature of 28°C, it increased isoflavone content by 38%.

Under all the environmental circumstances studied by Caldwell *et al.*, enriching the air with an extra 300 ppm of CO₂ increased the total isoflavone content of soybean seeds. The percent increases measured under the stress situations investigated were always greater than the percent increase measured under optimal growing conditions. Thus the direct effects of atmospheric CO₂ enrichment on the health-promoting properties of soybean seeds are likely universally beneficial and a boon to humans; Bernacchi *et al.* (2005) characterized the soybean as “the world’s most important seed legume.”

Ginseng (*Panax ginseng*), the roots of which are widely cultivated in China, South Korea, and Japan and have been used for medicinal purposes since Greek and Roman times, is known for its anti-inflammatory, diuretic, and sedative properties and is acknowledged to be an effective healing agent (Gillis, 1997; Ali *et al.*, 2005). Normally, four to six years are required for ginseng roots to accumulate the amounts of the various phenolic compounds needed to produce their health-promoting effects. In an important step in

the quest to develop an efficient culture system for the commercial production of ginseng root, Ali *et al.* (2005) investigated the effects of growing ginseng roots 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 fully 37% relative to the dry weight of roots produced in bioreactors in equilibrium with normal ambient air, and root dry mass was increased by 27% after 45 days at 25,000 ppm CO₂ and by a still smaller 9% after 45 days at 50,000 ppm CO₂. Although the optimum CO₂ concentration for ginseng root growth clearly 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 high CO₂ concentration, root growth was still greater than in ambient air.

Almost everything else measured by Ali *et al.* was even more dramatically enhanced by the ultra-high CO₂ concentrations they 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. 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 sets of conditions. In addition, there were equally large CO₂-induced increases in the activities of a large number of phenol biosynthetic enzymes.

Ali *et al.* note “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 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.

Stutte *et al.* (2008) studied *Scutellaria* plants, herbaceous perennials that possess numerous medicinal properties, noting they are “rich in physiologically active flavonoids that have a wide spectrum of pharmacological activity.” They say leaf extracts of *Scutellaria barbata* have been found to be “limiting to the growth of cell lines associated with lung, liver, prostate, and brain tumors (Yin *et al.*, 2004),” and “extracts of *S. lateriflora* and the isolated flavonoids from the extracts have been shown to have antioxidant, anticancer, and antiviral properties (Awad *et al.*, 2003).” They investigated how the growth of these important plants, and their significant medicinal properties, might be affected by the ongoing rise in the air’s CO₂ content.

Stutte *et al.* measured effects of elevated atmospheric CO₂ (1,200 and 3,000 ppm vs. a control value of 400 ppm) on plant biomass production and plant concentrations of six bioactive flavonoids—apigenin, baicalin, baicalein, chrysin, scutellarein, and wogonin—all of which, they write, “have been reported to have anticancer and antiviral properties,” as described in the review papers of Joshee *et al.* (2002) and Cole *et al.* (2007). These experiments were conducted in a large step-in controlled-environment chamber that provided a consistent light quality, intensity, and photoperiod to six small plant growth chambers that had “high-fidelity control of relative humidity, temperature, and CO₂ concentration.” Each chamber was designed to monitor nutrient solution uptake by six individual plants that they grew from seed for a period of 49 days.

With respect to plant productivity (fresh and dry weight production), the three U.S. researchers determined increasing the air’s CO₂ concentration from 400 to 1,200 ppm resulted in a 36% increase in shoot fresh weight in *S. barbata* and a 54% increase in shoot dry matter, with no further increases between 1,200 and 3,000 ppm CO₂. In *S. lateriflora*, the corresponding increases in going from 400 to 1,200 ppm CO₂ were 62% and 44%, and in going to 3,000 ppm CO₂, the total increases were 122% and 70%, respectively.

For total flavonoid concentrations in the plants’ vegetative tissues, Stutte *et al.* found, in *S. barbata* “the combined concentration of the six flavonoids measured increased by 48% at 1200 and 81% at 3000 ppm CO₂,” and for *S. lateriflora* they report “the total flavonoid content increased by over 2.4 times at 1200 and 4.9 times at 3000 ppm CO₂.” In consequence of the compounding effect of increases in both plant

biomass and flavonoid concentration, the total flavonoid content in *S. barbata* rose by 72% in going from 400 to 1,200 ppm CO₂, and by 128% in going to 3,000 ppm CO₂. In *S. lateriflora* the corresponding increases were 320% and 1,270%. Stutte *et al.* conclude their results indicate “the yield and pharmaceutical quality of *Scutellaria* species can be enhanced with controlled environment production and CO₂ enrichment,” and massively so, it appears. In addition, since they say more than 200 substances—of which more than 80% are flavonoids—have been found in a total of 65 *Scutellaria* species, it would also appear the “increased concentration of flavonoids through CO₂ enrichment,” as they conclude, “has the potential to enhance the production and quality of medicinal plants.”

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Climate Change Reconsidered II: Biological Impacts

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7.8.2 Common Food Plants

- The ongoing rise in the air’s CO₂ content 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.

Studies of the effects of atmospheric CO₂ enrichment on the quality of the plants that comprise our diets have typically lagged far behind studies designed to assess the effects of elevated CO₂ on the quantity of plant production. Some noteworthy exceptions were the early studies of Barbale (1970) and Madsen (1971, 1975), who discovered increasing the air’s CO₂ content produced a modest increase in the vitamin C concentration of tomatoes, and Kimball and Mitchell (1981), who demonstrated enriching the air with CO₂ also stimulated the tomato plant’s production of vitamin A. A few years later, Tajiri

(1985) found a mere one-hour-per-day doubling of the air's CO₂ concentration doubled the vitamin C contents of bean sprouts, and did so when applied over a period of only seven days.

Fast-forwarding a couple of decades, Idso *et al.* (2002) grew well-watered and fertilized sour orange trees out-of-doors at Phoenix, Arizona, in clear-plastic-wall open-top enclosures maintained at atmospheric CO₂ concentrations of either 400 or 700 ppm since November 1987, while evaluating the effects of the extra 300 ppm of CO₂ on the vitamin C concentrations of fully ripened fruit harvested over the eight-year period 1992–1999. In years when the production of fruit was approximately doubled by the extra CO₂, they found the fruit produced in the two CO₂ treatments were of approximately the same size, and the vitamin C concentration of the juice of the oranges grown in the CO₂-enriched air was enhanced by approximately 7% above that of the juice of the ambient-treatment oranges. In years when CO₂-enriched fruit numbers were more than doubled, however, the CO₂-enriched fruit were slightly smaller than the fruit produced in normal air, and the vitamin C concentration of the juice of the CO₂-enriched fruit rose even higher, to as much as 15% above that of the ambient-treatment fruit. In years when fruit numbers were less than doubled, the CO₂-enriched fruit were slightly larger than the ambient-treatment fruit, and the enhancement of the vitamin C concentration of the juice of the CO₂-enriched fruit was somewhat less than the base value of 7% typical of equal-size fruit.

With respect to the likely long-term equilibrium response of the trees, Idso *et al.* (2002) report that in five of the last six years of the study, “the 75% increase in atmospheric CO₂ concentration has increased: (1) the number of fruit produced by the trees by $74 \pm 9\%$, (2) the fresh weight of the fruit by $4 \pm 2\%$, and (3) the vitamin C concentration of the juice of the fruit by $5 \pm 1\%$.” The eight researchers conclude, “there is reason to believe that an atmospheric CO₂ enrichment of the magnitude expected over the current century may induce a large and sustained increase in the number of fruit produced by orange trees, a small increase in the size of the fruit, and a modest increase in the vitamin C concentration of the juice of the fruit, all of which effects bode well for this key agricultural product that plays a vital role in maintaining good health in human populations around the globe.”

Further support for the significance of these observations was provided by Idso and Idso (2001), who note “these findings take on great significance when it is realized that scurvy—which is brought on

by low intake of vitamin C—may be resurgent in industrial countries, especially among children (Ramar *et al.*, 1993; Gomez-Carrasco *et al.*, 1994), and that subclinical scurvy symptoms are increasing among adults (Dickinson *et al.*, 1994).” In addition, they report, “Hampl *et al.* (1999) have found that 12 to 20% of 12–18-year-old school children in the United States ‘drastically under-consume’ foods that supply vitamin C; while Johnston *et al.* (1998) have determined that 12 to 16% of U.S. college students have marginal plasma concentrations of vitamin C.” Hence, “since vitamin C intake correlates strongly with the consumption of citrus juice (Dennison *et al.*, 1998), and since the only high-vitamin-C juice consumed in any quantity by children is orange juice (Hampl *et al.*, 1999), the modest role played by the ongoing rise in the air's CO₂ content in increasing the vitamin C concentration of orange juice could ultimately prove to be of considerable significance for public health in the United States and elsewhere.”

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—for a period of 28 months (from early spring of 1998 through June 2000), harvesting their fruit at the commercially ripe stage in both 1999 and 2000 and analyzing them for antioxidant properties and flavonol contents.

Wang *et al.* note strawberries are good sources of natural antioxidants and state, “in addition to the usual nutrients, such as vitamins and minerals, strawberries are also rich in anthocyanins, flavonoids, and phenolic acids,” and “strawberries have shown a remarkably high scavenging activity toward chemically generated radicals, thus making them effective in inhibiting oxidation of human low-density lipoproteins (Heinonen *et al.*, 1998).” They note previous studies (Wang and Jiao, 2000; Wang and Lin, 2000) “have shown that strawberries have high oxygen radical absorbance activity against peroxyl radicals, superoxide radicals, hydrogen peroxide, hydroxyl radicals, and singlet oxygen.”

The researchers determined, first, that strawberries had higher concentrations of ascorbic acid (AsA) and glutathione (GSH) “when grown under enriched CO₂ environments.” In going from ambient to +300 ppm and +600 ppm CO₂, for example, AsA concentrations increased by 10 and 13%, respectively, and GSH concentrations increased by 3 and 171%, respectively. They also learned “an enriched CO₂ environment resulted in an increase in

phenolic acid, flavonol, and anthocyanin contents of fruit.” For nine flavonoids, for example, there was a mean concentration increase of $55 \pm 23\%$ in going from the ambient atmospheric CO₂ concentration to +300 ppm CO₂, and a mean concentration increase of $112 \pm 35\%$ in going from ambient to +600 ppm CO₂. In addition, the “high flavonol content was associated with high antioxidant activity.” As for the significance of these findings, Wang *et al.* note “anthocyanins have been reported to help reduce damage caused by free radical activity, such as low-density lipoprotein oxidation, platelet aggregation, and endothelium-dependent vasodilation of arteries (Heinonen *et al.*, 1998; Rice-Evans and Miller, 1996).”

Wang *et al.* write, “strawberry fruit contain flavonoids with potent antioxidant properties, and under CO₂ enrichment conditions, increased their AsA, GSH, phenolic acid, flavonol, and anthocyanin concentrations,” further noting “plants grown under CO₂ enrichment conditions also had higher oxygen radical absorbance activity against radicals in the fruit.”

With respect to a major staple crop, soybeans, Caldwell *et al.* (2005) write “the beneficial effects of isoflavone-rich foods have been the subject of numerous studies (Birt *et al.*, 2001; Messina, 1999),” and “foods derived from soybeans are generally considered to provide both specific and general health benefits.” Caldwell *et al.* examined how the isoflavone content of soybean seeds might be affected by the ongoing rise in the air’s CO₂ content, growing well-watered and fertilized soybean plants from seed to maturity in pots within two controlled-environment chambers, one maintained at an atmospheric CO₂ concentration of 400 ppm and one at 700 ppm. The chambers were initially kept at a constant air temperature of 25°C; at the onset of seed fill, air temperature was reduced to 18°C until seed development was complete, to simulate average outdoor temperatures at this stage of plant development. In a second experiment, this protocol was repeated, except the temperature during seed fill was maintained at 23°C, with and without drought (a third treatment). In a third experiment, seed-fill temperature was maintained at 28°C, with or without drought.

In the first experiment, where air temperature during seed fill was 18°C, the elevated CO₂ treatment increased the total isoflavone content of the soybean seeds by 8%. In the second experiment, where air temperature during seed fill was 23°C, the extra CO₂ increased total seed isoflavone content by 104%. In

the third experiment, where air temperature during seed fill was 28°C, the CO₂-induced isoflavone increase was 101%. When drought-stress was added as a third environmental variable, the extra CO₂ boosted total seed isoflavone content by 186% when seed-fill air temperature was 23°C, and at a seed-fill temperature of 28°C, it increased isoflavone content by 38%.

Under all environmental circumstances studied, therefore, enriching the air with an extra 300 ppm of CO₂ increased the total isoflavone content of soybean seeds. The percent increases measured under the stress situations were always greater than the percent increase measured under optimal growing conditions. Consequently, the direct effects of atmospheric CO₂ enrichment on the health-promoting properties of soybeans, which Bernacchi *et al.* (2005) characterize as “the world’s most important seed legume,” are likely universally beneficial.

Kim *et al.* (2005) note important flavonoids “are mainly found in the form of isoflavones in soybean seeds,” including “phytoestrogens with various biological potentials such as antioxidative, pharmaceutical, oestrogenic and anticarcinogenic properties, with some acting as antiestrogens and being used as anticancer agents (Peterson and Barnes, 1991; Anderson *et al.*, 1995; Anthony *et al.*, 1996; Arjmandi *et al.*, 1996; Holt, 1997; Chung *et al.*, 2000).” They grew well-watered plants from seed to maturity in pots of sandy loam soil within the closed-environment plant growth facility of the National Horticultural Research Institute of Korea, where the plants were exposed to natural solar radiation and the natural daily course of ambient air temperature or elevated air temperature (= ambient + 5°C) with either normal soil nitrogen content or added nitrogen equivalent to an extra 40 kg N/ha, and they were maintained at either ambient CO₂ (360 ppm) or elevated CO₂ (650 ppm). At the end of the growing season, the plants were harvested and their total biomass determined. The concentrations of 12 isoflavones found in their seeds—three aglycons, three glucosides, three acetyl conjugates, and three malonyl conjugates—were quantitatively analyzed

Kim *et al.* found the CO₂-induced increase in total plant biomass at normal ambient temperatures was 96% in the case of normal soil nitrogen and 105% in the case of added nitrogen, and at the warmer temperatures it was 59% in the case of normal soil nitrogen and 68% in the case of added nitrogen. With respect to seed isoflavone concentrations, the CO₂-induced increases of all 12 isoflavones were fairly similar. As a group, at normal ambient temperatures

the mean increase was 72% in the case of normal soil nitrogen and 59% in the case of added nitrogen, and at the warmer temperatures it was 72% in the case of normal soil nitrogen and 106% in the case of added nitrogen. Irrespective of soil nitrogen status and air temperature, therefore, increases in the air's CO₂ content produced large increases in soybean biomass, as well as soybean seed concentrations of 12 major isoflavones.

Schonhof *et al.* (2007) stated the glucosinolates contained in broccoli plants comprise a group of bioactive compounds responsible for many physiological effects, including enhancing the plant's flavor and helping to prevent cancer in people who consume them, citing Mikkelsen *et al.* (2002). In a set of three experiments conducted in a controlled greenhouse environment, Schonhof *et al.* grew well-watered and fertilized broccoli plants in large soil-filled containers at ambient (430–480 ppm) and elevated (685–820 ppm) atmospheric CO₂ concentrations to the stage where fully developed heads could be harvested for glucosinolate analyses. They report the roughly 65% increase in atmospheric CO₂ concentration increased the fresh weight of the broccoli heads by approximately 7% and increased the total glucosinolate concentration of the broccoli inflorescences by 14%, due primarily to identical 37% increases in two particular glucosinolates: glucoiberin and glucoraphanin. The four researchers conclude atmospheric CO₂ enrichment “can enhance the health-promoting quality of broccoli because of induced glucosinolate content changes.”

Jin *et al.* (2009) grew well-watered and fertilized spinach from seed (five to each 3.5-liter pot filled with a loam soil) for approximately three weeks in controlled-environment chambers containing air of either 350 ppm or 800 ppm CO₂. They harvested the plants, weighed them, and measured the concentrations of several of the nutritive substances contained in their leaves. As best as can be determined from the graphs of their results, the extra 450 ppm of CO₂ increased the fresh weight of the spinach shoots by about 67% and their dry weight by approximately 57%. In addition, it boosted the soluble sugar concentrations of their leaves by approximately 29% and soluble protein concentrations by about 52%. The extra CO₂ also increased spinach leaf concentrations of ascorbate, glutathione, and total flavonoids by 21%, 16%, and 3%, respectively.

La *et al.* (2009) noted “epidemiological studies show there is a negative relationship between Brassicaceae vegetable intake and the risk of a number of cancers (Wattenberg, 1993; Kohlmeier and

Su, 1997; Price *et al.*, 1998),” adding, “it has been widely recognized that some of the cancer-chemoprotective activities in these vegetables are attributable to their contents of glucosinolates (Zhao *et al.*, 1992; Wattenberg, 1993; Tawfiq *et al.*, 1995; Fahey *et al.*, 1997; Rosa *et al.*, 1997; Holst and Williamson, 2004).” They set out to determine what effect the ongoing rise in the air's CO₂ content might have on the production of these important cancer-fighting agents in yet another common food plant.

The five scientists placed pairs of seedlings of Chinese kale in 1.8-L pots “fixed in a foam cavity with sponge” within growth chambers maintained at either 350 or 800 ppm CO₂, where the plant's roots were immersed in culture solutions treated with either 5.0 mmol nitrogen (N) per L (low N), 10 mmol N per L (medium N), or 20 mmol N per L (high N) and allowed to grow for 35 days. The plants then were separated into their primary morphological parts and weighed, and their bolting stems were ground into powder for glucosinolate analyses.

“Regardless of N concentration,” the researchers write, the elevated CO₂ treatment “significantly increased plant height [15.64%], stem thickness [11.79%], dry weights of the total aerial parts [11.91%], bolting stems [15.03%], and roots [16.34%].” Also, the elevated CO₂ increased the total glucosinolate concentrations of the bolting stems in the low and medium N treatments by 15.59% and 18.01%, respectively, compared with those at ambient CO₂, although there was no such effect in the high N treatment. Consequently, in terms of the total amount of glucosinolate production within the bolting stems of Chinese kale, these results suggest increases of 33 to 36% may be obtained for plants growing in low to medium N conditions in response to a 450 ppm increase in the air's CO₂ concentration.

