Earth's Vegetative Future

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Key Findings

The key findings of this chapter are listed below.

- Rising atmospheric CO₂ and warming temperatures, both of which IPCC claims constitute a significant threat to the biosphere, benefited agriculture in the ancient past and in the twentieth century.
- Empirical studies suggest a future warming of the climate coupled with rising atmospheric CO₂ levels will boost global agricultural production and help meet the food needs of the planet's growing population.

- When model-based studies fully account for the growth-enhancing and water-conserving benefits of atmospheric CO₂ enrichment, they project significant gains for future agricultural production.
- The vigor of the terrestrial biosphere has been increasing with time, revealing a great greening of the planet that extends across the globe.
- Satellite-based analyses of net terrestrial primary productivity (NPP) reveal an increase of around 6–13% since the 1980s.
- There is no empirical evidence to support the model-based claim that future carbon uptake will

diminish on a global scale due to rising temperatures.

- Earth's land surfaces were a net *source* of CO₂carbon to the atmosphere until about 1940. From 1940 onward, the terrestrial biosphere has become, in the mean, an increasingly greater *sink* for CO₂carbon.
- Over the past 50 years, global carbon uptake has doubled from 2.4 ± 0.8 billion tons in 1960 to 5.0 ± 0.9 billion tons in 2010.
- The observed greening of the Earth has occurred in spite of the many real and imagined assaults on the planet's vegetation over this time period, including fires, disease, outbreaks of pests, deforestation, and climatic changes (primarily in temperature and precipitation).
- The atmosphere's rising CO₂ content—which IPCC considers to be the chief culprit behind its concerns about the future of the biosphere—is most likely the primary cause of the observed greening trends.
- In the future, plants should be able to adjust their physiology to accommodate a warming of the magnitude and rate of rise typically predicted by climate models to accompany the projected future increase in atmospheric CO₂ content.
- The rise in the air's CO₂ concentration and its antitranspiration effect, which improves plant wateruse efficiency, are enhancing and will continue to enhance the vegetative productivity of Africa.
- The rise of the air's CO₂ concentration and temperature to their highest values of the past century enhanced the terrestrial vegetative productivity of all parts of Asia, including deserts, forests, grasslands, and the Tibetan Plateau.
- Evergreen vegetation, woody plants, and other plant life have increased across Australia over the past 200 years as a result of CO₂ enrichment.
- Over the last two decades of the twentieth century, Europe as a whole became greener and much of it is seeing an increase in woodlands due to the recent rise in atmospheric CO₂, which has tended to offset the detrimental effects of climate change in the region.

- Opposite the forecasts promulgated by the models used by IPCC, land-based plants of the Arctic and near-Arctic regions of North America are thriving, thanks in large part to the ongoing rise in the atmosphere's CO₂ concentration and global warming.
- Late twentieth-century increases in air temperature and atmospheric CO₂ concentration did not negatively affect plant communities in the eastern United States. Rather, the temperature and CO₂ increases significantly enhanced local and regional productivity, and there is little reason to think such enhancements will not continue throughout the foreseeable future.
- The late twentieth-century rise in temperature and atmospheric CO₂ concentrations improved the productivity of plant communities in the central region of the United States, notwithstanding model-based concerns to the contrary.
- The late twentieth-century rise in temperature and atmospheric CO₂ improved the productivity of plant communities in the western region of the United States, notwithstanding model-based projections of unprecedented ecological disaster due to rising temperatures and drought.
- Warmer temperatures and higher CO₂ concentrations are resulting in net primary productivity increasing across tropical South America, overcoming the effects of deforestation, forest fires, and incursions by human civilization into natural areas.
- It is likely the greening of the planet will continue in the future, even if the largest temperature increases predicted by the models occur, because the optimum temperature for plant growth and development typically rises with increasing levels of atmospheric CO₂. This response, coupled with expected increases in plant photosynthetic rates from the rise in the air's CO₂ concentration, is more than enough to compensate for any temperature-induced plant stress caused by global warming.
- Real-world observations reveal plants have many ways of adjusting to changes in climate in addition to their ability to spread from places of rising warmth to cooler habitats, and these observations suggest the planet's current assemblage of plants

is likely to be around a good deal longer than many theoretical models have predicted.

- A major cause of biodiversity reductions is not rising atmospheric CO₂ concentrations, but instead the direct encroachment of man upon the world of nature. Anthropogenic global warming, to whatever extent it exists, is helping plants overcome these assaults and thrive despite the growing human presence.
- As good as things currently are for world agriculture, and as much better as they are expected to become as the atmospheric CO₂ content continues to rise, there may be additional substantial room for both natural selection and bioengineering to remove the constraints of low CO₂ adaptation in several important agricultural crops and thereby create novel genotypes able to exploit high CO₂ conditions to their—and our—advantage.
- The ongoing rise in atmospheric CO₂ content is likely exerting significant selection pressure on Earth's naturally occurring terrestrial plants, which should improve their performance in the face of various environmental stressors via the process of microevolution. Plants may be much better prepared than most scientists once thought to meet whatever climatic challenges, including global warming, the future may pose for them.
- Evidence continues to accumulate for substantial heritable variation of ecologically important plant traits, including root allocation, drought tolerance, and nutrient plasticity, which suggests rapid evolution based on epigenetic variation alone should be possible.