Gwynn-Jones *et al.* (2012) note “dwarf shrub berries are particularly valued by the human populations at Northern Latitudes as an autumn harvest, but are also consumed by a wide range of animals (Anderson, 1985).” They note the fruit of these shrubs contain high concentrations of flavonoids and anthocyanins (Heinonen *et al.*, 1998; Faria *et al.*, 2005; Heinonen, 2007), which can scavenge cancer-causing free-radicals (Martin-Aragon *et al.*, 1998; Taruscio *et al.*, 2004) and reduce the oxidative stress caused by these compounds in animals (Johnson and Felton, 2001). They state “there is already laboratory evidence suggesting that the consumption of *Vaccinium myrtillus* berry flavonoids by small mammals can increase the antioxidant capacity of their blood plasma which could promote

their fitness,” citing Talavera *et al.* (2006).

In an open-top chamber study conducted at the Abisko Scientific Research Station in Northern Sweden, Gwynn-Jones *et al.* assessed the impact of atmospheric CO₂ enrichment (600 vs. 360–386 ppm) on the berry quality of *Vaccinium myrtillus* and *Empetrum hermaphroditum* in the final year (2009) of a 17-year experiment. As best as can be determined from the 10 researchers’ graphically presented results, it appears the mean concentration of quercetin glycosides in *V. myrtillus* was increased by approximately 46% by the approximate mean CO₂ concentration increase of 227 ppm. In *E. hermaphroditum*, syringetin glycoside concentrations were increased by about 36% by the extra CO₂, and five anthocyanins had their concentrations increased as follows: delphinidin-3-hexoside by about 51%, cyanidin-3-hexoside by about 49%, petunidin-3-hexoside by about 48%, malvidin-3-pentoside by about 46%, and malvidin-3-hexoside by about 59%. Gwynn-Jones *et al.* conclude, “consumers of *E. hermaphroditum* may gain higher antioxidant intake at elevated CO₂,” and “some European bird species show preferential feeding towards berries with higher antioxidant contents (Catoni *et al.*, 2008), which could have important implications for the palatability and, therefore, seed dispersal of these species.”

It is becoming increasingly evident the ongoing rise in the air’s CO₂ content 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. As these foods make their way onto our dinner tables, they improve our health and help us better contend with the multitude of diseases and other maladies that regularly afflict us. It is possible, if not likely, that the lengthening of human lifespan that has occurred over the past half-century or more—as described by Horiuchi (2000) and Tuljapurkar *et al.* (2000)—may in some significant part be due to the concomitant CO₂-induced increases in the concentrations of the many health-promoting substances found in the various plant-derived foods we eat. Yet these real and many benefits continue to be ignored by IPCC.

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7.8.3 Medicinal Plants

- Atmospheric CO₂ enrichment 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.

Studies of the effects of atmospheric CO₂ enrichment on the amounts and concentrations of various health-promoting substances produced by medicinal or “health food” plants have lagged behind studies designed to assess the effects of elevated CO₂ on the quantity of plant production. Nevertheless, enough research has been conducted on this topic to reveal atmospheric CO₂ enrichment positively impacts these important substances.

Stuhlfauth *et al.* (1987), for example, found a near-tripling of the air’s CO₂ content increased the dry weight production of the woolly foxglove plant (which produces the cardiac glycoside digoxin used in the treatment of cardiac insufficiency) by 63% under dry conditions and by 83% when well-watered, and the concentration of digoxin within the plant dry mass was enhanced by 11% under well-watered conditions and by 14% under conditions of water stress. Stuhlfauth and Fock (1990) obtained similar results in a field study, with a near-tripling of the air’s CO₂ content leading to a 75% increase in plant dry weight production per unit land area and a 15% increase in digoxin per unit dry weight of plant material, resulting in an actual doubling of total digoxin yield per hectare of cultivated land.

Idso *et al.* (2000) grew spider lily plants out-of-doors at Phoenix, Arizona in clear-plastic-wall open-top enclosures that had their atmospheric CO₂ concentrations maintained at either 400 or 700 ppm for two consecutive two-year growth cycles. The 75% increase in the air’s CO₂ concentration increased aboveground plant biomass by 48% and belowground (bulb) biomass by 56%. In addition, the extra CO₂ increased the concentrations of five bulb constituents possessing anticancer and antiviral properties. Mean percentage increases in these concentrations were, the researchers write, “6% for a two-constituent (1:1) mixture of 7-deoxynarciclasine and 7-deoxy-trans-dihydronarciclasine, 8% for pancratistatin, 8% for trans-dihydronarciclasine, and 28% for narciclasine, for a mean active-ingredient percentage concentration increase of 12%.” Combined with the 56% increase in bulb biomass, these percentage concentration increases resulted in a mean active-ingredient increase of 75% for the 75% increase in the air’s CO₂ concentration. The substances described above have been shown to be effective in fighting a number of devastating human maladies, including leukemia; ovary sarcoma; melanoma; and brain, colon, lung, and renal cancers, as well as Japanese encephalitis and yellow, dengue, Punta Tora, and Rift Valley fevers.

Zobayed and Saxena (2004) studied St. John’s wort, a perennial herb native to Europe and West Asia that has been used for treatment of mild to moderate depression, inflammation, and wound healing (Brolis *et al.*, 1998; Stevinson and Ernst, 1999), and which has been reported to be a potential source for anticancer, antimicrobial, and antiviral medicines (Schempp *et al.*, 2002; Pasqua *et al.*, 2003). The two scientists grew shoots of the plant for 42 days under well-watered and fertilized conditions within a greenhouse, where the air’s CO₂ concentration averaged 360 ppm, as well as in computer-controlled environment chambers maintained at a mean CO₂ concentration of 1,000 ppm, with all other environmental conditions being comparable between the two treatments.

On the final day of the study, Zobayed and Saxena determined the net photosynthetic rates of the plants in the CO₂-enriched chambers were 124% greater than those of the plants growing in ambient air, and their dry weights were 107% greater. The extra 640 ppm of CO₂ in the high-CO₂ treatment increased plant concentrations of hypericin and pseudohypericin (two of the major health-promoting substances in the plants) by just over 100%. Consequently, the 180% increase in the air’s CO₂

content more than doubled the dry mass produced by the well-watered and fertilized St. John's wort plants, and it more than doubled the concentrations of hypericin and pseudohypericin found in their tissues. Thus the CO₂ increase more than quadrupled the total production of these two health-promoting substances.

Mosaleeyanon *et al.* (2005) also studied St. John's wort, growing well-watered and fertilized seedlings for 45 days in controlled-environment chambers at low, medium, and high light intensities (100, 300, and 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively) at atmospheric CO₂ concentrations of 500, 1,000, and 1,500 ppm. On the 45th day of their experiment, the plants were harvested, and the hypericin, pseudohypericin, and hyperforin (another important health-promoting substance) they contained were extracted from their leaves and quantified.

Under all three light intensities employed in the study, the four researchers found the 1,000-ppm increase in atmospheric CO₂ concentration experienced in going from 500 to 1,500 ppm produced total plant biomass increases of approximately 32%. Over this same CO₂ range, hypericin concentrations rose by 78, 57, and 53%, respectively, under the low, medium, and high light intensities. Pseudohypericin concentrations rose by 70, 57, and 67%, and hyperforin concentrations rose by 102, 23, and 3%. Compared to plants growing out-of-doors in air of 380 ppm CO₂ and at light intensities on the order of 1,770 $\mu\text{mol m}^{-2} \text{s}^{-1}$, Mosaleeyanon *et al.* discovered total plant biomass was fully 30 times greater in the high-light, high-CO₂ controlled-environment treatment, and under the same conditions the concentrations of hypericin and pseudohypericin were 30 and 41 times greater. Thus the researchers demonstrated growing St. John's wort plants in CO₂-enriched air in controlled-environment chambers can enormously enhance both plant biomass and hypericin and pseudohypericin contents.

Ziska *et al.* (2005) grew well-watered and fertilized tobacco and jimson weed plants from seed in controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 378 ppm (ambient) or 690 ppm (elevated) and mean air temperatures of either 22.1 or 27.1°C for 50 and 47 days after planting for tobacco and jimson weed, respectively. They sampled the plants at weekly intervals beginning at 28 days after planting for tobacco and 16 days for jimson weed, to determine the effects of these treatments on three plant alkaloids possessing important pharmacological properties: nicotine, in the case of tobacco, and atropine and scopolamine, in the case of jimson weed. At the time

of final harvest they found the elevated CO₂ had increased the aboveground biomass production of tobacco by approximately 89% at 22.1°C and 53% at 27.1°C, and had increased that of jimson weed by approximately 23% and 14% at the same respective temperatures. The extra CO₂ also was found to have reduced the concentration of nicotine in tobacco and increased the concentration of scopolamine in jimson weed, but it had no significant effect on the concentration of atropine in jimson weed.

The two significant changes (reduced nicotine in tobacco and increased scopolamine in jimson weed) likely would be characterized as beneficial by most people; as the six scientists report, nicotine is acknowledged to have significant negative impacts on human health, and scopolamine is used as a sedative and as "an antispasmodic in certain disorders characterized by restlessness and agitation, (e.g., delirium tremens, psychosis, mania and Parkinsonism)." Nevertheless, Ziska *et al.* state "it can be argued that synthetic production of these secondary compounds alleviates any concern regarding environmental impacts on their production from botanical sources," but they note "developing countries (i.e., ~75% of the world population) continue to rely on ethno-botanical remedies as their primary medicine (e.g. use of alkaloids from jimson weed as treatment for asthma among native Americans and in India)." In addition, "for both developed and developing countries, there are a number of economically important pharmaceuticals derived solely from plants whose economic value is considerable (Raskin *et al.*, 2002)."

Another plant with an impressive history of medicinal use is ginseng. Well-known for its anti-inflammatory, diuretic, and sedative properties, and long acknowledged to be an effective healing agent (Gillis, 1997), ginseng is widely cultivated in China, South Korea, and Japan, where it has been used for medicinal purposes since Greek and Roman times. Normally, ginseng roots take four to six years to accumulate the amounts of the various phenolic compounds needed to produce their health-promoting effects.

Ali *et al.* (2005) investigated the consequences of growing ginseng plants 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 are the effects of the ultra-high CO₂ concentrations on root growth and whether they would be toxic and lead to biomass reductions or even

root death. The answer, according to Ali *et al.*'s experiment was a resounding *no*. After 45 days of growth at 10,000 ppm CO₂, root dry weight was increased by about 37% relative to the dry weight of roots produced in bioreactors in equilibrium with ambient air, and it was increased by a lesser 27% after 45 days at 25,000 ppm CO₂ and by a still smaller 9% after 45 days at 50,000 ppm CO₂. Consequently, although the optimum CO₂ concentration for ginseng root growth likely resides somewhere below 10,000 ppm, the concentration at which root growth is reduced below that characteristic of ambient air resides somewhere above 50,000 ppm, for even at that extremely high CO₂ concentration, root growth was still greater than it was in ambient air.

Almost everything else measured by Ali *et al.* was even more dramatically enhanced by the ultra-high CO₂ concentrations. 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. Total root flavonoid concentrations were enhanced by 228%, 383%, and 232%, respectively; 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%. There were equally large CO₂-induced increases in the activities of a large number of phenol biosynthetic enzymes.

Ali *et al.* state "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 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. It should be further noted that as the air's CO₂ content continues to climb, it likely will bring forth a substantial natural increase in the concentrations of health-promoting substances in ginseng and other medicinal plants, leading to better human health the world over. It is likely this phenomenon already has played some role in the lengthening of human life span that has occurred since the dawn of the Industrial Revolution, as described by Horiuchi (2000) and Tuljapurkar *et al.* (2000), when the air's CO₂ concentration rose from roughly 280 ppm to its current value of close to 400 ppm.

Zou (2005) studied the brown seaweed *Hizikia*

fusiforme, which serves as both a health-promoting food and a delicacy in China, Japan, and Korea. The researcher collected specimens from intertidal rocks along the coast of Nanao Island, Shantou (China) and maintained them in glass aquariums in filtered natural seawater enriched with 60 µM NaNO₃ and 6.0 µM NaH₂PO₄, where the plants were continuously aerated with either ambient air of 360 ppm CO₂ or CO₂-enriched air of 700 ppm CO₂. Zou measured the seaweed's relative growth and nitrogen assimilation rates as well as its nitrate reductase activity. Zou reports the slightly less than a doubling of the air's CO₂ concentration increased the seaweed's mean relative growth rate by about 50%, its mean rate of nitrate uptake during the study's 12-hour light periods by around 200%, and its nitrate reductase activity by approximately 20% over a wide range of substrate nitrate concentrations.

Zou notes "the extract of *H. fusiforme* has an immune-modulating activity on humans and this ability might be used for clinical application to treat several diseases such as tumors (Suetsuna, 1998; Shan *et al.*, 1999)." He also states the alga is "becoming one of the most important species for seaweed mariculture in China, owing to its high commercial value and increasing market demand." In addition, Zou reports "the intensive cultivation of *H. fusiforme* would remove nutrients more efficiently with the future elevation of CO₂ levels in seawater, which could be a possible solution to the problem of ongoing coastal eutrophication," which in turn suggests rising atmospheric CO₂ concentrations may additionally assist in the amelioration of this important environmental problem.

Hoshida *et al.* (2005) grew the marine alga unicellular *Nannochloropsis* sp. alga in batch culture under normal (370 ppm) and elevated (3,000 and 20,000 ppm) air CO₂ concentrations in an attempt to learn how elevated CO₂ impacted the alga's ability to produce eicosapentaenoic acid (EPA), a major polyunsaturated omega-3 fatty acid that may play an important role in human health related to the prevention of certain cardiovascular diseases (e.g. atherosclerosis, thrombogenesis) and the inhibition of tumor growth and inflammation, as described by Dyerberg *et al.* (1978), Hirai *et al.* (1989), Kinsella *et al.* (1990), and Sanders (1993).

The five researchers note "Nitsan *et al.* (1999) showed that supplementing the diet of hens with *Nannochloropsis* sp. led to an increased content of n-3 fatty acids in the egg yolk, indicating an additional role in enhancing the nutritional value of eggs," and they report "feeding *Nannochloropsis* sp. to rats

caused a significant increase in the content of n-3 polyunsaturated fatty acids (Sukenik *et al.*, 1994),” suggesting the alga may play an “important role as the source for n-3 polyunsaturated fatty acids in human nutrition.”

The Japanese scientists found “maximum EPA production was obtained when 20,000 ppm CO₂ was supplied 12 hours prior to the end of the exponential growth,” and “total EPA production during 4-day cultivation was about twice that obtained with ambient air.” They also report other researchers have obtained similar results, noting EPA is found mainly in thylakoid membranes (Sukenik *et al.*, 1989; Hodgson *et al.*, 1991), and prior experiments have shown “the amount of stroma thylakoid membrane increased in several plants under elevated CO₂ concentrations (Griffin *et al.*, 2001).” In addition, “in *Synechococcus lividus*, reduction and synthesis of thylakoid membrane occurred by CO₂ deprivation and elevation, respectively (Miller and Holt, 1977),” and “in *Chlorella vulgaris*, altering the ambient CO₂ concentration varied fatty acid composition (Tsuzuki *et al.*, 1990).” Finally, Hoshida *et al.* report, “the effect of CO₂ on fatty acid composition and/or fatty acid content had been reported in algae and higher plants (Tsuzuki *et al.*, 1990; Sergeenko *et al.*, 2000; He *et al.*, 1996; Radunz *et al.*, 2000),” and “increased EPA production caused by elevated CO₂ concentration was reported in *P. tricornutum* (Yongmanitchai and Ward, 1991).” Consequently, as the atmospheric CO₂ concentration continues to rise, concentrations of omega-3 fatty acids will be widely enhanced in both aquatic and terrestrial plants.

Ziska *et al.* (2008) note, “among medicinal plants, the therapeutic uses of opiate alkaloids from poppy (*Papaver* spp.) have long been recognized,” and they considered it important “to evaluate the growth and production of opiates for a broad range of recent and projected atmospheric carbon dioxide concentrations,” which they did for the wild poppy (*P. setigerum*). The authors grew well-watered and fertilized plants from seed within growth chambers maintained at atmospheric CO₂ concentrations of 300, 400, 500, and 600 ppm for a period of 90 to 100 days, quantifying plant growth and the production of the alkaloids morphine, codeine, papaverine, and noscapine, which were derived from latex obtained from capsules produced by the plants.

Relative to the plants grown at 300 ppm CO₂, those grown at 400, 500, and 600 ppm produced approximately 200, 275, and 390% more aboveground biomass, respectively, as best as can be determined from the researchers’ bar graphs. In

addition, “reproductively, increasing CO₂ from 300 to 600 ppm increased the number of capsules, capsule weight and latex production by 3.6, 3.0 and 3.7 times, respectively, on a per plant basis,” so, ultimately, “all alkaloids increased significantly on a per plant basis.” They conclude, “as atmospheric CO₂ continues to increase, significant effects on the production of secondary plant compounds of pharmacological interest (i.e. opiates) could be expected.” These effects, they write, “are commonly accepted as having both negative (e.g. heroin) and positive (e.g. codeine) interactions with respect to public health.”

Vurro *et al.* (2009) note thyme (a well-known culinary and medicinal herb) has “a considerable economic value in the nutraceutical and pharmaceutical industry (Vardar-Uenlue *et al.*, 2003; Konyalioglu *et al.*, 2006),” and “thyme essential oil possesses *per se* considerable antioxidant capacity (Economou *et al.*, 1991), and may therefore contribute towards the control of antioxidant status in the leaves.” They grew well-watered one-year-old thyme plants for three additional months (10 June–10 September) in pots (filled with 40% sand, 25% clay, and 35% silt) out-of-doors within a mini-free-air CO₂-enrichment (FACE) system at Ravenna, Italy. The air’s CO₂ concentration was maintained at approximately 500 ppm (during daylight hours only), and control plants were continuously exposed to air of approximately 370 ppm CO₂. They measured a number of plant characteristics at the end of each of the three months of the study.

The four researchers state “none of the plants grown under high levels of CO₂ for 90 days presented either significant differences in fresh weight and dry weight compared with controls, or macroscopic alteration of morphogenesis (number and length of nodes/internodes, branching, leaf area and chlorosis, etc.), at any of the sampling times.” However, “in plants grown under elevated CO₂, a relative increase in oil yield of 32, 34 and 32% was, respectively, recorded in the first, second and third sampling-time (July, August and September),” and they observed a “general depression of the oxidative stress under elevated CO₂” that led to a “down-regulation of leaf reactive oxygen species-scavenging enzymes under elevated CO₂.” In layman’s terms, the Italian scientists say their results pointed to “a ‘low cost’ life strategy for growth under elevated CO₂, not requiring synthesis/activation of energy-intensive and expensive metabolic processes.” This change in behavior should allow the plants to invest more energy in the production of essential plant oils that have, as Vurro *et al.* describe it, “considerable economic value in the

nutraceutical and pharmaceutical industry.”

Goncalves *et al.* (2009) write, “the impact of elevated carbon dioxide concentration on the quality of berries, must, and red wine (with special reference to volatile composition, phenolic content, and antioxidant activity) made from Touriga Franca, a native grape variety of *Vitis vinifera* L. for Port and Douro wine manufacturing grown in the Demarcated Region of Douro [northern Portugal], was investigated during 2005 and 2006.” The six Portuguese researchers grew grapevines in open-top chambers maintained at either 365 or 550 ppm CO₂, finding, “in general, the increase of CO₂ did not affect berry characteristics” and “did not significantly change the total antioxidant capacity of the red wines.” They write, “thirty-five volatile compounds belonging to seven chemical groups were identified,” and, “generally, the same volatile compounds were present in all of the wines.” Although some of these compounds were “slightly affected,” they note “the red wine quality remained almost unaffected.” Thus, Goncalves *et al.* say their study shows “the predicted rise in CO₂ might strongly stimulate grapevine photosynthesis and yield without causing negative impacts on the quality of grapes and red wine.”

Bindi *et al.* (2001) conducted a two-year (1996, 1997) FACE study of 20-year-old grapevines (*Vitis vinifera* L., cv Sangiovese) near Rapolano, Siena (Italy). They enriched the air around the plants to 550 and 700 ppm (compared to ambient CO₂ levels in those two years that averaged 363 ppm, per Mauna Loa data), measuring numerous plant parameters in the process, including—after the fermentation process was completed—“the principal chemical compounds that determine the basic red wine quality.” They report “elevated atmospheric CO₂ levels had a significant effect on biomass components (total and fruit dry weight) with increases that ranged from 40 to 45% in the 550 ppm treatment and from 45 to 50% in the 700 ppm treatment.” In addition, “acid and sugar contents were also stimulated by rising CO₂ levels up to a maximum increase in the middle of the ripening season (8–14%),” but as the grapes reached the maturity stage, the CO₂ effect on these parameters gradually disappeared. In terms of various health-promoting substances contained in the wine itself, in response to the ~50% increase in atmospheric CO₂ concentration in going from ~363 to ~550 ppm CO₂, as can be calculated from the bar graphs of their results, the concentrations of total polyphenols, total flavonoids, total anthocyanins, and non-anthocyanin flavonoids in the wine rose by approximately 19%, 33%, 31%, and 38%, respectively. Bindi *et al.*

conclude, “the expected rise in CO₂ concentrations may strongly stimulate grapevine production without causing negative repercussions on quality of grapes and wine,” and in fact their data suggest the ongoing rise in the air’s CO₂ content might slightly enhance the health-protective properties of the wine.

Oliveira *et al.* (2010) write, “there is a growing interest in the use of inulin as a health food ingredient, as an alternative for low-calorie sweeteners, and as a dietary fiber and fat substitute (Ritsema and Smeekens, 2003).” In addition, they say “it is suggested” a daily intake of low amounts of inulin or its derivatives promotes the growth of beneficial bacteria in the intestinal tract, as well as anti-tumor effects, citing Roberfroid (2005). Hence, they studied *Vernonia herbacea*, a plant from the Brazilian Cerrado that accumulates inulin-type fructans in underground organs called rhizophores. The five Brazilian researchers grew well-watered and fertilized *V. herbacea* plants from rhizophore fragments for two months and then transferred them in groups of three to 3-L pots containing forest soil. The plants were maintained in open-top chambers in a glasshouse for 120 days at atmospheric CO₂ concentrations of either 380 or 760 ppm, and the scientists measured the plants’ net photosynthetic rates, water use efficiencies, and fructan concentrations after 15, 30, 60, 90, and 120 days of treatment, as well as above- and below-ground biomass at the end of the experiment.

Oliveira *et al.* write, the “plants under elevated CO₂ presented increases in height (40%), photosynthesis (63%) and biomass of aerial (32%) and underground (47%) organs when compared with control plants.” In addition, “water use efficiency was significantly higher in treated plants, presenting a 177% increase at day 60.” They found fructan concentration remained unchanged, but because of the significant CO₂-induced increase in underground organ biomass, “a 24% increase in total fructan yield occurred.”

Ghasemzadeh *et al.* (2010) write, “free radicals and single oxygen are recognized as major factors causing various chronic diseases such as cancer, diabetes, *etc.*,” and as a result, they note, “the health maintenance function of antioxidant components in various foods has received much attention,” citing Byers and Guerrero (1995) and Namiki (1990). They further observe, “phenolic acids and flavonoids are antioxidants with health benefits such as anti-inflammatory and anti-tumor effects (Heijnen *et al.*, 2001; Chun *et al.*, 2003; Harborne and Williams, 2000; Chen, 2004),” specifically noting “Sung-jin *et*

al. (2008) showed that some flavonoid components in green tea are effective in inhibiting cancer or induce mechanisms that may kill cancer cells and inhibit tumor invasion.”

The Malaysian researchers grew two varieties of Malaysian young ginger (*Zingiber officinale*)—Halia Bentong and Halia Bara—from rhizomes planted in a drip-irrigated 1:1 mixture of burnt rice husk and coco peat in polyethylene bags placed within controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 400 or 800 ppm for a period of 16 weeks. They then harvested the plants and analyzed their leaves and rhizomes for a wide variety of phenolics and flavonoids, along with their free radical scavenging power, which is a measure of their ability to prevent dangerous reactive oxygen species from attacking various parts of the body and causing a large number of potentially life-threatening maladies. Malaysian young ginger is one of the medicinal/food plants used by Polynesians for more than 2,000 years in treating cancer, diabetes, high blood pressure, and many other illnesses

Ghasemzadeh *et al.* found, on average, “flavonoid compounds increased 44.9% in leaves and 86.3% in rhizomes of Halia Bentong and 50.1% in leaves and 79% in rhizomes of Halia Bara when exposed to elevated carbon dioxide conditions.” Phenolic compounds increased even more: by 79.4% in leaves and 107.6% in rhizomes of Halia Bentong and 112.2% in leaves and 109.2% in rhizomes of Halia Bara. In addition, the increase in the CO₂ concentration from 400 to 800 ppm increased the free radical scavenging power by 30.0% in Halia Bentong and 21.4% in Halia Bara. Also, “the rhizomes exhibited more enhanced free radical scavenging power, with 44.9% in Halia Bentong and 46.2% in Halia Bara.”

The three scientists say their results indicate “the yield and pharmaceutical quality of Malaysian young ginger varieties can be enhanced by controlled environment production and CO₂ enrichment.”

Ghasemzadeh and Jaafar (2011) also focused on ginger (*Zingiber officinale* Roscoe), noting it is “an important horticultural crop in tropical Southeast Asia” and is the Asian continent’s “most widely used herb.” It “contains several interesting bioactive constituents and possesses health promoting properties (Rozanida *et al.*, 2005).” Ghasemzadeh and Jaafar lament “no information is available on the effect of CO₂ concentration on the polyphenolic content and scavenging capacity against active oxygen species of Malaysian young ginger varieties.”

The two Malaysian scientists grew two varieties

of ginger (Halia Bentong and Halia Bara) from rhizomes placed in polyethylene bags filled with a 1:1 mixture of burnt rice husk and coco peat for a period of 16 weeks in controlled-environment chambers maintained at two atmospheric CO₂ concentrations (400 and 800 ppm). They measured a number of important plant properties during and after the growing period.

In response to the increase in the air’s CO₂ content, Ghasemzadeh and Jaafar state, their research showed the rate of photosynthesis was increased by 65% in Halia Bentong and by 46% in Halia Bara, which led to total biomass increases of 48% in Halia Bentong and 76% in Halia Bara. Total flavonoids in the new rhizomes of Halia Bentong and Halia Bara rose by 82% and 118%, respectively, and total phenolics in the same two varieties rose by 154% and 183%, respectively.

The two researchers say their study revealed “ginger has good free radical scavenging ability and therefore can be used as a radical inhibitor or scavenger, acting possibly as a primary antioxidant.” Also, increasing the CO₂ content of the atmosphere “can enhance the antioxidant activity of ginger extract, especially in its rhizomes,” which can be of great value because it thereby “increases the concentrations of several therapeutic compounds.”

Ibrahim and Jaafar (2011) report “the antioxidant properties in food have been a focus of interest in recent years due to the health maintenance functions of these components that can help reduce the risk of chronic diseases such as cancer, hypertension and diabetes.” This phenomenon, they note, “is attributed to the high scavenging activity of antioxidants towards free radicals that are usually associated with these diseases (Namiki, 1990; Byers and Guerrero, 1995).” They used a randomized complete block design 3 by 3 experiment to study and distinguish the relationships among production of secondary metabolites, total phenolics, total flavonoids, glutathione, oxidized glutathione, soluble carbohydrate, and antioxidant activities of the Malaysian medicinal herb *Labisia pumila* Blume under three levels of CO₂ enrichment (400, 800, and 1,200 ppm) for 15 weeks.

The two Universiti Putra Malaysia researchers write, “secondary metabolites, glutathione, oxidized glutathione and antioxidant activities in a descending manner came from the leaf enriched with 1200 ppm CO₂ > leaf 800 ppm CO₂ > leaf 400 ppm CO₂ > stem 1200 ppm CO₂ > stem 800 ppm CO₂ > stem 400 ppm CO₂ > root 1200 ppm CO₂ > root 800 ppm CO₂ > root 400 ppm CO₂,” and “correlation analyses

revealed strong significant positive coefficients of antioxidant activities with total phenolics, flavonoids, glutathione and oxidized glutathione,” indicating “an increase in antioxidative activity of *L. pumila* under elevated CO₂ might be up-regulated by the increase in production of total phenolics, total flavonoids, glutathione, oxidized glutathione and soluble sugar.” Ibrahim and Jaafar conclude their study results imply “the medicinal potential of herbal plants such as *L. pumila* can be enhanced under elevated CO₂, which simultaneously improved the antioxidative activity that was indicated by the high oxygen radical absorbance activity against peroxyl radicals, superoxide radicals, hydrogen peroxide and hydroxyl radicals.”

Also studying *Labisia pumila* Blume, Jaafar *et al.* (2012) wrote, “plant antioxidants have been a focus of attention in recent years due to the health preservation functions of these components that can help reduce the threat of chronic diseases such as cancer, diabetes and hypertension.” These benefits, they note, are “attributed to the high scavenging activity of antioxidants towards free radicals that are usually associated with these diseases (Byers and Guerrero, 1995).” Among this group of plant compounds are phenolic acids and flavonoids, both of which exhibit, they state, “high anti-inflammatory and anti-carcinogenic activities (Heijnen *et al.*, 2001; Chun *et al.*, 2003).” In addition, phenolics and flavonoids can function as reducing agents, free radical scavengers, and quenchers of singlet oxygen formation (Chan *et al.*, 2008). Many of the components of polyphenols have been proven to have significant roles in curing cancer and other human ailments (Harborne and Williams, 2000).

Jaafar *et al.* conducted a split plot 3 x 3 experiment designed to examine the impact of 15 weeks of exposure to three concentrations of CO₂ (400, 800, and 1,200 ppm) on the phenolic and flavonoid compound profiles—as well as the antioxidant activities—of three varieties (*alata*, *pumila*, and *lanceolata*) of *Labisia pumila* Benth. or kaci fatimah, as it is commonly known throughout Southeast Asia. They describe the latter as “a sub-herbaceous plant with creeping stems from the family Myrsinaceae that is found widespread in Indochina and throughout the Malaysian forest”; it has historically been used to help maintain a healthy female reproductive system.

The three Malaysian researchers report that when exposed to elevated CO₂ (1200 ppm), “gallic acid increased tremendously, especially in var. *alata* and *pumila* (101–111%), whilst a large quercetin increase was noted in var. *lanceolata* (260%), followed closely

by *alata* (201%).” They also found “caffeic acid was enhanced tremendously in var. *alata* (338–1100%) and *pumila* (298–433%),” and “rutin continued to increase by 262% after CO₂ enrichment.” In addition, they note naringenin was enhanced by 1,100% in var. *pumila*. Finally, they report “the increase in production of plant secondary metabolites in *L. pumila* was followed by enhancement of the antioxidant activity under exposure of elevated CO₂.”

Moghaddam *et al.* (2011) explain *Centella asiatica* or Gotu Kola is a small herbaceous annual plant that has been used as a medicinal herb or nutraceutical in Ayurvedic, African, and traditional Chinese medicine for more than 2,000 years, valued for its mildly antibacterial, antiviral, and anti-inflammatory properties. It also has been used as a rejuvenating diuretic herb that is purported to clear toxins, reduce inflammations and fevers, improve healing and immunity, improve memory, and provide a balancing effect on the nervous system.

The six scientists grew well-watered and fertilized *C. asiatica* plants for four to five weeks in individual polybags filled with a 1:1:1 mix of sand, coco dust, and compost within controlled environment chambers, where CO₂ concentrations of 400 and 800 ppm were maintained, the researchers write, “for two hours every day between 8:30 to 10:30 am.” At the end of these four- to five-week periods the plants were harvested and their leaves assessed for total biomass and total flavonoid content. The latter substance is considered to be the source of the many health benefits attributed to the species.

Moghaddam *et al.* report the daily two-hour 400 ppm increase in the controlled environment chambers’ atmospheric CO₂ concentration led to a 193% increase in *C. asiatica* leaf biomass, a 264% increase in plant water use efficiency, and a 171% increase in leaf total flavonoid content. The six scientists conclude, “collectively, the enhancement in yield and quality provides an economic motivation to produce a consistent pharmaceutical-grade product for commercial purposes,” via what they describe as “controlled environment plant production.” It also stands to reason the ongoing rise in the atmosphere’s CO₂ concentration should be gradually increasing the medicinal potency of *C. asiatica* plants either growing wild or cultivated out-of-doors.

Ibrahim and Jaafar (2012) studied the oil palm *Elaeis guineensis* (Jacq.)—the highest-yielding vegetable oil producer in the world—which has gained wide recognition because of the health-promoting properties of some of its flavonoids and phenolics, which the two scientists describe as

“natural antioxidants that may reduce oxidative damage to the human body,” citing Mandel and Youdim (2004). For 15 weeks, the pair of researchers grew initially-five-month-old seedlings of three progenies of oil palm (deli AVROS, Deli Yangambi, and Deli URT) within growth chambers maintained at atmospheric CO₂ concentrations of either 400, 800, or 1,200 ppm, measuring a large number of important plant properties and processes.

Ibrahim and Jaafar discovered the production of total flavonoids and phenolics was highest under 1,200 and lowest at 400 ppm CO₂, and “the antioxidant activity, as determined by the ferric reducing/antioxidant potential (FRAP) activity increased with increasing CO₂ levels.” In leaves, for example, they found the quantity of “total flavonoids was enhanced by 86% and 132%, respectively, in 800 and 1200 ppm compared to 400 ppm CO₂,” and total phenolics “increased by 52% to 91% under elevated CO₂ compared to the ambient CO₂ condition.” Ibrahim and Jaafar say their findings “suggest that enrichment with higher than ambient CO₂ level is able to enhance the production of gallic acid and rutin in oil palm seedlings.” This finding is important because these bioactive components, as they describe them, “act as free radical scavengers, and hence can reduce the possibilities of major diseases such as cancers of leukemia, breast, bone and lung,” citing Kaufman *et al.* (1999) and Wink (1999).

In light of the research discussed above, it is clear atmospheric CO₂ enrichment 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 (Horiuchi, 2000; Tuljapurkar and Boe, 2000). As the atmosphere’s CO₂ content continues to rise, humanity may be helped even more in this regard in the years and decades to come.

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Climate Change Reconsidered II: Biological Impacts

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7.8.4 Health-Harming Substances

- There appears to be little reason to expect any significant CO₂-induced increases in human-health-harming substances produced by plants as the atmosphere's CO₂ concentration continues to rise.

Whereas IPCC makes no mention of the CO₂-induced enhancement of certain health-promoting substances in plants, as described in the subsections above, it is quick to point out the possibility of a CO₂-induced enhancement in certain health-harming substances. The research on that topic is the focus of this subsection.

Wayne *et al.* (2002) grew common ragweed plants from seed in controlled-environment glass-houses maintained at ambient (350 ppm) and enriched (700 ppm) atmospheric CO₂ concentrations for 84 days. They then sampled the pollen from the central plants of each stand, assessed the pollen's characteristics, and harvested all mature seeds and above-ground shoot material. They report, "stand-level pollen production was 61% higher in elevated versus ambient CO₂ environments" and "CO₂-induced growth stimulation of stand shoot biomass was similar to that of total pollen production." Although the researchers admit it would be "challenging to accurately predict the future threat to public health caused by CO₂-stimulated pollen production"—because "it is likely that plant pollen production will also be influenced by factors expected to change in concert with CO₂, including temperature, precipitation, and atmospheric pollutants"—they nevertheless suggest "the incidence of hay fever and related respiratory diseases may increase in the future."

Weber (2002) discussed the study of Wayne *et al.* in a guest editorial published in the same issue of the *Annals of Allergy, Asthma & Immunology*. He begins by noting "one can always wonder whether such manipulations [i.e., those employed in Wayne *et al.*'s study] have any relationship to present reality, or indeed, conditions that one can expect in the near future," and then proceeds methodically to his

conclusion: "it would be premature to assume that increased pollen grain numbers necessarily lead to an increased aeroallergen exposure."

Weber notes, "allergenic activity of short ragweed will vary from year to year, even from the same source and supplier (Maasch *et al.*, 1987)," and he cites Lee *et al.* (1979) as having found "varying potency in plants at the same site from year to year, which [were] attributed to seasonal climatic differences, primarily of rainfall." The latter researchers found a four-fold range in the allergenic potency of ragweed pollen within a single county in Illinois (USA). Consequently, Weber concludes "a constant relationship between pollen mass and allergenic protein content is not a given," and it will remain speculative until scientists determine whether "the increased pollen grains seen with the increased ambient CO₂ levels maintain the same ratio of allergenic proteins."

A further demonstration of the tenuousness of the suggestion of Wayne *et al.*—that "the incidence of hay fever and related respiratory diseases may increase in the future" because of the near-universal growth-promoting effects of atmospheric CO₂ enrichment—is provided by Rogers *et al.* (2006). They collected and vernalized ragweed seeds by sowing them in containers kept in a refrigerator maintained at 4°C. They transferred one-third of the seeded containers at 15-day intervals to glasshouse modules maintained at atmospheric CO₂ concentrations of either 380 or 700 ppm, and the seeds were allowed to germinate (also at 15-day intervals, with the middle germination date approximating that of plants currently growing naturally in the vicinity of where the seeds were collected). They kept the seeds under well-watered and fertilized conditions until the seeds senesced. The researchers then harvested the seeds and conducted assessments of plant and allergenic pollen biomass.