Introduction

A remarkable global phenomenon occurred throughout much of the twentieth century that the authors of IPCC's reports pretend never occurred despite hundreds of scholarly studies documenting its extent, causes, and consequences. The phenomenon is a gradual yet dramatic increase in biospheric productivity, or more simply, the greening of the Earth. According to IPCC's assumptions, theories, and models, this should not be occurring, indeed *cannot* be occurring. And yet, as this chapter will document, the evidence is overwhelming.

The aerial fertilization effect caused by the rise in

 CO_2 following the last deglaciation, combined with its transpiration-reducing effect that in turn led to a large increase in the water use efficiencies of the world's major C_4 founder crops, was the global trigger that made human agriculture possible. By dramatically increasing the yields of the first crops, that natural rise in CO_2 made modern civilization possible. Far from being a crisis, it was a miracle.

Fast-forward to the modern era and we are witnessing a rise in CO₂ levels similar to what occurred some 22,000 to 7,000 years ago. Once again, agricultural production is increasing throughout the world and across all types of landscapes, including plants and areas where improvements in human cultivation techniques cannot explain the improvement. Could global warming be good? In China, home to a fifth of all of humanity, Liu et al. (2004) report "all of China would benefit from climate change in most scenarios." Julien et al. (2006) say of the last two decades of the twentieth century, "Europe as a whole has a tendency to greening," and much of it is "seeing an increase in its wood land proportion." Extensive research has found the benefits of global warming on agriculture are occurring globally, across Asia, North America, and South America.

Nor is there evidence this greening is soon to end. Ballantyne *et al.* (2012) conclude, "although present predictions indicate diminished C uptake by the land and oceans in the coming century, with potentially serious consequences for the global climate, as of 2010 there is no empirical evidence that C uptake has started to diminish on the global scale." Their results clearly indicate just the opposite appears to be the case, with global carbon uptake doubling over the past half-century. Their research refutes the hypothesis of Canadell *et al.* (2007) and Raupach *et al.* (2008), who claimed to have detected a decreasing trend in the efficiency of the planet's carbon sinks, and it vindicates the many studies revealing an increasing greening of planet Earth.

IPCC feigns ignorance of this reality. Its authors seem still to be in the thrall of two authors who, two decades ago, wrote CO_2 -induced changes in global climate were expected to occur "too fast for evolutionary processes such as natural selection to keep pace," and this phenomenon "could substantially enhance the probability of extinction of numerous species" (Root and Schneider (1993)). This famous but unsubstantiated declaration has pervaded the publications of IPCC ever since ... but it never has been proven correct. It is more likely to be incorrect.

This chapter begins, in Section 4.1, with a

discussion of how the rise in CO_2 levels boosted food production globally in the past and how models that include the fertilizing effects of CO_2 suggest a future warming of the climate coupled with rising CO_2 levels will boost future global agricultural production, helping to meet the food needs of the planet's growing population. Section 4.2 surveys the extensive literature on the greening of the Earth, first presenting global studies and then studies focusing on specific continents, and finally studies that ask whether rising temperatures could check or offset the greening trend.

Section 4.3 reviews evidence on the impact of the rise in CO_2 levels on biodiversity and finds that impact to be positive. Similarly, Section 4.4. looks at the impact of the rise in CO_2 levels on plant extinctions and finds CO_2 makes extinctions less likely to occur. Finally, Section 4.5 asks whether plants can in fact evolve fast enough to adapt to a world with higher levels of CO_2 , higher temperatures, and more drought. The evidence is clear that many plant species can make significant adaptations to changes in their environment in just a few generations.

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4.1 Agricultural and Food Production

According to IPCC, over the past century or so the atmosphere's temperature and CO_2 concentration have risen at rates (and to levels) not seen for millennia in the case of temperature and millions of years in the case of CO_2 . Section 4.1.1 examines how the modern increase in temperature and CO_2 affected agriculture and food production in the past, and Section 4.1.2 provides an appraisal of how they might affect them in the future.

4.1.1 The Past

• Rising atmospheric CO₂ and warming temperatures, both of which IPCC claims constitute a significant threat to the biosphere, benefited agriculture in the ancient past and in the twentieth century.

According to Cunniff *et al.* (2008), "early agriculture was characterized by sets of primary domesticates or 'founder crops' that were adopted in several independent centers of origin," all at about the same time, and "this synchronicity suggests the involvement of a global trigger." Further noting Sage (1995) saw a causal link between this development and the rise in atmospheric CO₂ concentration that followed deglaciation (a jump from about 180 to 270 ppm), they hypothesized the aerial fertilization effect caused by the rise in CO₂ combined with its transpiration-reducing effect led to a large increase in the water use efficiencies of the world's major C₄ founder crops, and that this development was the global trigger that launched the agricultural enterprise.

To test this hypothesis, Cunniff et al. designed "a controlled environment experiment using five modern day representatives of wild C₄ crop progenitors, all 'founder crops' from a variety of independent centers." The five C₄ crops employed in their study were Setaria viridis, Panicum miliaceum var. ruderale. Pennisetum violaceum. Sorghum arundinaceum, and Zea mays subsp. parviglumis. They were grown individually in small pots filled with a 1:1 mix of washed sand and vermiculite for 40-50 days in growth chambers maintained at atmospheric CO₂ concentrations of either 180, 280, or 380 ppm, characteristic of glacial, post-glacial, and modern times, respectively.

Cunniff *et al.* report the "increase in CO_2 from glacial to postglacial levels [180 to 280 ppm] caused a significant gain in vegetative biomass of up to 40%," together with "a reduction in the transpiration rate via

decreases in stomatal conductance of ~35%," which led to "a 70% increase in water use efficiency, and a much greater productivity potential in water-limited conditions." The five researchers write, "these key physiological changes could have greatly enhanced the productivity of wild crop progenitors after deglaciation ... improving the productivity and survival of these wild C₄ crop progenitors in early agricultural systems." They further note "the lowered water requirements of C₄ crop progenitors under increased CO₂ would have been particularly beneficial in the arid climatic regions where these plants were domesticated."

Expanding on their work two years later, Cunniff et al. (2010) conducted a second set of experiments designed to further study the physiological and yield responses to glacial and post-glacial atmospheric CO₂ concentrations of modern representatives of the wild crop progenitors, but this time they included an analysis of C₃ and C₄ cereals. Once again, their experimental work was conducted in the laboratory in controlled-environment chambers maintained at atmospheric CO₂ concentrations of either 180 or 280 ppm. Cunniff et al. report "both the C₃ and C₄ species responded positively to rising CO₂ from the glacial to post-glacial level," with vegetative biomass near-doubling and yield rising by 50% in the C_3 species, consistent with the findings of Polley et al. (1992) and Dippery et al. (1995), and with a 10-15% yield enhancement under well-watered conditions in the C₄ species, consistent with the findings of Polley et al. (1996), Ziska and Bunce (1997), and Ward et al. (1999). In the case of the C_4 species, which typically are found in semi-arid environments, they discovered the transpiration-reducing effect of atmospheric CO₂ enrichment had a considerably larger positive impact on plant growth and yield. They write, "this stronger response of photosynthesis to soil drying in the C₄ species could represent an important route for rising CO₂ to stimulate biomass accumulation in a semi-arid environment," citing Cunniff (2009).

Cunniff *et al.* state the data described in their paper "provide experimental support for Sage's CO_2 limitation hypothesis, showing that atmospheric conditions of the last glacial period would have placed direct and indirect limitations on the productivity of crop progenitors." Although they also note the hypothesis does not explain why the domestication of crops occurred, they opine "it does offer evidence-based explanations of why agriculture did not begin earlier." It is logical to conclude civilizations of the past, which could not have existed without agriculture, were largely made possible by the increase in the atmospheric CO_2 content that accompanied deglaciation, and that people of today are likewise indebted to this phenomenon as well as to the additional 100 ppm of CO_2 the atmosphere has subsequently acquired.

A number of studies reveal the important role of temperature in agricultural production. Following the centuries-long cold period of the Little Ice Age (sixteenth through nineteenth centuries), global agriculture production has benefited from the warmer climate of the twentieth and twenty-first centuries.

Shen *et al.* (2005), for example, derived and analyzed long-term (1901–2002) temporal trends in the agroclimate of Alberta, Canada, reporting "an earlier last spring frost, a later first fall frost, and a longer frost-free period are obvious all over the province." They also say May–August precipitation in Alberta increased 14% from 1901 to 2002, and annual precipitation exhibited a similar increasing trend, with most of the increase coming in the form of lowintensity events. They note "the area with sufficient corn heat units for corn production, calculated according to the 1973–2002 normal, had extended to the north by about 200–300 km, when compared with the 1913–32 normal, and by about 50–100 km, when compared with the 1943–72 normal."

These changes, Shen *et al.* write, "imply that Alberta agriculture has benefited from the last century's climate change" and "the potential exists to grow crops and raise livestock in more regions of Alberta than was possible in the past." They also state the increase in the length of the frost-free period "can greatly reduce the frost risks to crops and bring economic benefits to Alberta agricultural producers." In addition, they note the northward extension of the corn heat unit boundary sufficient for corn production "implies that Alberta farmers now have a larger variety of crops to choose from than were available previously." Shen *et al.* say "there is no hesitation for us to conclude that the warming climate and increased precipitation benefit agriculture in Alberta."