As best as can be determined from the graphical representations of Rogers *et al.*'s data, the end-of-season CO₂-induced increase in aboveground plant biomass was about 16% for the date of emergence typical of the present, and the corresponding increase in pollen production was about 32%. For the 15-day earlier date of emergence, which was chosen to represent "anticipated advances of spring several decades into the future" based upon projected rates of future global warming, the end-of-season CO₂-induced change in aboveground plant biomass was only about +3%, and the end-of-season CO₂-induced change in pollen production was actually a negative 3%.

The most meaningful way of viewing the results, then, is to determine the change in pollen production that would occur in going from today's atmospheric CO₂ concentration and date-of-onset of spring (380 ppm, middle date of germination) to the elevated CO₂ concentration and earlier date-of-onset of biological spring (700 ppm, 15-day earlier date of germination); when this is done, the production of allergenic pollen is seen to rise by just 1–2%.

Caporn *et al.* (1999) studied bracken, a weed that poses a 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 and high levels of fertilization. They found the elevated CO₂ consistently increased rates of net photosynthesis in bracken from 30 to 70%, depending on soil fertility and time of year. The elevated CO₂ did not increase total plant dry mass or the dry mass of any plant organs, including rhizomes, roots, and fronds. The only significant effect of the elevated CO₂ on bracken growth was observed in the normal nutrient regime, where elevated CO₂ reduced the area of bracken fronds.

Matros *et al.* (2006) grew tobacco plants in pots filled with quartz sand placed in controlled-climate chambers maintained at either 350 or 1,000 ppm CO₂ for eight weeks, irrigating them daily with a complete nutrient solution containing either 5 or 8 mM NH₄NO₃. Some of the plants in each treatment were mechanically infected with potato virus Y (PVY) when they were six weeks old. At the end of the study, the researchers report, the 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. In addition, with respect to the PVY part of the study, they found the plants grown at high CO₂ “showed a markedly decreased spread of virus.”

Matros *et al.* report “tobacco plants grown under elevated CO₂ show a slight decrease of nicotine contents,” and “elevated CO₂ resulted in reduced spread of PVY.” Most people likely would consider both of these impacts beneficial; potato virus Y is economically important because it infects many crops and ornamental plants throughout the world, and nicotine is nearly universally acknowledged to have significant negative effects on human health (Topliss *et al.*, 2002).

Mohan *et al.* (2006) investigated the effects of an extra 200 ppm of atmospheric CO₂ on the growth and

development of *Toxicodendron radicans*, commonly known as poison ivy, as well as its effect on the plant's toxicity, over a period of six years at the Duke Forest FACE facility, where the noxious vine grew naturally in a loblolly pine plantation's understory. The researchers surrounded clumps of it with 4 cm plastic-mesh enclosures to protect them from damage by indigenous white-tailed deer. This long and detailed study revealed atmospheric CO₂ enrichment increased poison ivy photosynthesis by 77% and boosted its water use efficiency by 51%. At the end of the study's sixth year, the aboveground biomass of poison ivy plants in the CO₂-enriched plots was 62% greater than that of poison ivy plants in the ambient-treatment plots. In addition, the high-CO₂-grown plants produced “a more allergenic form of urushiol,” the substance that produces the plant's allergic reaction in humans.

Not unsurprisingly, the seven scientists say their findings indicate under future levels of atmospheric CO₂, poison ivy “may grow larger and become more noxious than it is today.” And so it may, but the story is not quite that simple, as the next study indicates.

Londre and Schnitzer (2006) studied woody vines or lianas, focusing on changes over a period of 45 years in 14 temperate deciduous forests of southern Wisconsin (USA). During that time (1959–1960 to 2004–2005), the air's CO₂ concentration rose by 65 ppm, the mean annual air temperature of the region rose by 0.94°C, and its mean winter air temperature rose by 2.40°C, but its mean annual precipitation did not change. The researchers found, contrary to their initial hypothesis, “liana abundance and diameter did not increase in the interiors of Wisconsin (USA) forests over the last 45 years.” *Toxicodendron radicans*, or poison ivy—which they note “grew markedly better under experimentally elevated CO₂ conditions than did competing trees” in the study of Mohan *et al.* (2006)—decreased in abundance over this time period, and significantly.

The two researchers say their study suggests “lianas are limited in the interiors of deciduous forests of Wisconsin by factors other than increased levels of CO₂.” It is likely, for example, the growth of interior-forest lianas was limited by the enhanced tree growth provided by the CO₂ increase, which resulted in the trees becoming more competitive with the vines because of CO₂-induced increases in tree leaf numbers, area, and thickness, all of which would lead to less light being transmitted to the lianas growing beneath the forest canopy. This phenomenon apparently negated the enhanced propensity for growth that was provided the vines by the increase in

the atmosphere's CO₂ concentration—the potential growth was not realized because the declining light intensity prevented it.

Londre and Schnitzer provide support for this reasoning in their finding that “compared to the forest interior, lianas were >4 times more abundant within 15 m of the forest edge and >6 times more abundant within 5 m of the forest edge.” The two researchers note this “strong gradient in liana abundance from forest edge to interior” “was probably due to light availability.” In addition, they say their results “are similar to findings in tropical forests, where liana abundance is significantly higher along fragmented forest edges and within tree fall gaps.”

In conclusion, there appears to be little reason to expect any significant CO₂-induced increases in human-health-harming substances produced by plants as the atmosphere's CO₂ concentration continues to rise.

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Appendix 1

Acronyms

ABS	abscisic acid	BTDV	bluetongue disease virus
AGB	aboveground biomass	BVOC	biogenic volatile organic compound
aDGVM	adaptive dynamic global vegetation model	BYDV	barley yellow dwarf virus
ADS	Asian dust storm	C	carbon
AFLP	amplified fragment length polymorphism	C₃	C ₃ carbon fixation pathway for photosynthesis
AGW	anthropogenic global warming	C₄	C ₄ carbon fixation pathway for photosynthesis
AM	arbuscular mycorrhizal	Ca	CO ₂ concentration in the air
AMF	arbuscular mycorrhizal fungi	CAM	crassulacean acid metabolism
AMI	acute myocardial infarction	CASA	Carnegie-Ames-Stanford Approach
AMO	Atlantic Multidecadal Oscillation	CBD	cerebrovascular disease
APSIM	Agricultural Production Systems Simulator	CBSC	carbon-based secondary compounds
AO/NAO	Arctic Oscillation/North Atlantic Oscillation	CCA	canonical correspondence analysis
APS	atmospheric pollen season	CDC	Canadian Drought Code
ARPEGE	Action de Recherche Petite Echelle Grande Echelle (Research Project on Small and Large Scales)	CEC	carbon exchange capacity
AsA	ascorbic acid	CER	CO ₂ exchange rate
AVHRR	Advanced Very High Resolution Radiometer	CERES	Crop Environment Resources Synthesis
Ba	barium	CEVSA	Carbon Exchanges in the Vegetation-Soil-Atmosphere System
BAI	basal area index	CH₂ClI	iodocarbon chloriodomethane
BioCON	Biodiversity, Carbon Dioxide, and Nitrogen Effects on Ecosystem Functioning	CH₃Cl	methyl chloride
BIOME3	Biogeochemical Model	CH₄	methane
BP	before present	CH₂I₂	diiodomethane
BSW	bog surface wetness	CHD	coronary heart disease
Bt	<i>Bacillus thuringiensis</i>	CLEH	climate-linked epidemic hypothesis
BTD	bluetongue disease	CO₂	carbon dioxide
		CPR	Continuous Plankton Recorder
		CS₂	carbon disulfide
		CSIRO	Commonwealth Scientific and Industrial Research Organization (Australia)

Climate Change Reconsidered II: Biological Impacts

Cu	copper	GPCP	Global Precipitation Climatology Project
CVD	cardiovascular disease	GPP	gross primary production
CZCS	Coastal Zone Color Scanner	gr	gram(s)
DAE	days after emergence	GSH	glutathione
DAS	days after seeding	GtC	gigatons of carbon
DBH	diameter at breast height	H₂O₂	hydrogen peroxide
DGGE	denaturant gradient gel electrophoresis	H₂S	hydrogen sulfide
DHZR	dihydrozeatin ribosidem	HC1	Hidden Cave (Guadalupe Mountains)
DIC	dissolved organic carbon	HR	heterotrophic respiration
DM	dry matter	HSG	hematite stained grain
DMS	dimethyl sulfide	IAA	indole-3 acetic acid
DNA	deoxyribonucleic acid	IC	ischemic stroke
DOC	dissolved organic carbon	IE	infection efficiency
DTR	diurnal temperature range	IMAR	Inner Mongolia Autonomous Region
ECM	ectomycorrhizal	iPA	isopentenyl adenosine
EF-Tu	protein synthesis elongation factor	IPCC	Intergovernmental Panel on Climate Change
ENSO	El Niño-Southern Oscillation	IPCC 2007-I	Intergovernmental Panel on Climate Change – Group 1 Contribution
EPA	Environmental Protection Agency	IPCC 2007-II	Intergovernmental Panel on Climate Change – Group II Contribution
EU	European Union	IPCC 2007-III	Intergovernmental Panel on Climate Change – Group III Contribution
EVI	Enhanced Vegetation Index	IPCC-FAR	Intergovernmental Panel on Climate Change – First Assessment Report
FA	fluctuating asymmetry	IPCC-SAR	Intergovernmental Panel on Climate Change – Second Assessment Report
FACE	free-air CO ₂ enrichment	IPCC-TAR	Intergovernmental Panel on Climate Change – Third Assessment Report
FACTS	Forest Atmosphere Carbon Transfer and Storage	IPCC-AR4	Intergovernmental Panel on Climate Change – Fourth Assessment Report
FATI	free-air temperature increase	IPCC-AR5	Intergovernmental Panel on Climate Change – Fifth Assessment Report
FAO	Food and Agriculture Organization	IUCN	International Union for Conservation of Nature
Fe	iron	IWUE (iWUE)	intrinsic water use efficiency
FRAP	ferric reducing/antioxidant potential	ka	thousand years
GA3	gibberellic acid	kDa	kilodalton
GAM	generalized additive model	KPRNA	Konza Prairie Research Natural Area
GBR	Great Barrier Reef	kS	specific conductivity
GCM	General Circulation Models	LBM	larch budmoth
GCTE	Global Change and Terrestrial Ecosystems	LCLUC	land cover/land use change
GDP	Gross Domestic Product		
GIMMS	Global Inventory Modeling and Mapping Studies		
GLO-PEM	Global Production Efficiency Model		
gNDVI	Normalized Difference Vegetation Index over the Growing Season		

Appendix 1: Acronyms

LGM	Last Glacial Maximum	PDO	Pacific Decadal Oscillation
LIA	Little Ice Age	PDSI	Palmer Drought Severity Index
LIG	last interglacial	PET	physiologically equivalent temperature
LST	land surface temperature	PETM	Palaeocene-Eocene Thermal Maximum
m	meter	PHACE	prairie heating and CO ₂ enrichment
Ma	million years	PIH	primary intracerebral hemorrhagic stroke
Ma BP	million years before present	PM	particulate matter
MAAT	mean annual air temperature	PNL	progressive nitrogen limitation
MODIS	moderate resolution imaging spectroradiometer	PNUE	photosynthetic nitrogen use efficiency
Mg	megagram	POM	particulate organic matter
MWP	Medieval Warm Period	PopFACE	poplar free-air CO ₂ enrichment
MXD	maximum latewood density	ppb	parts per billion
N	nitrogen	PPB	purple phototrophic bacteria
N₂O	nitrous oxide	ppm	parts per million
NaCl	sodium chloride	ppmv	parts per million by volume
NAO	North Atlantic Oscillation	PRECIS	Providing Regional Climates for Impact Studies
NAS	National Academy of Sciences (USA)	PSII	photosystem II
NASA	National Aeronautics and Space Administration (USA)	RD	respiratory disease
NDVI	Normalized Difference Vegetation Index	Rda	area-based dark respiration
NEP	net ecosystem production	Rdm	mass-based dark respiration
NEE	net ecosystem exchange	rDNA	ribosomal deoxyribonucleic acid
NEEa	annual net ecosystem exchange	RERCA	recent rate of carbon accumulation
NH₄	ammonium	ROS	reactive oxygen species
NIPCC	Nongovernmental International Panel on Climate Change	RSV	respiratory syncytial virus
NOAA	National Oceanic and Atmospheric Administration (USA)	RTI	respiratory tract infection
NPP	net primary productivity	RWP	Roman Warm Period
NUE	nitrogen use efficiency	SACC	screen-aided CO ₂ control
O₃	ozone	SB	Southern Beaufort Sea
OCS	carbonyl sulfide	SCC	Swiss canopy crane
OM	organic matter	SCD	sudden cardiac death
ORNL	Oak Ridge National Laboratory (USA)	SCPDSI	self-calibrating Palmer Drought Severity Index
OTC	open-top chamber	SeaWiFS	Sea-Viewing Wide Field-Of-View Sensor
P	phosphorous	SEPP	Science and Environmental Policy Project
PAR	photosynthetically active radiation	SET	surface elevation table
Pg	petagram	SLR	sea-level rise
PAL	Pathfinder AVHRR [Advanced Very High Resolution Radiometer] Land	SO₂	sulfur dioxide

Climate Change Reconsidered II: Biological Impacts

SOC	soil organic carbon	TRMM	Tropical Rainfall Measuring Mission
SOM	soil organic matter	TRW	tree-ring width
SOS	start of spring	TSD	temperature-dependent sex determination
SPAR	soil-plant-atmosphere-research	UCD	unusually cold day
SPM	Summaries for Policymakers	UN	United Nations
SPS	sucrose-phosphate synthase	UNEP	United Nations Environment Program
SST	sea surface temperatures	UNFCCC	United Nations Framework Convention on Climate Change
TBARS	thiobarbituric acid reactive substance	UNT	unified neutral theory
TBE	tick-borne encephalitis	UV	ultraviolet
TBEV	tick-borne encephalitis virus	VOC	volatile organic compound
TDR	time domain reflectometry	VPD	vapor pressure deficit
TEM	terrestrial ecosystem model	VSP	vegetative storage protein
Tg	teragram	WH	Western Hudson Bay
Tmax	maximum temperature	WHO	World Health Organization
Tmin	minimum temperature	WMO	World Meteorological Organization
TMI	Tropical Rainfall Measuring Mission Microwave Imager	WSC	water-soluble carbohydrate
Topt	optimum temperature	WT	wild type
TP	Tibetan Plateau	WUE	water use efficiency
TRFO	tropical rainforest	ZR	zeatin riboside

Appendix 2

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Appendix 3

Table 1.1.1 — Plant Dry Weight (Biomass) Responses to Atmospheric CO₂ Enrichment

Table 1.1.1 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 percent enhancement, the adjusted 300 ppm CO₂ growth response was calculated as $(300/350) \times 60\% = 51\%$.

The data in this 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. New data are added to the database at approximately weekly intervals and can be accessed free of charge at the center's Web site 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.

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Abelmoschus esculentus [Okra]	1	8%	0%
Abies alba [Silver Fir]	5	33.20%	11.60%
Abies faxoniana [Minjiang Fir]	4	20.30%	2.90%
Abutilon theophrasti [Velvet Leaf]	14	32.10%	13.70%
Acacia karroo [Sweet Thorn]	3	53.70%	5.90%
Acacia aneura [Mulga Acacia]	1	0%	0%
Acacia auriculiformis [Acacia, Earleaf]	1	0%	0%
Acacia catechu [Black Cutch]	7	71.10%	10.70%
Acacia coleii [Acacia]	1	89%	0%
Acacia coriacea [Wiry Wattle]	1	50%	0%
Acacia dealbata [Silver Wattle]	1	106%	0%
Acacia implexa	1	77%	0%
Acacia irrorata	1	64%	0%

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Acacia magium [Brown Saiwood]	3	19%	6.90%
Acacia mearnsii [Black Wattle]	1	48%	0%
Acacia melanoxylon [Blackwood]	1	164%	0%
Acacia minuta [Coastal Scrub Wattle]	2	110%	22.60%
Acacia nilotica [Gum Arabic Tree]	11	241.50%	53.90%
Acacia saligna [Orange Wattle]	1	55%	0%
Acacia tetragonophylla [Acacia]	1	55%	0%
Acer barbatum [Southern Sugar Maple]	1	95%	0%
Acer pensylvanicum [Striped Maple]	4	28.80%	8.40%
Acer pseudoplatanus [Sycamore]	3	34.30%	12.80%
Acer rubrum [Red Maple]	13	44.20%	13.30%
Acer saccharum [Sugar Maple]	12	48.30%	13.10%
Achillea millefolium [Yarrow]	3	24.70%	12.60%

Climate Change Reconsidered II: Biological Impacts

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Aechmea cuculata x a. fasciata [Bromelaid Cv. Maya]	1	-6%	0%
Aechmea fasciata [Silver Vase Bromeliad]	5	26.20%	14.90%
Aechmea magdalenae [Understory Herb]	1	30%	0%
Agave deserti [Desert Agave]	4	34.80%	10.30%
Agave salmiana [Agave]	1	43%	0%
Agave vilmoreniana [Leaf Succulent]	2	14%	9.90%
Agropyron repens [C ₃ Grass]	1	41%	0%
Agropyron smithii [Western Wheatgrass]	3	50.30%	42.20%
Agrostemma githago [Corncockle]	1	21%	0%
Agrostis canina [Velvet Bentgrass]	1	124%	0%
Agrostis capillaris [Colonial Bentgrass]	9	37.10%	11.70%
Ailanthus excelsa [Indian Tree Of Heaven]	1	49%	0%
Albizia procera [Tall Albiza]	8	125.60%	16.30%
Allium fistulosum [Scallion]	1	135%	0%
Allotriopsis semialata [Cockatoo Grass]	6	41.20%	3.70%
Alnus maximowiczii [Alder Tree]	4	0.80%	6.20%
Alnus glutinosa [Black Alder]	6	32.50%	6.10%
Alnus hirsuta [Manchurian Alder]	7	17.10%	5.70%
Alnus incana [Mountain Alder]	1	50%	0%
Alnus rubra [Red Alder]	6	34.50%	7.70%
Amaranthus hybridus [Slim Amaranth]	6	14%	5.60%
Amaranthus hypochondriacus [Grain Amaranth]	2	5.50%	3.90%
Amaranthus retroflexus [Redroot Amaranth]	17	6.40%	3.30%
Amaranthus tricolor [Amaranth]	1	20%	0%
Amaranthus viridis [Slender Amaranth]	4	-2.30%	3.20%
Ambrosia artemisiifolia [Annual Ragweed]	13	28.80%	7%
Ambrosia dumosa [White Burrobush]	2	164%	36.10%
Ambrosia trifida [Great Ragweed]	3	26%	8.20%
Amorpha canescens [Leadplant]	3	40.30%	63.30%
Amur Silvergrass [Miscanthus sacchariflorus]	1	-27%	0%
Ananas comosus [Pineapple]	2	5%	9.20%
Andropogon appendiculatus [Vlei Bluegrass]	6	50.50%	6.90%
Andropogon gerardii [Big Bluestem]	12	20.30%	7.20%
Andropogon virginicus [Broomsedge]	2	0%	0%
Anemone cylindrica [Candle Anemone]	1	84%	0%
Anthoxanthum odoratum [Sweet Vernal Grass]	1	170%	0%
Anthyllis vulneraria [Common Kidney]	6	45.30%	17.50%