Qian *et al.* (2010) derived a set of agroclimatic indices representing Canadian climatic conditions, which they analyzed for trends sure to prove useful for agricultural production planning for many years to come. They used a homogenized temperature dataset consisting of daily maximum and minimum air temperatures obtained from 210 meteorological stations distributed across Canada that cover the period 1895– 2007, along with an adjusted precipitation dataset developed at the Climate Research Division of Environment Canada. They found "a significant lengthening of the growing season due to a significantly earlier start and a significantly later end of the growing season," adding, "significant positive trends are also observed for effective growing degreedays and crop heat units at most locations across the country." Qian et al. report "the occurrence of extremely low temperatures had become less frequent during the non-growing season, implying a more favorable climate for overwinter survival." and "the total numbers of cool days, frost days, and killingfrost days within a growing season had a decreasing trend," so "crops may also be less vulnerable to cold stress and injury during the growing season." Their work revealed "extreme daily precipitation amounts and 10-day precipitation totals during the growing season have been increasing" and "significant trends associated with increased availability of water during the growing season are identified."

Clearly, the global warming that brought an end to the debilitating cold of the Little Ice Age and ushered the planet into the Current Warm Period is proving to be a benefit to Canada.

Hicke and Lobell (2004) calculated cropland net primary production (NPP) in the central part of the United States (South Dakota, Nebraska, Kansas, Missouri, Iowa, Minnesota, Wisconsin, and Illinois) using U.S. Department of Agriculture information together with crop-specific parameters that convert agronomic data into carbon fluxes for the period 1972–2001. Total cropland area exhibited no temporal trend over the study period, but "both NPP (flux per unit area) and P (spatially aggregated flux) increased during the study period (46 and 51%, respectively)."

These results indicate agricultural productivity in the central United States increased, and dramatically so, over the last three decades of the twentieth century, contrary to frequent claims that rising air temperatures and CO_2 concentrations will have negative effects on agriculture. Possible drivers of this increased agricultural productivity, according to Hicke and Lobell, include "improved cultivars, better fertilizer and pest management, more favorable climate, shifts to productive crop types, and economic influences (Duvick and Cassman, 1999; Evans, 1997; Lobell and Asner, 2003)."

Moonen *et al.* (2002) studied agriculturally important data collected from 1878 to 1999 on the outskirts of Pisa, Italy. Meteorological parameters routinely measured over this period were daily maximum, minimum, and mean air temperature plus daily rainfall. Agrometeorological parameters included the date of first autumn frost, date of last spring frost, length of growing season, number of frost days, lengths of dry spells, potential evapotranspiration, reference evapotranspiration, soil moisture surplus, theoretical irrigation requirement, number of days with soil moisture surplus, and number of days with soil moisture deficit.

Moonen et al.'s analysis found "extremely cold temperature events have decreased and extremely warm temperature events have remained unchanged." They suggest these observations may be attributed to the increase in cloud cover that would be expected to occur in a warming world, since more clouds would reduce midday heating and thereby offset much, if not all, of the impetus for global warming during the hottest part of the day. At night, the increased cloud cover would enhance the atmosphere's greenhouse effect, thereby adding to the long-term warming trend. Moonen et al. conclude, "no negative effects can be expected on crop production from this point of view." They found a real "silver lining" in the latter of these cloud feedback phenomena: "the number of frost days per year had decreased significantly resulting in a decrease in risk of crop damage." Hence, they say the time of planting spring crops could be safely advanced by many days, noting the length of the growing season increased by fully 47 days during the period they studied.

With respect to rainfall, Moonen *et al.* found a somewhat analogous situation. On an annual basis, the incidence of extremely high rainfall events did not appear to have changed, but there was an increase in the incidence of very low rainfall events. The one exception to this rule on a seasonal basis was a decrease in high rainfall events in the spring, which might be expected to increase drought risk at that time of year. However, when the maximum length of dry spells was assessed on a seasonal basis, the only significant change observed was a lengthening of this parameter in the autumn. Autumn is the wettest season of the year in Pisa, Italy; the researchers conclude "no increased drought risk is to be expected."

The bottom line with respect to water in agriculture is the balance between what is received via rainfall and what is lost via evapotranspiration, as this difference is what determines the soil moisture balance. Although there was a downward trend in yearly rainfall at Pisa over the past 122 years (due to the decrease of high rainfall events in the spring), there also was a nearly offsetting downward trend in evapotranspiration (possibly induced by enhanced daytime cloud cover), so there were "no significant changes in soil water surplus or deficit on an annual basis." The scientists noted a significant decrease in the number of surplus soil moisture days in the autumn, but because autumn is the wettest season of the year, they write, "this indicates a reduced flooding risk in autumn, which could have positive effects on workability of the soil and imply a reduction of erosion."

Thus Moonen *et al.* conclude, concomitant with the warming of the Northern Hemisphere over the past 122 years, "extreme events in Pisa have not changed in a way that is likely to negatively affect crop production." More often than not, the changes demonstrated to have occurred seem to have had positive impacts on agriculture. Moonen *et al.* say "there is no doubt regarding the reality of the observed changes."

Fengjin and Lianchun (2011) write, "the damage from extreme low temperature events during the warm season in Northeast China is one of the major disasters that affect agriculture in China," noting "rice, sorghum, corn, soybeans, and other major crops are all vulnerable to low-temperature damage." They computed temporal trends in the frequency of occurrence of extreme minimum temperatures during Northeast China's warm season (May to September) during the years 1956–2005, concurrently calculating trends in the region's annual average near-surface air temperature, after which they compared the former dependent trend with the latter independent trend.