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Vetch]			
Arabidopsis thaliana [Thale Cress]	17	162.30%	51.20%
Arachis glabrata [Florigrade Peanut]	2	20.50%	1.10%
Arachis hypogaea [Peanut]	38	60.30%	16.10%
Armeria maritima [Thrift Seapink]	1	-45%	0%
Arrhenatherum elatius [Tall Oatgrass]	7	18.60%	9.60%
Artemisia absinthium [Absinth Sagewort]	2	161.50%	44.20%
Artemisia tridentata [Big Sagebrush]	4	24.30%	6.10%
Asclepias syriaca [Common Milkweed]	3	31%	15.50%
Asclepias tuberosa [Butterfly Milkweed]	1	108%	0%
Aster pilosus [White Oldfield Aster]	2	62.50%	26.50%
Austrodanthonia caespitosa [Wallaby Grass]	2	78%	4.20%
Avena barbata [Slender Oat]	6	22.80%	5.80%
Avena fatua [Wild Oat]	8	32.90%	8.40%
Avena sativa [Red Oat]	15	40.60%	15.40%
Avicennia germinans [Black Mangrove]	2	22.50%	5.30%
Azolla caroliniana [Water Fern]	3	28%	9.10%
Azolla filiculoides [Water Fern]	4	20.80%	3.80%
Azolla pinnata [Water Fern]	4	54.30%	27%
Bauhinia variegata [Mountain Ebony]	7	78.90%	9.10%
Bellis perennis [Lawn Daisy]	3	95.70%	0.30%
Beta vulgaris [Common Beet]	33	65.70%	19.30%
Betula ermanii [Birch, Ermans]	2	6%	0.70%
Betula maximowicziana [Birch, Monarch]	2	15%	1.40%
Betula alleghaniensis [Yellow Birch]	15	34.30%	10.20%
Betula nana [Bog Birch]	1	0%	0%
Betula pendula [European White Birch]	32	32.30%	4.80%
Betula platyphylla [Japanese White Birch]	6	15.80%	3.40%
Betula populifolia [Gray Birch]	4	19.80%	8.30%
Betula pubescens [Downy Birch]	4	25.50%	6.50%
Bouteloua curtipendula [Sideoats Grama]	2	7%	22.60%
Bouteloua eriopoda [Black Grama]	1	21%	0%
Bouteloua gracilis [Blue Grama]	8	2.10%	9.80%
Brachypodium pinnatum [Heath Falsebrome]	1	0%	0%
Brassica alboglabra [Chinese Broccoli]	2	9%	0.70%
Brassica campestris	6	55.80%	8.50%
Brassica carinata [Abyssinian Mustard]	2	28%	1.40%

Appendix 3 – Plant Dry Weight (Biomass) Responses

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Brassica juncea [India Mustard]	2	28.50%	1.80%
Brassica kaber [Field Mustard]	1	29%	0%
Brassica napus [Oilseed Rape]	38	43.80%	5.20%
Brassica nigra [Black Mustard]	2	40.50%	10.30%
Brassica oleracea [Broccoli]	5	28.80%	8.50%
Brassica rapa [Mustard]	1	21%	0%
Bromus erectus [Erect Brome]	7	34.60%	6.80%
Bromus hordeaceus [Soft Brome]	2	43%	9.90%
Bromus inermis [Smooth Brome]	1	-13%	0%
Bromus madritensis [Compact Brome]	2	7%	14.10%
Bromus mollis [Soft Brome]	2	53.50%	2.50%
Bromus rubens [Foxtail Brome]	2	25%	7.80%
Bromus sterilis [Poverty Brome]	1	0%	0%
Bromus tectorum [Cheatgrass]	1	36%	0%
Buchloe dactyloides [Buffalo Grass]	1	-5%	0%
Bulbophyllum longissimum [Orchid, Tropical]	4	15.50%	13.70%
Cajanus cajan [Pigeon Pea]	4	75%	20.50%
Calamagrostis angustifolia [Reed Grass]	24	14.80%	2.10%
Calamagrostis purpurea [Scandinavian Small Reed]	2	18%	7.80%
Calamagrostis epigeios [Chee Reedgrass]	2	98.50%	0.40%
Calcidiscus leptoporus [Marine Coccolithophore]	2	18.50%	3.20%
Calluna vulgaris [Heather]	9	17.10%	5.40%
Capsicum chinense [Yellow Lantern Chili]	1	49%	0%
Caragana intermedia [Deciduous Shrub of Semi-arid Northern China]	6	54.50%	4.50%
Cardamine hirsuta [Hairy Bittercress]	2	-0.50%	3.90%
Carex arenaria [Sand Sedge]	1	26%	0%
Carex bigelowii [Bigelow's Sedge]	1	0%	0%
Carex flacca [Heath Sedge]	5	73.80%	18.20%
Carex rostrata [Beaked Sedge]	1	44%	0%
Cariniana legalis [Jequitiba Tree]	2	20%	2.80%
Carpinus betulus [European Hornbeam]	3	35.30%	26.40%
Cassia fasciculata [Sleepingplant]	2	17.50%	27.20%
Cassia nictitans [Partridge Pea]	1	22%	0%
Cassia obtusifolia [Coffeeweed]	2	31.50%	7.40%
Castanea sativa [Sweet Chesnut]	4	12.80%	2.20%
Casuarina equisetifolia [Beach Sheoak]	1	54%	0%
Catopsis juncifolia [Bromeliad, Tropical]	4	13.30%	5.20%

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Cenchrus ciliaris [Buffel Grass]	1	242%	0%
Centaurea solstitialis [Yellow Star Thistle]	1	500%	0%
Centella asiatica [Centella]	1	145%	0%
Cerastium fontanum [Chickweed]	1	51%	0%
Ceratonia siliqua [Carob]	10	38.10%	9.70%
Ceratophyllum tetragonolobum	2	60%	42.40%
Chaetoceros muelleri [Marine Diatom]	2	18%	6.40%
Chamaecrista nictitans [Partridge Pea]	1	0%	0%
Chamaelucium uncinatum (Schauer) x Chamaelucium uncinatum (MS) [Lady Stephanie]	3	20.70%	3.40%
Chamerion angustifolium	1	228%	0%
Chamerops humilis [Mediterranean Fan Palm]	1	67%	0%
Chenopodium album [Lambsquarters]	20	46%	7.70%
Chenopodium bonus-henricus [Good King Henry]	1	21%	0%
Chlorella pyrenoidosa [Common Freshwater Microalga]	2	8%	0.70%
Chloris gayana [Rhodes Grass]	1	39%	0%
Cicer arietinum [Chickpea]	16	42.80%	3.80%
Cirsium arvense [Canadian Thistle]	3	83.30%	33.50%
Citrus [Ambersweet Orange Tree]	3	30.70%	1.20%
Citrus aurantium [Sour Orange Tree]	5	69.40%	9.10%
Citrus reticulata [Mandarin Orange Tree]	2	29.50%	3.90%
Citrus sinensis [Sweet Orange Tree]	2	38.50%	4.60%
Citrus sinensis x poncirus trifoliata [Carrizo Citrange]	2	40.50%	1.80%
Clarkia rubicunda [Ruby Chalice Fairyfan]	1	35%	0%
Coffea arabusta [Coffee]	2	175.50%	76.70%
Commelina benghalensis [Tropical Spiderwort]	1	61%	0%
Conium maculatum [Poison Hemlock]	1	21%	0%
Cornus florida [Eastern Flowering Dogwood]	2	121.50%	37.10%
Correa schlehtendalii	3	9.70%	0.30%
Crotalaria juncea [Sunn Hemp]	2	45%	9.90%
Croton urucurana [Dragons Blood Tree]	2	23.50%	4.60%
Cucumis melo [Cantaloupe]	3	4.70%	0.70%
Cucumis sativus [Garden Cucumber]	12	44.80%	6%
Cuphea viscosissima [Clammy Cuphea]	1	17%	0%
Cycas revoluta [Sago Palm]	1	172%	0%
Cynosurus cristatus [Crested Dogstailgrass]	1	30%	0%
Cyperus esculentus [Yellow Nutsedge]	1	16%	0%

Climate Change Reconsidered II: Biological Impacts

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Cyperus rotundus [Purple Nutsedge]	1	38%	0%
Dactylis glomerata [Orchardgrass]	15	18.30%	4.30%
Dalbergia latifolia [Indian Rosewood]	7	55.60%	7.80%
Danthonia richardsonii Cashmore [Wallaby Grass]	9	25%	8.60%
Datura stramonium [Jimsonweed]	3	36.70%	15.80%
Daucus carota [Carrot]	5	77.80%	32.30%
Deschampsia flexuosa [Wavy Hairgrass]	1	19%	0%
Desmazeria rigida [Ferngrass]	1	26%	0%
Digitalis purpurea [Purple Foxglove]	2	17.50%	2.50%
Digitaria natalensis [Natal Crabgrass]	6	13%	3.20%
Digitaria sanguinalis [Hairy Crabgrass]	2	39%	12.70%
Echinacea purpurea [Eastern Purple Coneflower]	4	191.50%	75.50%
Echinochloa crus-galli [Barnyard Grass]	19	49.80%	16.90%
Echium plantagineum [Salvation Jane]	4	15.80%	6.20%
Eichhornia crassipes [Common Water Hyacinth]	10	43.80%	12.20%
Elaeis guineensis [African Oil Palm]	1	89%	0%
Eleusine indica [Indian Goosegrass]	6	34%	17.40%
Elymus athericus	4	46.30%	20%
Elymus elymoides [Botlebrush Squirreltail]	1	24%	0%
Emiliana huxleyi [Marine Coccolithophores]	3	45%	34.70%
Epilobium hirsutum [Codlins and Cream]	1	9%	0%
Eragrostis curvula [Weeping Lovegrass]	7	48.10%	10.10%
Eragrostis orcuttiana [Annual Weed, C4]	1	462%	0%
Eragrostis racemosa [Narrowheart Lovegrass]	6	11.70%	1.80%
Erica tetralix [Crossleaf Heath]	4	23.80%	10.50%
Eriophorum vaginatum [Tussock Cottongrass]	5	105%	71.60%
Eucalyptus degluptax x e. camaldulensis [Eucalypt Hybrid]	2	45.50%	20.90%
Eucalyptus pauciflora [Snow Gum Tree]	10	67.10%	9.50%
Eucalyptus saligna [Sydney Blue Gum]	4	139.50%	46.80%
Eucalyptus cladocalyx [Sugargum]	2	87.50%	9.50%
Eucalyptus miniata [Darwin Woollybutt]	9	-2%	5.40%
Eucalyptus tetrodonta	9	132.80%	19.90%
Eupatorium adenophorum [Sticky Snakeroot]	5	27.40%	4.50%
Eupatorium japonicum [Pei Lan]	1	24%	0%
Eupatorium stoehadosmum [Orchid Herb]	3	15.30%	5.20%
Euphorbia lathyris [Myrtle Spurge]	2	36.50%	4.60%

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Fagopyrum esculentum [Common Buckwheat]	3	17.30%	9.90%
Fagus crenata [Japanese Beech]	1	31%	0%
Fagus grandifolia [American Beech]	1	88%	0%
Fagus sylvatica [European Beech]	23	23.60%	6%
Ferocactus acanthodes [California Barrelcactus]	1	30%	0%
Festuca rubra [Red Fescue]	4	29.50%	12%
Festuca arundinacea [Tall Fescue]	11	25.40%	7.20%
Festuca elatior [Tall Meadow Fescue]	1	40%	0%
Festuca ovina [Sheep Fescue]	6	47.70%	16.60%
Festuca pratensis [Meadow Fescue]	11	20.30%	10%
Flaveria trinervia [Clustered Yellowtops]	1	46%	0%
Fragaria x ananassa [Hybrid Strawberry]	4	42.80%	13.10%
Fraxinus americana [White Ash]	4	33.80%	7.30%
Fraxinus excelsior [European Ash]	10	13.40%	3.60%
Fraxinus pennsylvanica [Green Ash]	1	32%	0%
Galactia Elliottii [Elliott's Milkpea]	1	110%	0%
Gentianella germanica [Dwarf Gentian]	1	54%	0%
Ginkgo biloba [Maidenhair Tree]	1	78%	0%
Glycine max [Soybean]	190	45.50%	2.70%
Gmelina arborea [White Teak]	2	150.50%	6%
Gnaphalium affine [Cudweed]	1	21%	0%
Gonolobus ctenophorus	2	3.50%	12.40%
Gossypium hirsutum [Cotton]	41	58.40%	7.80%
Gracilaria lemaneiformis [Red Algae]	4	33.50%	13.90%
Grassland community in antwerp, belgium [Six Perennial Species]	1	48%	0%
Grassland, wyoming, usa [Four C ₃ Grasses In A Mixed-grass Prairie]	1	45%	0%
Grassland, Species-poor on a peaty gley soil	1	50%	0%
Grassland, Species-rich on a brown Earth soil over limestone	1	56%	0%
Guzmania Hilda [Guzmania]	1	63%	0%
Gypsophila paniculata [Babysbreath Gypsophila]	1	23%	0%
Hedera helix [English Ivy]	3	66%	10.60%
Helianthemum nummularium [Sun Rose]	1	0%	0%
Helianthus annuus [Sunflower]	13	36.50%	6.80%
Hemizonia congesta [Hayfield Tarweed]	2	48.50%	10.30%
Heterosigma akashiwo [A Marine Raphidophyte]	2	15%	2.10%
Heterotheca subaxillaris [Camphorweed]	1	20%	0%
Hizikia fusiforme [Hiziki (Brown	1	45%	0%

Appendix 3 – Plant Dry Weight (Biomass) Responses

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Seaweed))			
Holcus lanatus [Common Velvetgrass]	11	38.50%	10.40%
Hordeum vulgare [Barley]	35	34.60%	3.40%
Hydrilla verticillata [Water Thyme]	7	21.90%	3.30%
Hymenocallis littoralis [Spider Lily]	2	52%	2.80%
Hyparrhenia rufa [Jaragua]	2	33.50%	1.80%
Hypericum perforatum [St. John's Wort]	1	72%	0%
Hypnea spinella [Red Seaweed]	1	66%	0%
Hyptis suaveolens [Wild Spikenard]	1	1720%	0%
Ilex aquifolium [English Holly]	1	15%	0%
Ipomoea cairica [Mile A Minute Vine]	1	61%	0%
Ipomoea pes-caprae [Beach Morning Glory]	1	29%	0%
Ipomoea batatas [Sweet Potato]	6	33.70%	9.30%
Ipomoea hederacea [Ivyleaf Morningglory]	2	-21%	8.50%
Ipomoea lacunosa [Whitestar]	2	15%	14.80%
Juncus effuses [Soft Rush]	1	-5%	0%
Kielmeyera coriacea [Tropical Savanna Tree]	3	88.70%	55.50%
Koeleria macrantha [Prairie Junegrass]	1	2%	0%
Krameria erecta [Littleleaf Ratany]	2	102.50%	1.10%
Kummerowia striata [Japanese Clover]	1	26%	0%
Lactuca sativa [Garden Lettuce]	2	18.50%	6%
Lantana camara [Lantana]	3	131.70%	40.30%
Larix decidua [European Larch]	1	142%	0%
Larix kaempferi [Japanese Larch]	4	26.80%	10.30%
Larix laricina [Tamarack]	1	56%	0%
Larrea tridentata [Creosote Bush]	8	104.90%	22.90%
Lasthenia californica [California Goldfields]	2	27%	26.90%
Layia platyglossa [Coastal Tidytip]	1	12%	0%
Ledum palustre [Wild Rosemary]	1	0%	0%
Lemna gibba [Swollen Duckweed]	2	47%	11.30%
Lepidium latifolium [Pepperweed]	2	40%	7.10%
Lespedeza capitata [Roundhead Lespedeza]	3	333.70%	136.10%
Lespedeza cuneata [Chinese Lespedeza]	1	0%	0%
Leymus chinensis [Chinese Lyme-grass]	2	19.50%	8.80%
Linum usitatissimum [Common Flax]	2	68.50%	18.70%
Linum usitatissimum [Common Flax] in mixed stands with Linum usitatissimum	2	63.50%	15.90%
Liquidambar styraciflua [Sweetgum]	20	132.40%	23.50%

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Liriodendron tulipifera [Yellow Poplar]	3	34%	4.70%
Lolium multiflorum [Italian Ryegrass]	12	20%	3.80%
Lolium perenne [Perennial Ryegrass]	85	35.20%	4.60%
Lolium temulentum [Darnel Ryegrass]	3	44.70%	29.20%
Lomentaria articulata [Seaweed]	1	269%	0%
Lonicera japonica [Japanese Honeysuckle]	4	312.80%	73.70%
Lonicera sempervirens [Coral Honeysuckle]	1	30%	0%
Lotus corniculatus [Birdfoot Deer Vetch]	8	49.30%	12.90%
Lotus pedunculatus [Big Trefoil]	6	56%	26.50%
Lupinus angustifolius [Narrowleaf Lupine]	3	38%	7%
Lupinus luteus [European Yellow Lupine]	1	21%	0%
Lupinus perennis [Sundial Lupine]	11	56.40%	6.60%
Lycopersicon esculentum [Garden Tomato]	53	31%	3.50%
Lycopersicon lycopersicum [Tomato]	2	29.50%	5.30%
Macroptilium atropurpureum [Purple Bushbean]	1	43%	0%
Mangifera indica [Mango]	1	36%	0%
Manihot esculenta [Cassava]	4	13.80%	40.70%
Maranthos corymbosa	3	69%	14.30%
Medicago glomerata	1	17%	0%
Medicago lupulina [Black Medick]	6	45%	9.40%
Medicago minima [Burr Medick]	1	-6%	0%
Medicago sativa [Alfalfa]	85	37.40%	3.70%
Medicago truncatula [Barrelclover]	10	54.40%	6.30%
Melinis minutiflora [Molassesgrass]	2	32%	8.50%
Melinis repens [Red Natal Grass]	6	25.80%	7%
Mentha x piperita [Peppermint]	1	29%	0%
Microstegium vimineum [Nepalese Browntop]	3	-53.30%	15.60%
Mikania micrantha [Bittervine]	1	92%	0%
Miscanthus sacchariflorus [Amur Silvergrass]	1	-27%	0%
Molinia caerulea [Purple Moorgrass]	9	36.60%	9.40%
Nemophila menziesii [Menzies' Baby Blue Eyes]	1	0%	0%
Nicotiana tabacum [Cultivated Tobacco]	14	38.40%	7.40%
Nitzschia palea [Freshwater Diatom]	2	10%	4.90%
Nymphaea marliac [Water Lily]	2	162%	76.40%
Olea europaea [Olive Tree]	6	35.20%	14.10%
Onobrychis viciaefolia [Sainfoin]	1	21%	0%
Opuntia ficus-indica [Prickly Pear]	9	38.20%	13.30%

Climate Change Reconsidered II: Biological Impacts

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Orobancha minor [Hellroot]	1	0%	0%
Orontium aquaticum [Goldenclub]	12	19.80%	3%
Oryza sativa [Rice]	219	36.10%	2%
Oryzopsis hymenoides [Perennial Bunchgrass]	1	0%	0%
Paederia scandens [Chinese Fever Vine]	1	14%	0%
Panicum antidotale [Blue Panicgrass]	4	15.50%	6.30%
Panicum coloratum [Blue Panicgrass]	2	1%	15.60%
Panicum dichotomiflorum (Fall Panicgrass)	1	24%	0%
Panicum laxum [Lax Panicgrass]	4	30%	11%
Panicum maximum [Guineagrass]	1	-2%	0%
Panicum miliaceum [Broomcorn Millet]	1	-13%	0%
Panicum virgatum [Switchgrass]	1	-1%	0%
Papaver setigerum [Dwarf Breadseed Poppy]	1	390%	0%
Pascopyrum smithii [Western Wheatgrass]	5	63%	16.40%
Paspalum conjugatum [Hilograss]	1	18%	0%
Paspalum dilatatum [Dallas Grass]	2	71%	7.80%
Paspalum notatum [Bahagrass]	3	10%	1.90%
Paspalum plicatulum [Brownseed Paspalum]	1	9%	0%
Pasture in Switzerland (Orchard Grass and Red Clover)	12	29.10%	5.70%
Peanut, Rhizoma	1	57%	0%
Pelargonium x hortorum [Pelargonium]	3	3.30%	12.80%
Petalostemum villosum [Silky Prairie-Clover]	3	-9.30%	23.40%
Petunia hybrida [Petunia]	6	55%	9.80%
Phaeocystis [Phytoplankton]	1	0%	0%
Phalaris aquatica [Harding Grass]	13	24.60%	8.50%
Phalaris arundinacea [Canary Grass]	8	34.30%	12.10%
Pharus latifolius [Broad Stalkgrass]	1	144%	0%
Phaseolus acutifolius [Tepary Bean]	2	70%	9.90%
Phaseolus vulgaris [Garden Bean]	17	64.30%	20.30%
Phleum pratense [Timothy]	20	14.90%	3.40%
Phragmites communis [Wetland Reed]	1	-8%	0%
Phragmites japonica [Wetland Reed]	1	-11%	0%
Phyllanthus emblica [Emblie]	8	165%	16%
Physalis peruviana [Peruvian Groundcherry]	1	23%	0%
Phytolacca americana [American Pokeweed]	8	-2.40%	13.80%
[Phytoplankton]	1	7%	0%
Picea abies [Norway Spruce]	15	33.50%	4.90%

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Picea glauca [White Spruce]	7	106.10%	52.40%
Picea koraiensis [Spruce]	7	37.90%	8.70%
Picea mariana [Black Spruce]	17	37.70%	10.60%
Picea sitchensis [Sitka Spruce]	7	20.70%	5%
Pinus banksiana [Jack Pine]	3	18.30%	8.80%
Pinus densiflora [Japanese Red Pine]	9	22.40%	7.60%
Pinus eldarica [Eldarica Pine]	1	153%	0%
Pinus koraiensis [Korean Pine]	2	27%	15.60%
Pinus merkusii [Merkus Pine]	2	200%	43.10%
Pinus nigra [Black Pine]	1	22%	0%
Pinus palustris [Longleaf Pine]	8	19%	7.40%
Pinus ponderosa [Ponderosa Pine]	47	63.30%	11.60%
Pinus radiata [Monterey Pine]	1	36%	0%
Pinus strobus [Eastern White Pine]	3	31.70%	9%
Pinus sylvestris [Scots Pine]	63	35%	4.30%
Pinus taeda [Loblolly Pine]	67	60.90%	7.70%
Pinus uncinata [Mountain Pine]	1	0%	0%
Pisum sativum [Garden Pea]	29	29.20%	3.10%
Plantago erecta [Dwarf Plantain]	2	4.50%	11.70%
Plantago lanceolata [Narrowleaf Plantain]	11	46.20%	15.20%
Plantago major [Common Plantain]	3	31.70%	4.60%
Plantago maritima [Sea Plantain]	3	101.70%	27.90%
Plantago media [Hoary Plantain]	2	26.50%	5.30%
Plantago virginica [Virginia Plantain]	1	45%	0%
Poa alpina [Alpine Bluegrass]	2	79.50%	4.60%
Poa annua [Annual Bluegrass]	10	20.20%	9.10%
Poa pratensis [Kentucky Bluegrass]	9	113.90%	29.80%
Poa trivialis [Rough Bluegrass]	1	3%	0%
Polygonum cuspidatum [Japanese Knotweed]	3	48%	14.80%
Polygonum hydropiper [Marshpepper Knotweed]	2	40.50%	15.90%
Polygonum lapathifolium [Curlytop Knotweed]	5	19.40%	4.20%
Polygonum pensylvanicum [Pennsylvania Smartweed]	3	55.70%	1.80%
Polygonum persicaria [Spotted Ladysthumb]	2	38%	9.20%
Populus cathayana [Qing Yang]	4	39.80%	9.50%
Populus tremula x alba [Poplar, Hybrid]	2	17%	0.70%
Populus alba [White Poplar]	14	43.90%	4.70%
Populus deltoides [Eastern Cottonwood]	7	53.70%	13.60%

Appendix 3 – Plant Dry Weight (Biomass) Responses

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Populus deltoides x Populus deltoides [Robusta Poplar Clone]	6	63.30%	13.70%
Populus euramericana [Robusta Poplar]	18	110.30%	37.60%
Populus grandidentata [Bigtooth Aspen]	1	29%	0%
Populus nigra [Black Poplar]	15	53.90%	12.20%
Populus tremula x Populus tremula [Hybrid Aspen]	6	40.30%	18%
Populus tremuloides [Quaking Aspen]	35	58.10%	9.30%
Populus trichocarpa [Black Cottonwood]	5	124%	93.20%
Populus trichocarpa x Populus trichocarpa [Hybrid Poplar]	7	76.70%	23.40%
Prorocentrum minimum [A Marine Dinoflagellate]	2	20%	3.50%
Prosopis flexuosa [Deciduous Tree]	1	42%	0%
Prosopis glandulosa [Honey Mesquite]	13	37.70%	5.20%
Prunella vulgaris [Selfheal]	2	78%	17.70%
Prunus avium [Sweet Cherry]	8	59.80%	7.80%
Prunus laurocerasus [English Laurel]	1	56%	0%
Prunus persica [Peach Tree]	4	27.80%	0.80%
Prunus serotina [Black Cherry]	2	42%	1.40%
Pseudotsuga menziesii [Douglas-Fir]	6	9.70%	3.90%
Pteridium revolutum [Hairy Bracken]	3	49%	7.40%
Pteridium aquilinum [Bracken]	4	45.30%	20.50%
Pteris vittata [Ladder brake]	3	38.30%	6.90%
Puccinellia maritima [Seaside Alkaligrass]	4	61%	31%
Pueraria lobata [Leguminous Weed]	1	98%	0%
Pyrrosia piloselloides [Tropical Fern]	1	78%	0%
Pyrus pyrifolia [Asian Pear]	2	23.50%	5.30%
Quercus alba L. [White Oak]	6	146.70%	30.10%
Quercus cerrioides [Oak]	1	35%	0%
Quercus chapmanii Sargenti [Chapman's Oak]	3	278.70%	90.80%
Quercus geminata [Sand Live Oak]	6	8.70%	4.50%
Quercus ilex L. [Holly Oak]	4	38%	4.80%
Quercus margaretta [Sand Post Oak]	2	20.50%	14.50%
Quercus mongolica [Mongolian Oak]	6	54.30%	19.50%
Quercus myrtifolia Wild. [Myrtle Oak]	9	136.90%	56.30%
Quercus petraea (Mattuschka) Liebl. [Durmast Oak]	6	53.20%	18.70%
Quercus robur L. [Pedunculate Oak]	8	30.60%	12.80%
Quercus rubra L. [Northern Red Oak]	7	55.30%	25.20%
Quercus suber L. [Cork Oak]	4	46.80%	13.70%
Raphanus sativus [Wild Radish]	22	71.20%	12.20%

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Raphanus sativus x raphanistrum [Wild Radish]	1	33%	0%
Rhinanthus alectorolophus [European Yellowrattle]	2	75%	68.60%
Rhinanthus minor [Yellow Rattle]	1	50%	0%
Rhizophora mangle [American Mangrove]	3	39.30%	6.10%
Ricinus communis [Castor Bean]	7	53.60%	16.30%
Robinia pseudoacacia [Black Locust]	4	346%	242.10%
Rosa hybrida [Rose]	4	26.50%	7.90%
Rubus [Blackberry]	1	675%	0%
Rubus idaeus [Red Raspberry]	4	111.80%	32.80%
Rudbeckia hirta [Black-eyed Susan]	1	0%	0%
Rumex acetosella [Common Sheep Sorrel]	2	24%	2.10%
Rumex obtusifolius [Bitter Dock]	6	18.70%	12.50%
Saccharina latissima [Sugar Kelp]	74	35.10%	5.30%
Saccharum officinarum [Sugarcane]	11	34%	6.50%
Salix jiangsuensis [Willow]	2	38.50%	8.80%
Salix myrsinifolia [Dark Leaved Willow]	8	70.80%	13.70%
Salvia officinalis [Sage]	2	21%	11.30%
Salvia pitcheri [Pitcher Sage]	2	25.50%	2.50%
Sanguisorba minor [Small Burnet]	6	81.20%	15.20%
Schima superba [Subtropical Tree]	2	27.50%	11%
Schizachyrium scoparium [Little Bluestem]	9	18.20%	9%
Schoenoplectus americanus [Chairmaker's Bulrush]	1	27%	0%
Scindapsus aureus [Pothos]	1	39%	0%
Scirpus lacustris [Softstem Bulrush]	1	-2%	0%
Scirpus olneyi [Salt Marsh Sedge]	10	17.40%	7.70%
Sedum alfredii [Perennial Herb]	6	23.30%	2.40%
Senecio jacobaea [Ragwort]	1	21%	0%
Senecio vulgaris [Common Groundsel]	2	66%	25.50%
Sesbania vesicaria [Bagpod]	1	60%	0%
Setaria glauca [Yellow Bristle Grass]	1	16%	0%
Seteria faberi [Japanese Bristlegrass]	5	18.80%	6.70%
Seteria viridis [Green Bristlegrass]	4	16%	0.80%
Shorea leprosula	2	38.50%	11%
Silene cretica in mixed stands with Silene cretica [Common Flax]	2	98.50%	17.30%
Silene latifolia [White Campion]	6	43.50%	9%
Silene noctiflora [Night-flowering Catchfly]	1	44%	0%
Sinapis alba [White Mustard]	4	21.30%	4.10%

Climate Change Reconsidered II: Biological Impacts

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Solanum viarum [Tropical Soda Apple]	1	39%	0%
Solanum curtilobum [Shortlobe Solanum]	2	63%	5.70%
Solanum dulcamara [Climbing Nightshade]	10	46.50%	9.30%
Solanum lycopersicum [Tomato]	2	152.50%	23%
Solanum melongena [Eggplant]	1	41%	0%
Solanum muricatum [Pepino]	4	69.80%	20.50%
Solanum tuberosum [White Potato]	36	29.50%	3.30%
Solidago canadensis [Canadian Goldenrod]	2	1750%	1237.40%
Solidago rigida [Stiff Goldenrod]	1	27%	0%
Sorghastrum nutans [Yellow Indian Grass]	3	9.70%	14.40%
Sorghum bicolor [Sorghum]	28	19.90%	3.50%
Sorghum halepense [Johnsongrass]	3	-13%	14.30%
Sorghum sudanense [Sudan Grass]	1	14%	0%
Spartina densiflora [Dense Flowered Cordgrass]	3	24.30%	12.40%
Spartina alterniflora [Smooth Cordgrass]	2	0%	0%
Spartina anglica [Common Cordgrass]	3	19%	25.10%
Spergula arvensis [Corn Spurrey]	2	-20%	7.80%
Sphagnum cuspidatum [Toothed Sphagnum]	1	42%	0%
Sphagnum magellanicum [Magellan's Sphagnum]	1	26%	0%
Sphagnum papillosum [Papillose Sphagnum]	2	57.50%	0.40%
Sphagnum recurvum [Recurved Sphagnum]	4	12.30%	7%
Spinacia oleracea [Spinach]	3	24.30%	5.70%
Sporobolus indicus [Smut Grass]	1	-5%	0%
Sporobolus pyramidalis [Whorled Dropseed]	6	33.50%	21.70%
Stipa thurberiana [Thurber Needlegrass]	1	11%	0%
Striga hermonthica [Purple Witchweed]	1	-65%	0%
Stylosanthes hamata [Pencil Flower]	1	18%	0%
Stylosanthes scabra [Pencilflower]	2	72%	10.60%
Symphiocarpos orbiculatus [Buck Brush]	2	98.50%	42.10%
Syracosphaera pulchra [Marine Coccolithophore]	2	9%	2.80%
Taxodium distichum [Bald Cypress]	5	28%	5.40%
Taxus baccata [English Yew]	5	28%	5.40%
Tectona grandis [Teak, Common]	8	44.60%	7.20%
Terminalia arjuna [Terminalia]	8	190.60%	35.10%
Terminalia chebula [Myrobalan]	8	442.50%	52.50%
Themeda triandra [Kangaroo Grass]	9	54.90%	15.80%

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Thinouia tomentosa Standley	2	94%	28.30%
Thymus vulgaris [Thyme]	1	0%	0%
Toxicodendron radicans [Poison Ivy]	7	75.70%	13.70%
Trachypogon plumosus [C ₄ South American Grass]	2	-28.50%	3.20%
Tridens flavus [Purpletop Tridens]	1	0%	0%
Trifolium alexandrinum [Berseem]	1	41%	0%
Trifolium incarnatum [Crimson Clover]	2	21.50%	0.40%
Trifolium pratense [Purple Clover]	6	16.30%	3.70%
Trifolium repens [White Clover]	49	64.90%	15.70%
Trifolium subterraneum [Subterranean Clover]	1	756%	0%
Trigonella foenum-graecum [Fenugreek]	2	91%	33.20%
Triticum dicoccoides [Wheat]	1	378%	0%
Triticum monococcum [Einkorn Wheat]	1	180%	0%
Triticum aestivum [Common Wheat]	260	33.40%	1.80%
Triticum turgidum [Rivet Wheat]	8	26.30%	1.80%
Tropaeolum majus [Nasturtium]	3	42.30%	10.80%
Tsuga canadensis [Eastern Hemlock]	3	34%	4.50%
Typha angustifolia [Narrowleaf Cattail]	3	41.30%	8.50%
Typha x glauca [White Cattail]	1	16%	0%
Typha latifolia [Cattail]	2	12.50%	10.30%
Ulmus alata [Winged Elm]	1	30%	0%
Urtica dioica [Stinging Nettle]	1	26%	0%
Vaccinium myrtillus [Whortleberry]	6	60.70%	10%
Vallisneria spiralis [Corkscrew Vallisneria]	2	14%	5.70%
Vernonia herbacea [Fructan Accumulating Plant]	2	31%	4.20%
Veronica didyma [Gray Field Speedwell]	1	26%	0%
Vicia cracca [Bird Vetch]	1	47%	0%
Vicia faba [Faba Bean]	4	46.30%	13.50%
Vicia lathyroides [Spring Vetch]	1	114%	0%
Vigna angularis [Adzuki Bean]	4	60%	5.20%
Vigna mungo [Blackgram]	2	87%	19.80%
Vigna radiata [Mungbean]	2	31.50%	16.60%
Vigna unguiculata [Black-eyed Pea]	4	77%	10.80%
Viola x wittrockiana [Pansy]	1	30%	0%
Vitis vinifera [Grapevine, Common]	5	68.20%	16.60%
Vulpia microstachys [Small Fescue]	2	-4.50%	8.10%
Wedelia chinensis [Herb, Perennial]	2	47.50%	0.40%

Appendix 3 – Plant Dry Weight (Biomass) Responses

Plant Name	# of Studies	Mean CO ₂ Growth Response	Standard Error
Wedelia trilobata [Creeping Daisy]	2	59.50%	0.40%
Weeds, Unspecified	2	0%	0%
Xanthium strumarium var. Xanthium strumarium [Canada Cocklebur]	7	30.60%	6.40%
Yucca brevifolia [Joshua Tree]	1	65%	0%
Yucca schidigera [Mojave Yucca]	1	86%	0%
Yucca whipplei [Chaparral Yucca]	1	13%	0%
Zea mays [Corn]	24	24.10%	5%
Zingiber officinale [Ginger]	2	46.50%	7.40%
Zizania latifolia [Manchurian Wildrice]	1	-5%	0%
Zostera marina [Eelgrass, Common]	1	24%	0%

Appendix 4

Table 1.1.2 — Plant Photosynthesis (Net CO₂ Exchange Rate) Responses to Atmospheric CO₂ Enrichment

Table 1.1.2. 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 percent enhancement, the adjusted 300 ppm CO₂ growth response was calculated as $(300/350) \times 60\% = 51\%$.

The data in this 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. 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.