The two Beijing Climate Center researchers found for the 1956-2005 period, the overall rate of increase in the annual average temperature was 0.32°C per decade. But from 1970 to 2005 it was 0.49°C per decade, and "from 1990, the increasing trend in the annual average temperature has become much more significant." They further report, "the average number of extreme minimum temperature days during the warm season in the 1950s was 15.8 days; in the 1960s, the average was 16.5 days; in the 1970s, the average increased to 17.3 days, and this was similar in the 1980s." In the 1990s, the average number of extreme minimum temperature days "decreased sharply to 13.3 days," and since 2000 the number of extreme minimum temperature days has been "decreasing constantly with an average of 11.4 davs."

As warming accelerated across Northeast China over the latter part of the past half-century, there was a concomitant decrease in the number of extreme minimum temperature events during that region's warm season. Fengjin and Lianchun state a "decreased frequency of extreme low temperatures over the past few decades has also been reported in other regions, e.g., Australia and New Zealand (Salinger *et al.*, 2000; Stone *et al.*, 1996)." The two Chinese scientists say the decrease in extreme minimum temperature events in response to the warmer temperatures of the past few decades has enabled farmers in Northeast China to harvest greater amounts of rice, sorghum, corn, soybeans, and other major crops than would otherwise have been possible.

Chen et al. (2011) report corn acreage in Northeast China-specifically Heilongjiang, Jilin, and Liaoning provinces-"accounts for 26.3% of the corn area in the country and accounts for about 29.4% of Chinese total corn grain production." They note the corn production of this region "plays a significant role in ensuring Chinese food security," and "knowledge of the potential effects of climate change on corn production in Northeast China will be highly valuable, not only for China but also for the world." Chen et al. "performed a multiple regression analysis to study the relationship between corn growth and the key climatic factors of temperature and precipitation during the crop growing season and during specific months in Northeast China from 1965 to 2008," to learn "which variables of climate change and which month in the crop growing season were associated with yield variability over this 44-year period."

The six scientists determined the major climatic factor affecting corn yield in Northeast China is daily minimum temperature, particularly in the months of May and September. They found a warming of 1.0°C in the mean daily minimum temperature of either of these months may enhance corn yield by 303 kg/ha (May) or 284 kg/ha (September). They report growth duration-defined as the period from sowing to harvest (days to maturity)-rose by six days in Liaoning province and by seven days in Jilin and Heilongjiang provinces during the years 1950–2008, which encompassed the period of 1965-2008, when daily minimum temperature rose at a rate of 0.44°C per decade. They conclude, "in order to fully exploit the positive effects of global warming on corn production, new varieties should be adapted to the longer growing season." This adjustment could be described as a good example of man and nature working together to ensure maximum food security for a significant portion of humanity.

Magrin *et al.* (2005) evaluated twentieth-century changes in climate and the yields of the chief crops (soybean, wheat, maize, and sunflower) of nine areas of contrasting environment in Argentina's Pampas region, which accounts for more than 90% of the country's grain production. After determining lowfrequency upward trends in yield due to improvements in crop genetics and management techniques, as well as the aerial fertilization effect of the historical increase in the air's CO_2 concentration, they used annual yield anomalies and concomitant climatic anomalies to develop relations describing the effects of precipitation, temperature, and solar radiation on crop yields, to determine the effects of long-term changes in these climatic parameters on Argentina's agriculture.

Although noting "technological improvements account for most of the observed changes in crop yields during the second part of the 20th century"— which totaled 110% for maize, 56% for wheat, and 102% for sunflower—Magrin *et al.* report changes in climate between the periods 1950–1970 and 1970–1999 led to yield increases of 38% in soybean, 18% in maize, 13% in wheat, and 12% in sunflower.

These studies suggest rising atmospheric CO_2 concentrations and warmer temperatures—both of which IPCC claims to constitute significant threats to the biosphere, having reached levels IPCC describes as unprecedented over the past one to two millennia—were far from problematic for agriculture.

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4.1.2 The Future

Several researchers have expressed concerns about a looming food production crisis on the horizon, suggesting just a few decades from now the evergrowing human population of the planet will need a near-doubling of present-day agricultural production. One example is the brief Perspective article published in *Science*, where Running (2012) resurrected shades of Meadows *et al.*'s 1972 treatise on *The Limits to Growth*.

Noting "terrestrial plant production is the foundation of the biospheric carbon cycle" and that "water and atmospheric CO₂ are transformed into plant carbohydrate matter with the help of solar energy," Running states this plant matter "sustains the global food web and becomes the source of food, fiber and fuel for humanity." A problem Running sees, however, is that for more than 30 years, global net primary production (NPP) has "stayed near 53.6 Pg per year, with only ~1 Pg of inter-annual variability," citing two studies of which he was a coauthor (Nemani *et al.*, 2003; Zhao and Running, 2010). He thus speculates, "if global NPP is fixed by planetary constraints, then no substantial increase in plant growth may be possible."

If true, this would indeed have catastrophic consequences, for it is almost universally agreed, as Running writes, "the projected 40% increase in human population by 2050 CE, combined with goals to substantially improve standards of living for the poorest 5 billion people on Earth, implies at least a doubling of future resource demand by 2050." The most important of these resources is food.

But is a doubling of food production by midcentury realistic? Agriculture already consumes 38% of the world's land surface, and Running notes "many analyses now conclude that freshwater use for irrigation has already reached a planetary boundary." Furthermore, with "massive river pollution and ocean anaerobic dead zones," he states, "if anything, future increases in NPP must be achieved with less, not more, irrigation and fertilizer use." Others have noted additional challenges, such as Tilman *et al.* (2009) noting "land previously allocated to food production is transformed to bioenergy production, raising food prices for the people who can least afford it."

Has the planet reached a limit to its growth? In a 2012 paper published in *Nature*, titled "Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years," Ballantyne *et al.* (2012) suggest it has not. The five U.S. scientists state their mass balance analysis shows "net global carbon uptake has increased significantly by about 0.05 billion tonnes of carbon per year and that global carbon uptake doubled, from 2.4 ± 0.8 to 5.0 ± 0.9 billion tonnes per year, between 1960 and 2010." They conclude, "there is no empirical evidence that carbon uptake has started to diminish on the global scale." In fact, as their results indicate, just the opposite appears to be the case, with global carbon uptake actually *doubling* over the past half-century.

There are many reasons why this doubling has occurred: breeding of better crop varieties that are higher-yielding, more competitive with weeds, less tasty to insect pests, more nutritious, and more drought-resistant, as well as smarter ways of farming, improved technologies, and the worldwide aerial fertilization and transpiration-reducing effects of the historical and still-ongoing rise in the atmosphere's CO_2 content. The latter two phenomena benefit agriculture and nature simultaneously.

Also concerned about adequately meeting the food needs of a growing world population, Parry and Hawkesford (2010) note "food production needs to increase 50% by 2030 and double by 2050 to meet projected demands." They say while the demand for food is increasing, production is progressively being limited by "non-food uses of crops and cropland," such as the production of biofuels. In their UK homeland, for example, they note, "by 2015 more than a quarter of wheat grain may be destined for bioenergy production," which is both sad and puzzling, as they also point out "currently, at least one billion people are chronically malnourished and the situation is deteriorating," with more people "hungrier now than at the start of the millennium."

The two researchers turn their discussion to photosynthesis, the all-important process by which plants "convert light energy into chemical energy, which is used in the assimilation of atmospheric CO₂ and the formation of sugars that fuel growth and yield." These phenomena make this natural and lifesustaining process "a major target for improving crop productivity both via conventional breeding and biotechnology," they write.

Next to a plant's need for carbon dioxide is its

need for water, the availability of which, in the words of Parry and Hawkesford, "is the major constraint on world crop productivity." They state, "since more than 80% of the [world's] available water is used for agricultural production, there is little opportunity to use additional water for crop production," because as populations increase, "the demand to use water for other activities also increases." Hence they conclude, "a real and immediate challenge for agriculture is to increase crop production with less available water."

They provide an example of a success story: the Australian wheat variety Drysdale, which gained fame "because it uses water more efficiently." This valued characteristic was achieved "by slightly restricting stomatal aperture and thereby the loss of water from the leaves." They note this ability "reduces photosynthetic performance slightly under ideal conditions," but it enables plants to "have access to water later in the growing season thereby increasing total photosynthesis over the life of the crop."

Of course, Drysdale is but one variety of one crop, and the ideal goal would be to get nearly all varieties of all crops to use water more efficiently. That goal in fact can be reached without doing anything new, because allowing atmospheric CO_2 concentrations to rise will cause the vast majority of plants to reduce the apertures of their stomata and thereby lower the rate at which water vapor escapes from them into the air. The result is even better than that produced by the breeding of Drysdale, because the extra CO_2 in the air more than overcomes the photosynthetic reduction that results from the partial closure of plant stomatal apertures, allowing even more yield to be produced per unit of water transpired in the process.

Human ingenuity can make the situation better still, by breeding and selecting crop varieties that perform better under higher atmospheric CO₂ concentrations than the varieties people currently rely upon, and by employing various technological means of altering them. Humanity can succeed even though "the United Nations Millennium Development Goal of substantially reducing the world's hungry by 2015 will not be met," as Parry and Hawkesford conclude. This truly seems to be the path to take, as they write "at least one billion people are chronically malnourished and the situation is deteriorating," with more people "hungrier now than at the start of the millennium."

Ainsworth *et al.* (2008) argue for breeding major crop varieties upon which the world depends for food to best take advantage of the ongoing rise in the atmospheric CO_2 content. The international consor-

tium of 32 scientists from 12 countries notes, "the growing world population, increasing demands for grains for animal feeds, land loss to urban expansion and demand for bioenergy production are exerting more and more pressure on global agricultural productivity." They state, "a major challenge for plant biologists, agronomists and breeders will be to provide germplasm and seed material that maximize future crop production," particularly in the context of rising atmospheric CO₂ concentrations that provide "a unique opportunity to increase the productivity of C_3 crops." They say "only a fraction of available germplasm of crops has been tested for CO₂ responsiveness," and "further research is needed to elucidate the mechanisms of yield response to CO₂, to assess the genetic diversity available for improving responsiveness and to devise efficient schemes for selection for adaptation to rising ambient CO₂, whether based on conventional plant breeding or systems biology approaches for selecting and engineering improved genetics."