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
Abelmoschus esculentus [Okra]	1	27%	0%
Abies alba [Silver Fir]	2	37.50%	15.20%
Abutilon theophrasti [Velvet Leaf]	6	46.70%	10.30%
Acacia catechu [Black Cutch]	1	24%	0%
Acacia nigrescens [Knob Thorn]	1	16%	0%
Acacia melanoxylon [Blackwood]	1	19%	0%
Acacia minuta [Coastal Scrub Wattle]	1	21%	0%
Acacia nilotica [Gum Arabic Tree]	4	71.50%	31.20%
Acer mono [Shantung Maple]	4	40.80%	15.10%
Acer rubrum [Red Maple]	17	94.80%	22.60%
Acer saccharinum [Silver Maple]	8	18.50%	7.80%
Acer saccharum [Sugar Maple]	3	64%	9%
Achillea millefolium [Yarrow]	5	27%	15.70%
Ackama rosaefolia [Small Bushy Tree]	1	-20%	0%
Acmena acuminatissima [Tree]	2	40.50%	1.10%
Actinidia deliciosa [Kiwifruit]	1	113%	0%
Adenocaulon bicolor [American Trailplant]	2	38.50%	2.50%
Aechmea [CAM Bromeliad]	1	58%	0%
Agathis microstachya [Semi-Evergreen Rainforest Tree]	1	50%	0%
Agathis robusta [Queensland Kauri]	1	56%	0%
Agave deserti [Desert Agave]	2	34.50%	3.20%
Agave salmiana [Pulque Agave]	2	39.50%	6.70%
Agave vilmoreniana [Leaf Succulent]	2	37.50%	26.50%
Agropyron repens [Couch Grass]	3	42%	18.50%
Agropyron smithii [Western Wheatgrass]	2	-4.50%	6%
Agrostis canina [Velvet Bentgrass]	1	38%	0%
Agrostis capillaris [Colonial Bentgrass]	3	46.30%	20.20%

Climate Change Reconsidered II: Biological Impacts

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
Albizia procera [Tall Albizia]	2	121%	19.10%
Alnus maximowiczii [Alder Tree]	4	32.80%	5.90%
Alnus firma [Alder]	4	83.50%	6.40%
Alnus glutinosa [Black Alder]	3	51%	11.80%
Alnus hirsuta [Manchurian Alder]	11	23.10%	11.80%
Alnus rubra [Red Alder]	8	73.90%	10.60%
Alocasia macrorrhiza [Giant Taro]	2	79%	18.40%
Alternanthera crucis [West Indian Joyweed]	1	91%	0%
Amaranthus viridis [Slender Amaranth]	2	-7%	6.40%
Amaranthus hybridus [Slim Amaranth]	2	2.50%	1.80%
Amaranthus hypochondriacus [Grain Amaranth]	1	9%	0%
Amaranthus retroflexus [Redroot Amaranth]	5	10.20%	4.20%
Ambrosia artemisiifolia [Annual Ragweed]	3	37.70%	5.20%
Ambrosia cordifolia [Tuscon Burr Ragweed]	3	45.70%	3.80%
Ambrosia dumosa [White Burrobush]	4	85%	28%
Amorpha canescens [Leadplant]	1	24%	0%
Anacardium excelsum	1	19%	0%
Anagallis arvensis [Scarlet Pimpernel]	1	45%	0%
Ananas comosus [Pineapple]	3	168.30%	55.80%
Andropogon gerardii [Big Bluestem]	14	23.10%	5.70%
Andropogon glomeratus [Bushy Bluestem]	2	-1%	3.50%
Anemone cylindrica [Candle Anemone]	3	57.30%	18.50%
Anemone raddeana [Anemone]	2	65%	24.70%
Anthoxanthum odoratum [Sweet Vernal Grass]	1	109%	0%
Anthyllis vulneraria [Common Kidney Vetch]	4	27.80%	10.30%
Antirrhoea trichantha	1	33%	0%
Apple	2	105.50%	18.70%
Arabidopsis thaliana [Mouse Ear Cress]	9	56.20%	17%
Arachis hypogaea [Peanut]	7	44.30%	8.60%
Arbutus unedo [Strawberry Tree]	4	91.30%	32.10%
Armeria maritima [Thrift Seapink]	1	46%	0%
Arrhenatherum elatius [Tall Oatgrass]	1	39%	0%
Artemisia tridentata [Big Sagebrush]	2	31%	12.70%
Asparagus officinalis [Garden Asparagus]	1	25%	0%
Avena barbata [Slender Oat]	2	52%	5.70%
Avena fatua [Wild Oat]	2	53%	11.30%
Avena sativa [Red Oat]	2	32.50%	3.90%

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
Azolla pinnata [Water Fern]	2	35%	24.70%
Bauhinia variegata [Mountain Ebony]	1	16%	0%
Begonia x hiemalis [Begonia]	2	70%	21.20%
Beilschmiedia pendula [Slugwood]	4	21.30%	7.70%
Beta vulgaris [Common Beet]	11	62.20%	9.30%
Betula ermanii [Birch, Ermans]	2	53%	2.10%
Betula albosinensis [Chinese Red Birch]	1	65%	0%
Betula alleghaniensis [Yellow Birch]	6	35%	5.90%
Betula davurica [Dahurian Birch]	1	52%	0%
Betula maximowicziana [Monarch Birch]	8	31%	10.30%
Betula nanal [Bog Birch]	1	0%	0%
Betula nigra [River Birch]	1	40%	0%
Betula papyrifera [Paper Birch]	57	60.80%	10.90%
Betula pendula [European White Birch]	7	28.60%	7.80%
Betula platyphylla [Broadleaf White Birch]	9	24.40%	7.10%
Betula pubescens Ehrh. [Downy Birch]	4	113.50%	67.20%
Bothriochloa caucasica [Caucasian Bluestem]	2	15.50%	11%
Bouteloua curtipendula [Sideoats Grama]	2	18.50%	2.50%
Bouteloua gracilis [Blue Grama]	4	49.80%	23%
Brachychiton populneum [Whiteflower Kurrajong]	1	75%	0%
Brachyglottis repanda [Rangiora]	1	120%	0%
Brachypodium pinnatum [Heath Falsebrome]	1	59%	0%
Brassica campestris [Rape Seed Mustard]	2	90.50%	37.10%
Brassica carinata [Abyssinian Mustard]	2	34.50%	10.30%
Brassica juncea [India Mustard]	2	50.50%	24.40%
Brassica napus [Canola]	12	63.50%	20.10%
Brassica nigra [Black Mustard]	2	39%	11.30%
Bromus erectus [Erect Brome]	6	30.20%	9.50%
Bromus inermis [Smooth Brome]	4	36%	9.40%
Bromus madritensis [Compact Brome]	1	12%	0%
Bromus sterilis [Poverty Brome]	1	45%	0%
Bromus tectorum [Cheatgrass]	1	56%	0%
Bryum pseudotriquetrum [Common Green Bryum Moss]	2	47.50%	10.30%
Bryum subrotundifolium	2	28.50%	8.10%
Buchloe dactyloides [Buchloe dactyloides]	1	27%	0%
Cajanus cajan [Pigeonpea]	2	137.50%	26.50%
Calamagrostis epigeios [Chee Reedgrass]	1	27%	0%

Appendix 4 – Plant Photosynthesis (Net CO₂ Exchange Rate) Responses

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
Calluna vulgaris [Heather]	20	114.50%	48.50%
Calophyllum longifolium [Tropical Tree]	1	-15%	0%
Caloplaxa trachyphylla [Lichen]	1	38%	0%
Capsicum annuum [Bell Pepper]	3	41%	15.50%
Carex bigelowii [Bigelow's Sedge]	1	0%	0%
Carex curvula dominated alpine grassland	2	66.50%	15.20%
Carex flacca [Heath Sedge]	1	55%	0%
Carex paleacea [Chaffy Sedge]	1	34%	0%
Cariniana legalis [Jequitiba Tree]	2	39.50%	11%
Carpinus betulus [European Hornbeam]	4	14.80%	6.40%
Carya glabra [Pignut Hickory]	3	57.30%	22.80%
Carya ovata [Shagbark Hickory]	1	35%	0%
Castanea sativa [Sweet Chesnut]	2	66.50%	37.80%
Castanopsis hystrix [Chinkapin]	2	57%	3.50%
Cecropia longipes	1	17%	0%
Cenchrus ciliaris	1	31%	0%
Centella asiatica [Centella]	1	33%	0%
Ceratonia siliqua [Carob]	6	40.50%	7.50%
Cercis canadensis [Eastern Redbud]	3	127.30%	48%
Chamaenerion angustifolium [Narrowleaved Fireweed]	1	96%	0%
Chenopodium album [Lambsquarters]	6	43.30%	8.90%
Cirsium arvense [Canadian Thistle]	4	56.50%	8%
Cistus salviifolius [Cistus]	1	53%	0%
Citrus aurantium [Sour Orange]	12	111.60%	15.30%
Citrus madurensis [Calamondin]	2	195%	74.20%
Citrus paradisi Macfad. budded to Citrus paradisi Blanco (Cleopatra mandarin) rootstock [Marsh Grapefruit]	2	60%	4.90%
Citrus paradisi Macfad. budded to Citrus paradisi (L.) Raf. rootstock [Marsh Grapefruit]	2	70%	14.10%
Citrus reticulata [Mandarin Orange]	2	45.50%	8.80%
Citrus sinensis (L.) Osbeck budded to Citrus sinensis Blanco (Cleopatra mandarin) rootstock [Washington Naval Orange]	2	52.50%	10.30%
Citrus sinensis (L.) Osbeck budded to Citrus sinensis (L.) Raf. rootstock [Washington Naval Orange]	2	43.50%	8.10%
Citrus sinensis (L.) Osbeck x Citrus sinensis Blanco (Cleopatra mandarin) [Valencia Orange]	2	42.50%	15.90%
Citrus sinensis (L.) Osbeck x Citrus sinensis (L.) Raf. [Valencia Orange]	2	54.50%	5.30%
Citrus sinensis [Sweet Orange]	2	57%	4.90%
Citrus sinensis x poncirus trifoliata [Carrizo Citrange]	2	76.50%	9.50%

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
Cladonia rangiferina (L.) Wigg. [Fruticose Lichen]	1	31%	0%
Claoxylon sandwicense [Po'ola]	3	100%	12.50%
Coffea arabusta [Coffee]	2	271%	65.10%
Collema furfuraceum [Jelly Lichen]	1	42%	0%
Cordia alliodora [Spanish Elm]	1	41%	0%
Corynocarpus laevigatus [Karaka Nut]	1	79%	0%
Crocospaera watsonii [Diazotrophic Cyanobacterium]	2	71%	38.20%
Croton urucurana [Dragons Blood Tree]	2	47%	17.70%
Cucumis melo [Cantaloupe]	4	56.80%	0.70%
Cucumis sativus [Garden Cucumber]	5	112.20%	68.60%
Cucurbita pepo [Zucchini]	2	34%	6.40%
Cyperus esculentus [Yellow Nutsedge]	1	-26%	0%
Cyperus rotundus [Purple Nutsedge]	1	6%	0%
Dactylis glomerata [Orchardgrass]	12	39.30%	7.20%
Dalbergia latifolia [Indian Rosewood]	1	9%	0%
Daucus carota [Carrot]	8	105.30%	38%
Dendrosenecio brassica [Afro-alpine Giant Rosette Plant]	1	65%	0%
Dendrosenecio keniodendron [Afro-alpine Giant Rosette Plant]	1	52%	0%
Digitalis purpurea [Purple Foxglove]	1	78%	0%
Digitaria sanguinalis [Hairy Crabgrass]	3	75.30%	32.70%
Dodonaea viscosa [Florida Hopbush]	1	42%	0%
Echinochloa crus-galli [Barnyard Grass]	8	24.40%	4.40%
Elaeis guineensis [African Oil Palm]	1	105%	0%
Elatostema repens [Tropical Rain Forest Herb]	1	68%	0%
Eleusine indica [Indian Goosegrass]	1	72%	0%
Elymus elymoides [Bottlebrush Squirreltail]	1	21%	0%
Elymus repens [Couch Grass]	1	176%	0%
Emiliania huxleyi [Marine Coccolithophorid]	5	47.80%	13.10%
Encelia frutescens [Button Brittlebush]	1	30%	0%
Entandrophragma angolense [West African Mahogany]	3	63.30%	7.20%
Epilobium hirsutum [Codlins and Cream]	1	62%	0%
Eragrostis orcuttiana [Annual Weed, C4]	1	-44%	0%
Eriogonum inflatum [Native American Pipeweed]	2	42.50%	15.90%
Eucalyptus deglupta x e. camaldulensis [Rainbow Eucalyptus X Red River Gum Hybrid]	2	44%	20.50%
Eucalyptus saligna [Sydney Blue Gum]	8	42.30%	9.80%
Eucalyptus sideroxylon [Red Ironbark]	6	68.80%	9%
Eucalyptus urophylla [Rose Gum Tree]	2	67.50%	15.20%

Climate Change Reconsidered II: Biological Impacts

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
Eucalyptus and Eucalyptus [Forest Canopy in Lysimeter]	1	53%	0%
Eucalyptus cladocalyx [Sugargum]	2	47.50%	27.20%
Eucalyptus microtheca [Coolibah Tree]	1	57%	0%
Eucalyptus polyanthemus [Silver Dollar Gum]	1	75%	0%
Eucalyptus tetrodonta	3	26.30%	8.40%
Eupatorium adenophorum [Sticky Snakeroot]	5	35%	3.80%
Eupatorium japonicum [Pei Lan]	4	21.50%	6.80%
Eupatorium stoechadosmum [Orchid Herb]	3	19.70%	8.80%
Evernia mesomorpha [Ring Lichen]	1	60%	0%
Fagus crenata [Japanese Beech]	6	29.50%	5.70%
Fagus grandifolia [American Beech]	1	96%	0%
Fagus sylvatica [European Beech]	14	58.70%	8.90%
Fargesia rufa [Bamboo, Dwarf]	2	39.50%	6%
Fargesia denudata [Bamboo]	1	40%	0%
Feijoa sellowiana [Pineapple Guava]	1	55%	0%
Ferocactus acanthodes [California Barrelcactus]	1	30%	0%
Festuca arundinacea [Tall Fescue]	2	46.50%	2.50%
Festuca pratensis [Meadow Fescue]	2	34.50%	1.80%
Festuca rupicola [Fescue]	2	112.50%	54.10%
Ficus insipida	1	47%	0%
Ficus obtusifolia [Amate]	1	76%	0%
Filipendula vulgaris [Dropwort]	3	273.70%	81.70%
Flaveria floridana [Florida Yellowtops]	1	25%	0%
Flaveria pringlei [Yellowtops]	1	33%	0%
Flaveria trinervia [Clustered Yellowtops]	3	9%	3.70%
Fontinalis antipyretica [Antifever Fontinalis Moss]	2	235%	166.20%
Fragaria x ananassa [Hybrid Strawberry]	14	72.60%	12.50%
Fraxinus lanceolata [Green Ash]	1	60%	0%
Fraxinus pennsylvanica [Green Ash]	5	62.40%	12.90%
Freshwater Benthic Algae	1	68%	0%
Geum reptans [Avens]	1	84%	0%
Geum rivale [Water Avens]	1	31%	0%
Ginkgo biloba [Maidenhair Tree]	6	54%	15.80%
Glycine max [Soybean]	98	50.40%	7.40%
Gmelina arborea [White Teak]	1	114%	0%
Gossypium hirsutum [Cotton]	20	44.20%	5.20%
Gracilaria lemaneiformis [Red Alga]	2	20%	10.60%
Helianthus annuus [Sunflower]	19	51.80%	6.50%

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
Helianthus petiolaris [Prairie Sunflower]	2	20%	0%
Heterotheca subaxillaris [Camphorweed]	1	17%	0%
Hevea brasiliensis [Rubber Tree]	8	85.90%	3.90%
Holcus lanatus [Common Velvetgrass]	1	85%	0%
Hordeum marinum [Sea Barley]	3	40.30%	7%
Hordeum vulgare [Barley]	25	56.80%	8.30%
Hylocomium splendens [Splendid Feather Moss]	1	100%	0%
Hymenaea courbaril [Stinkingtoe]	1	70%	0%
Hyparrhenia rufa [Jaragua]	1	70%	0%
Hypnea spinella [Red Seaweed]	1	32%	0%
Hyptis suaveolens [Wild Spikenard]	1	88%	0%
Ipomoea cairica [Mile A Minute Vine]	1	56%	0%
Ipomoea carnea [Gloria De La Manana]	1	62%	0%
Ipomoea pes-caprae [Beach Morning Glory]	1	35%	0%
Ipomoea batatas [Sweet Potato]	5	39.40%	10.80%
Jatropha curcas [Purging Nut]	3	49.30%	6.20%
Jatropha gossypifolia [Bellyache Bush]	1	73%	0%
Juglans nigra [Black Walnut]	1	24%	0%
Kalankoe blossfeldiana	1	47%	0%
Koeleria cristata [June Grass]	4	242.50%	189.90%
Krameria erecta [Littleleaf Ratany]	4	115.80%	28.60%
Lactuca serriola [Prickly Lettuce]	1	60%	0%
Lantana camara [Lantana]	1	245%	0%
Larix decidua [European Larch]	3	62.70%	4.80%
Larix kaempferi [Japanese Larch]	4	38.80%	16.80%
Larix laricina [Tamarack]	1	47%	0%
Larrea tridentata [Creosote Bush]	10	103.60%	24.40%
Lasthenia californica [California Goldfields]	1	47%	0%
Lecanora muralis [An Epilithic Lichen]	1	42%	0%
Ledum palustre [Wild Rosemary]	1	0%	0%
Lemna gibba [Swollen Duckweed]	2	55.50%	3.90%
Lespedeza capitata [Roundhead Lespedeza]	1	14%	0%
Leucadendron coniferum [Dune Conebush]	2	38%	14.10%
Leucadendron laeureolum [Golden Conebush]	2	28.50%	5.30%
Leucadendron meridianum [Limestone Conebush]	2	18%	10.60%
Leucadendron xanthoconus [Sickle-leaf Conebush]	2	59%	9.90%
Leymus chinensis [Chinese Lyme-grass]	2	133.50%	32.20%

Appendix 4 – Plant Photosynthesis (Net CO₂ Exchange Rate) Responses

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
Liquidambar styraciflua [Sweetgum]	18	105.10%	21.80%
Liriodendron tulipifera [Yellow Poplar]	13	64.40%	12.40%
Lobelia telekii [Afro-alpine Giant Rosette Plant]	1	52%	0%
Lolium mutiflorum [Italian Ryegrass]	3	18.30%	2.80%
Lolium perenne [Perennial Ryegrass]	32	39.80%	3.70%
Lolium temulentum [Darnel Ryegrass]	2	23.50%	1.80%
Lotus corniculatus [Birdfoot Deer Vetch]	1	38%	0%
Luehea seemannii	2	20%	2.10%
Lupinus arizonicus [Arizona Lupine]	3	15.70%	6.50%
Lupinus perennis [Sundial Lupine]	4	57.30%	27%
Lycopersicon esculentum [Garden Tomato]	14	24.30%	4.90%
Lyonia mariana [Piedmont Staggerbush]	1	27%	0%
Malvastrum rotundifolium [Desert Fivespot]	3	33%	5.70%
Manihot esculenta [Cassava]	2	7%	34.60%
Medicago lupulina [Black Medic]	1	46%	0%
Medicago glomerata	1	16%	0%
Medicago minima [Burr Medick]	1	0%	0%
Medicago sativa [Alfalfa]	19	24.60%	3.80%
Melinis minutiflora [Molassesgrass]	2	7.50%	12.40%
Metasequoia glyptostroboides [Dawn Redwood]	3	86.30%	42.80%
Mikania micrantha [Bittervine]	1	70%	0%
Nauclea diderrichii [Pioneer Tropical Tree]	3	69.70%	2.20%
Nicotiana sylvestris [South American Tobacco]	1	55%	0%
Nicotiana tabacum [Cultivated Tobacco]	9	68%	14.90%
Nostoc commune	1	5%	0%
Nothofagus cunninghamii [Myrtle Beech]	3	24.70%	13.20%
Nothofagus fusca [Red Beech]	3	40%	1.70%
Nymphaea marliac [Water Lily]	3	39.70%	12.40%
Oenothera primiveris [Desert Eveningprimrose]	1	23%	0%
Olea europaea [Olive]	10	50.20%	12.60%
Olearia ilicifolia [Holly-Leaved Daisybush]	1	79%	0%
Opuntia ficus-indica [Prickly Pear]	7	26.70%	4.30%
Ormosia pinnata [Tree]	2	45%	2.80%
Orontium aquaticum [Goldenclub]	7	72.10%	9.30%
Oryza sativa [Rice]	79	46.80%	4.80%
Oryzopsis hymenoides [Perennial Bunchgrass]	1	47%	0%
Pachysandra terminalis [Japanese Spurge]	1	70%	0%

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
Paederia scandens [Chinese Fever Vine]	1	3%	0%
Panicum antidotale [Blue Panicgrass]	2	-2.50%	4.60%
Panicum dichotomiflorum [Fall Panicgrass]	1	18%	0%
Panicum laxum [Lax Panicgrass]	2	8.50%	5.30%
Panicum maximum [Guineagrass]	2	16%	3.50%
Panicum miliaceum [Broomcorn Millet]	2	12%	2.10%
Panicum virgatum [Switchgrass]	1	64%	0%
Parmelia caperata [Foliose Lichen]	1	16%	0%
Parmelia kurokawae [Foliose Lichen]	1	30%	0%
Parmelia praesignis [Flavopunctelia Lichen]	1	60%	0%
Parmelia reticulata [Netted Rimelia Lichen]	1	63%	0%
Pascopyrum smithii [Western Wheatgrass]	6	61.20%	14.90%
Paspalum dilatatum [Dallas Grass]	4	80.80%	18.40%
Paspalum notatum [Bahia grass]	1	24%	0%
Peanut, Rhizoma	1	40%	0%
Pelargonium x hortorum [Pelargonium]	3	19.30%	8.80%
Peltigera canina [Felt Lichen]	1	24%	0%
Peltigera membranacea [Membranaceous Felt Lichen]	1	83%	0%
Peltigera polydactyla [Foliose Lichen]	1	83%	0%
Peltigera rufescens [Felt Lichen]	1	83%	0%
Petalostemum villosum [Silky Prairie Clover]	1	32%	0%
Phalaenopsis [Orchid]	2	191%	2.10%
Phalaris arundinacea [Canary Grass]	32	29.60%	2%
Phalaris aquatica [Harding Grass]	2	39.50%	17.30%
Phaseolus vulgaris [Garden Bean]	24	55.80%	10.30%
Phillyrea angustifolia [False Olive]	2	75%	10.60%
Phleum pratense [Timothy]	3	30.30%	3.20%
Phyllanthus emblica [Emblic]	2	71%	21.90%
Phytolacca americana [American Pokeweed]	1	56%	0%
Picea glauca [White spruce]	1	197%	0%
Picea abies [Norway Spruce]	14	52.60%	6.60%
Picea koraiensis [Spruce]	1	73%	0%
Picea mariana [Black Spruce]	5	33.60%	9.20%
Picea sitchensis [Sitka Spruce]	2	23%	4.20%
Pinus tabulaeformis [Chinese Red Pine]	2	60.50%	4.60%
Pinus banksiana [Pine, Jack]	4	34.80%	6.20%
Pinus densiflora [Pine, Japanese Red]	5	26.40%	8%

Climate Change Reconsidered II: Biological Impacts

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
<i>Pinus eldarica</i> [Pine, Eldarica]	2	133%	0%
<i>Pinus koraiensis</i> [Pine, Korean]	3	58.30%	9.70%
<i>Pinus merkusii</i> [Pine, Merkus]	2	44.50%	3.20%
<i>Pinus patula</i> [Mexican Yellow Pine]	1	47%	0%
<i>Pinus ponderosa</i> [Ponderosa Pine]	10	45.90%	8.80%
<i>Pinus radiata</i> [Monterey Pine]	13	40.20%	3.80%
<i>Pinus sylvestris</i> [Scots Pine]	22	70.10%	25.20%
<i>Pinus taeda</i> [Loblolly Pine]	48	87.60%	9.80%
<i>Pinus uncinata</i> [Mountain Pine]	2	44%	7.10%
<i>Piper auritum</i> [Vera Cruz Pepper]	2	67.50%	5.30%
<i>Piper hispidum</i> [Jamaican Pepper]	2	77.50%	15.90%
<i>Pisum sativum</i> [Garden Pea]	4	37.80%	5%
<i>Plantago asiatica</i> [Plantago Asiatica]	2	38%	4.90%
<i>Plantago erecta</i> [Dwarf Plantain]	1	43%	0%
<i>Plantago lanceolata</i> [Narrowleaf Plantain]	7	67.60%	21.30%
<i>Plantago maritima</i> [Sea Plantain]	1	-30%	0%
<i>Platanus occidentalis</i> [American Sycamore]	1	60%	0%
<i>Poa annua</i> [Annual Bluegrass]	6	62%	14%
<i>Poa cookii</i> [Bluegrass]	1	55%	0%
<i>Poa pratensis</i> [Kentucky Bluegrass]	4	153.30%	54.10%
<i>Poa trivialis</i> [Rough Bluegrass]	1	41%	0%
<i>Polygonum cuspidatum</i> [Japanese Knotweed]	3	32.70%	3.50%
<i>Polygonum sachalinense</i> [Giant Knotweed]	5	46.60%	8.30%
<i>Polygonum persicaria</i> [Spotted Ladysthumb]	2	-2.50%	1.80%
<i>Populus tremula</i> x <i>alba</i> [Hybrid Poplar]	1	23%	0%
<i>Populus tremula</i> x <i>populus tremuloides</i> [Hybrid Aspen]	1	113%	0%
<i>Populus alba</i> [White Poplar]	6	79.80%	16.40%
<i>Populus cathayana</i> [Poplar]	9	24.60%	4.40%
<i>Populus deltoides</i> [Eastern Cottonwood]	9	32.60%	6.60%
<i>Populus euramericana</i> [Robusta Poplar]	25	77.20%	14.70%
<i>Populus fremontii</i> [Fremont's Cottonwood]	3	30.70%	15.90%
<i>Populus grandidentata</i> [Bigtooth Aspen]	3	181.70%	60.70%
<i>Populus nigra</i> [Black Poplar]	6	73.20%	18.30%
<i>Populus tremula</i> x <i>Populus tremula</i> [Hybrid Aspen]	3	28.70%	3.30%
<i>Populus tremuloides</i> [Quaking Aspen]	54	80.30%	10.70%
<i>Populus trichocarpa</i> x <i>populus deltoides</i> [Hybrid Poplar]	2	37.50%	8.80%
<i>Potentilla crantzii</i> [Alpine Cinquefoil]	1	25%	0%

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
<i>Prochlorococcus</i> [Marine Picocyanobacterium]	2	5.50%	2.50%
<i>Prunus armeniaca</i> [Apricot]	4	62.80%	4.20%
<i>Prunus avium</i> [Sweet Cherry]	1	38%	0%
<i>Prunus persica</i> [Peach]	4	37.50%	8.70%
<i>Prunus serotina</i> [Black Cherry]	3	63.70%	5.70%
<i>Pseudobombax septenatum</i> [Tropical Tree]	1	68%	0%
<i>Pseudopanax arboreus</i> [Puahou]	1	69%	0%
<i>Pseudotsuga menziesii</i> [Douglas-Fir]	17	32%	5.30%
<i>Psychotria limonensis</i> [Forest Shrub]	1	65%	0%
<i>Pteridium aquilinum</i> [Bracken]	8	93.80%	7.30%
<i>Puccinellia maritima</i> [Seaside Alkaligrass]	5	84%	17.80%
<i>Pyrrosia piloselloides</i> [Tropical Fern]	1	19%	0%
<i>Pyrus pyrifolia</i> [Asian Pear]	4	64.50%	8.50%
<i>Quercus alba</i> [White Oak]	3	142%	38.30%
<i>Quercus chapmanii</i> [Chapman's Oak]	4	53%	4.10%
<i>Quercus crispula</i> [Mongolian Oak]	2	19%	3.50%
<i>Quercus geminata</i> [Sand Live Oak]	6	15.70%	5.90%
<i>Quercus ilex</i> [Holly Oak]	11	91.40%	30.10%
<i>Quercus mongolica</i> [Mongolian Oak]	24	74.80%	13.50%
<i>Quercus myrtifolia</i> [Myrtle Oak]	9	60.60%	7.70%
<i>Quercus petraea</i> [Durmast Oak]	2	23.50%	0.40%
<i>Quercus pubescens</i> [Downy Oak]	5	136.80%	58.50%
<i>Quercus robur</i> [Pedunculate Oak]	9	35.80%	6.20%
<i>Quercus rubra</i> [Northern Red Oak]	16	63%	10.40%
<i>Quercus suber</i> [Cork Oak]	3	28.70%	16.90%
<i>Ramalina menziesii</i> [Menzies' Cartilage Lichen]	1	20%	0%
<i>Ranunculus acris</i> [Tall Buttercup]	1	36%	0%
<i>Ranunculus</i> [Buttercup]	1	47%	0%
<i>Ranunculus glacialis</i> [Glacier Buttercup]	3	44%	8.90%
<i>Raphanus raphanistrum</i> [Wild Radish]	2	32%	7.10%
<i>Raphanus sativus</i> [Wild Radish]	8	30.40%	7%
<i>Raphanus sativus</i> x <i>raphanistrum</i> [Wild Radish]	1	109%	0%
<i>Rhaphiolepis indica</i> [Indian Hawthorn]	1	79%	0%
<i>Rhizophora mangle</i> [American Mangrove]	2	11.50%	0.40%
<i>Rhytidiadelphus triquetrus</i> [Rough Goose Neck Moss]	1	66%	0%
<i>Ricinus communis</i> [Castor Bean]	2	34%	0%
<i>Rosa hybrida</i> [Rose]	1	35%	0%

Appendix 4 – Plant Photosynthesis (Net CO₂ Exchange Rate) Responses

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
Rudbeckia hirta [Blackeyed Susan]	1	5%	0%
Rumex acetosa [Common Sorrel]	1	53%	0%
Saccharum officinarum [Sugarcane]	9	455.10%	417.80%
Salix jiangsuensis [Willow]	2	30%	12.70%
Salvia nemorosa [Woodland Sage]	2	277.50%	136.10%
Salvia pitcheri [Pitcher Sage]	2	26.50%	1.80%
Salvia pratensis [Introduced Sage]	1	47%	0%
Sanguisorba minor [Small Burnet]	5	31.60%	4%
Schima superba [Sub-tropical Tree]	2	26%	6.40%
Schizachyrium scoparium [Little Bluestem]	4	59.30%	17.70%
Schoenoplectus americanus [Chairmaker's Bulrush]	1	27%	0%
Scirpus maritimus [Seaside Bulrush]	1	55%	0%
Scirpus oleyi [Salt Marsh Sedge]	8	57.80%	10.80%
Scirpus robustus [Sedge]	2	60%	10.60%
Scrophularia desertorum [Desert Figwort]	3	50%	21%
Sequoia sempervirens [Coastal Redwood]	3	77.70%	31.40%
Setaria faberi [Japanese Bristlegrass]	4	15%	7.10%
Setaria viridis [Green Bristlegrass]	1	13%	0%
Shorea leprosula	2	57%	1.40%
Silene noctiflora [Night-flowering Catchfly]	1	42%	0%
Solanum curtilobum [Shortlobe Solanum]	1	46%	0%
Solanum dulcamara [Climbing Nightshade]	6	28.80%	3.10%
Solanum muricatum [Pepino]	2	74%	7.10%
Solanum tuberosum [White Potato]	15	33.20%	5.50%
Solidago rigida [Stiff Goldenrod]	3	15%	5.40%
Sorghastrum nutans [Indian Grass]	3	371%	293.50%
Sorghum bicolor [Sorghum]	19	21.30%	2.80%
Sorghum halapense [Johnsongrass]	1	12%	0%
Spartina densiflora [Dense Flowerd Cordgrass]	6	17.50%	4.40%
Spartina maritima [Small Cordgrass]	3	68%	4.20%
Spartina patens [Saltmeadow Cordgrass]	6	12.30%	4.30%
Spartina alterniflora [Smooth Cordgrass]	1	19%	0%
Spartina anglica [Common Cordgrass]	1	33%	0%
Spergularia maritima [Media Sandspurry]	1	81%	0%
Sphagnum fuscum [Sphagnum]	3	89.30%	6.60%
Spinacia oleracea [Spinach]	5	46.80%	11.40%
Stenocereus queretaroensis [Tree Cactus]	1	30%	0%

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
Stipa thurberiana [Thurber needlegrass]	1	56%	0%
Stylosanthes hamata [Pencil Flower]	1	44%	0%
Swietenia macrophylla [Honduras Mahogany]	1	26%	0%
Symphiocarpus orbiculatus [Buch Brush]	2	105%	43.80%
Synechococcus [Unicellular Marine Picocyanobacterium]	1	48%	0%
Talinum triangulare	1	357%	0%
Taxodium distichum [Cyprus, Bald]	7	95.10%	26.90%
Tectona grandis [Teak]	2	24%	9.20%
Terminalia arjuna [Terminalia]	2	194.50%	3.90%
Terminalia chebula [Myrobalan]	2	147.50%	37.10%
Tetragastris panamensis [Tropical Tree]	1	14%	0%
Themeda triandra [C ₄ grass]	2	19%	3.50%
Theobroma cacao [Cacao]	1	32%	0%
Toxicodendron radicans [Poison Ivy]	1	116%	0%
Trachypogon plumosus [A C ₄ South American Grass]	2	38.50%	2.50%
Trifolium repens [White Clover]	22	49.40%	7.40%
Trifolium subterraneum [Subterranean Clover]	1	19%	0%
Triticum durum [Wheat, Durum]	2	59%	25.50%
Triticum aestivum [Common Wheat]	109	67.10%	8.60%
Tussock Tundra	2	237.50%	19.40%
Typha augustifolia [Narrowleaf Cattail]	1	57%	0%
Typha latifolia [Common Cattail]	1	1%	0%
Typha x glauca [White Cattail]	1	0%	0%
Urtica dioica L. [Stinging Nettle]	1	126%	0%
Vaccinium myrtillus [Whortleberry]	2	47%	9.20%
Vernonia herbacea [Fructan Accumulating Plant]	1	50%	0%
Viburnum marisii [Flowering Shrub]	1	63%	0%
Vicia faba [Faba Bean]	7	52.30%	10.50%
Vigna radiata [Mungbean]	2	178%	18.40%
Vigna unguiculata [Blackeyed Pea]	5	65.60%	14.90%
Virola surinamensis [Tropical Tree]	1	31%	0%
Vitis vinifera [Grapevine, Common]	3	73.70%	21%
Vitis californica [California Wild Grape]	1	57%	0%
Vulpia microstachys [Small Fescue]	1	125%	0%
Wedelia chinensis [Herb, Perennial]	2	45.50%	6.70%
Wedelia trilobata [Creeping Daisy]	2	74%	1.40%
Xanthium strumarium L. [Rough Cocklebur]	4	30.80%	12.90%
Zea mays L. [Corn]	23	26.10%	10.60%

Climate Change Reconsidered II: Biological Impacts

Plant Name	Number of Studies	Mean CO ₂ Growth Response	Standard Error
Zingiber officinale [Ginger]	2	41.50%	5.30%
Zostera noltii [Dwarf Eelgrass]	1	33%	0%

\$154.00

THE NONGOVERNMENTAL INTERNATIONAL PANEL ON CLIMATE CHANGE

The Nongovernmental International Panel on Climate Change (NIPCC) is an international network of scientists first convened in 2003 to examine the same climate data used by the United Nations-sponsored Intergovernmental Panel on Climate Change (IPCC). Unlike IPCC, NIPCC is not a government agency and does not receive government funding. Whereas the mission of IPCC is to justify control of greenhouse gas emissions, NIPCC has no agenda other than discovering the truth about climate change.

CLIMATE CHANGE RECONSIDERED

Climate Change Reconsidered is a publication series produced by NIPCC and published by The Heartland Institute. Series editors Craig D. Idso, Robert M. Carter, and S. Fred Singer have assembled and oversee an international team of scholars devoted to producing a thorough and unbiased review of the extensive research on climate change. Four volumes were published prior to the present publication: *Nature, Not Human Activity, Rules the Climate* (2008), *Climate Change Reconsidered: The 2009 Report of the Nongovernmental International Panel on Climate Change (NIPCC)* (2009), *Climate Change Reconsidered: The 2011 Interim Report of the Nongovernmental International Panel on Climate Change (NIPCC)* (2011), and *Climate Change Reconsidered II: Physical Science* (2013). All are available for purchase from The Heartland Institute and for free online at www.climatechangereconsidered.org and www.nipccreport.org.

CCR II: BIOLOGICAL IMPACTS

The current report, *Climate Change Reconsidered II: Biological Impacts*, is the most comprehensive and up-to-date review of science on the impacts of climate change. This report combines the research and analysis of previous volumes in the series with new research published as recently as the first quarter of 2014 (well after the cut-off date for IPCC's *Fifth Assessment Report*). This volume tracks and critiques the expected 2014 report of the IPCC's Working Group II on "Impacts, Adaptation, and Vulnerability." A third and final volume of CCR-II series, *Human Welfare, Energy, and Policies*, is being released concurrently with the present volume.

ABOUT THE COAUTHORS

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