The first step in meeting these objectives, according to the researchers, "is to create facilities for field screening the yield response to elevated CO_2 across a wide range of germplasm," and doing so under "conditions and management that reflect dominant agronomic practices and provide as natural an environment as possible." They recommend free air CO_2 enrichment (FACE) experimentation, which these scientists say meets many of these criteria and presents a minimally obtrusive interaction with the natural environment.

Although FACE systems are often considered expensive to construct and operate, Ainsworth *et al.* note "the net cost is compensated for by economies of scale, and the cost per unit ground area is considerably less than alternative systems." This is very important, as they explain, because "the new research requires investigating large numbers of genotypes," and "to investigate the association of CO_2 responsiveness with a single quantitative trait locus mapping population, approximately 150 inbred lines would need to be investigated."

The world-renowned group of scientists concludes, "because it may take 10–15 years to move from discovery of new advantaged genetics to commercial cultivars of annual grain crops, developing a robust strategy and supporting the planned work with the best possible facilities should be an urgent priority."

Zhu *et al.* (2010) embrace an alternative strategy for boosting agricultural production. They say meeting the global increase in agricultural demand during this century "is predicted to require a doubling of global production," but "the world has limited capacity to sustainably expand cropland," and this capacity is actually "shrinking in many developed countries." The three researchers contend, "meeting future increases in demand will have to come from a near doubling of productivity on a land area basis." They suggest "a large contribution will have to come from improved photosynthetic conversion efficiency," for which they estimate "at least a 50% improvement will be required to double global production."

The researchers focus on photosynthetic conversion efficiency because experimental evidence has found increases in the atmosphere's CO_2 concentration boost the photosynthetic rates of nearly all plants, and those rate increases generally lead to equivalent increases in plant productivity on a landarea basis. They examined the prospects for boosting photosynthetic conversion efficiency in an entirely different way: genetically, without increasing the atmosphere's CO_2 content.

The three scientists write, "Improving photosynthetic conversion efficiency will require a full suite of tools including breeding, gene transfer, and synthetic biology in bringing about the designed alteration to photosynthesis." For some of these "near-term" endeavors, they write, "implementation is limited by technical issues that can be overcome by sufficient investment." But a number of "mid-term" goals could take 20 years to achieve, and "even when these improvements are achieved, it may take an additional 10-20 years to bring such innovations to farms in commercial cultivars at adequate scale." And they write of still longer-term goals for which "too little of the science has been undertaken to identify what needs to be altered to effect an increase in yield." They acknowledge some of what they envision may not even be possible, such as developing a form of rubisco that exhibits a significant decrease in oxygenation activity, or designing C₃ crops to utilize the C₄ form of photosynthetic metabolism. The focus of Ainsworth et al. (2008) appears to be a far better path to pursue: conducting research to "elucidate the mechanisms of yield response to CO₂, to assess the genetic diversity available for improving responsiveness and to devise efficient schemes for selection for adaptation to rising ambient CO2, whether based on conventional plant breeding or systems biology approaches for selecting and engineering improved genetics."

Godfray *et al.* (2010) note, "more than one in seven people today still do not have access to sufficient protein and energy from their diet and even more suffer some form of micronutrient malnourishment," citing the FAO (2009). They write, although "increases in production will have an important part to play" in correcting this problem and keeping it from worsening in the future, mankind "will be constrained by the finite resources provided by the Earth's lands, oceans and atmosphere." This set of difficulties they describe at the end of their review as a "perfect storm."

The first question they ask in regard to how mankind might successfully navigate this highly restricted terrain is: "How can more food be produced sustainably?" They say the primary solution to food shortages of the past had been "to bring more land into agriculture and to exploit new fish stocks," but they quickly note there is precious little remaining of either of these resources. They conclude, "the most likely scenario is that more food will need to be produced from the same or less land," because "we must avoid the temptation to sacrifice further the Earth's already hugely depleted biodiversity for easy gains in food production, not only because biodiversity provides many of the public goods upon which mankind relies, but also because we do not have the right to deprive future generations of its economic and cultural benefits."

The key to meeting these diverse requirements simultaneously is in Godfray *et al.*'s statement, "greater water and nutrient use efficiency, as well as tolerance of abiotic stress, are likely to become of increasing importance." As discussed previously, rising carbon dioxide can bring about all of these changes in mankind's crops. Rising concentrations of atmospheric CO_2 increase the photosynthetic prowess of essentially all plants, while generally reducing the rate at which they transfer water from the soil to the air. In addition, an increase of CO_2 in the atmosphere tends to enhance the efficiency with which plants utilize nutrients in constructing their tissues and producing the edible portions that essentially all of Earth's animals and humans depend on.

Each of the important benefits noted above has been discussed in great detail in the preceding chapters of this volume. In the material that follows, we limit our discussion to studies that directly imply general trends regarding these global benefits. Section 4.1.2.1 examines the findings of several empirical studies from which trends in future agricultural production can be inferred, and Section 4.1.2.2 presents a review of several model-based studies that shed additional light on the subject.

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4.1.2.1 Empirical Studies

• Empirical studies suggest a future warming of the climate coupled with rising atmospheric CO₂ levels will boost global agricultural production and help meet the food needs of the planet's growing population.

As discussed in the preceding chapters of this volume, numerous studies attest to the growth-enhancing, water-conserving, and stress-alleviating benefits of CO_2 enrichment for plants. In the present subsection, therefore, we limit our discussion to studies from which we can infer general trends in future agricultural production.

According to Tian *et al.* (2012), "more than 20% of the world's food consumers depend on wheat (*Triticum aestivum* L.), which is produced on an area of over 200 million hectares worldwide (Ortiz *et al.*, 2008)." They note "winter wheat area accounts for more than 80% of this total," and "it is typically grown in the seasons of winter and spring where warming is mainly anticipated." China, the writers note, is the world's largest producer of winter wheat, and more than 70% of the crop is sown in the country's eastern provinces on the Yangtze Delta Plain.

Tian *et al.* "conducted a five-year field warming experiment since 2004 with a facility of Free Air Temperature Increase (FATI) in Nanjing, Jiangsu province," in which their objectives were "to investigate the actual responses of winter wheat phenophase, biomass production and grain yield to anticipated warming [~1.5°C] under field conditions" where "there were no water and nitrogen limitations for winter wheat growth, which is common in East China." They studied *Triticum aestivum* L. cv Yangmai 11, a local cultivar having a "high yield potential."

The 1.5°C increase in temperature significantly advanced crop phenophases, leading to a reduction in the length of the entire growth period of about 10 days, with the result that grain yields rose due to "the mitigation of low temperature limitation during the pre-anthesis phase and to the avoidance of hot-dry stress during the post-anthesis phase." The researchers found the areas of flag leaves and total green leaves at anthesis, as well as the 1,000-grain weight of the plants, were 36.0, 19.2, and 5.9% higher in the warmed plots than in the unaltered control, respectively. The net effect of these warmth-induced changes was a mean grain yield increase of 16.3%, and they therefore conclude "anticipated warming

may facilitate winter wheat production in East China."

Ortiz et al. (2008) reviewed some of the approaches for ameliorating the oft-predicted negative impacts climate change may have on wheat production in some of the most important wheat growing areas of the world. They write, "to adapt and mitigate the climate change effects on wheat supplies for the poor, germplasm scientists and agronomists are developing heat-tolerant wheat germplasm, as well as cultivars better adapted to conservation agriculture," noting these encouraging results include "identifying sources of alleles for heat tolerance and their introgression into breeding populations through conventional methods and biotechnology." They report "wheat geneticists and physiologists are also assessing wild relatives of wheat as potential sources of genes with inhibitory effects on soil nitrification." This activity could lead to significantly reduced emissions of nitrous oxide from agricultural soils and thereby shrink the impetus for global warming provided by this powerful trace greenhouse gas, which molecule-for-molecule is about 300 times more radiatively active than CO2. Ortiz et al. conclude important technology and knowledge will ultimately flow to farmers and enable them "to face the risks associated with climate change."

Bunce (2008) grew adequately fertilized plants of four varieties of the common garden bean (Phaseolus vulgaris)-Matterhorn (a great northern bean), Jaguar (a black bean), Red Hawk (a kidney bean), and Brown Beauty (a snap bean)-from seed to maturity under standard field conditions at Beltsville, Maryland (USA) in open-top chambers. They made photosynthetic measurements of mature upper-canopy leaves in full sunlight at midday during the pod-filling stages of four growing seasons and determined final seed yields and other plant characteristics at harvest. They found an extra 180 ppm of CO₂ in the CO₂enriched chambers (a concentration increase of close to 50% during daylight hours) resulted in a mean long-term stimulation of midday net photosynthesis of approximately 18% in the Matterhorn and Jaguar bean varieties, and an increase of twice that much (36%) in the Red Hawk and Brown Beauty cultivars. In terms of dry mass seed yield, the Matterhorn variety experienced a CO₂-induced increase of about 39%, followed by Red Hawk at 21%, Brown Beauty at 18%, and Jaguar with a 10% decline in seed yield. As Bunce reports, "the highest yielding variety at ambient CO₂ [Jaguar] was out-yielded by a different variety at elevated CO₂ [Matterhorn]."

These observations make it clear there is

significant variability in seed yield response to atmospheric CO_2 enrichment among the four bean varieties tested by Bunce. In addition, it is equally clear there was no *a priori* way of knowing which of the four cultivars would respond best to an increase in atmospheric CO_2 concentration, or that one would actually respond negatively. Bunce's experiment demonstrates the great need to perform a host of such studies on the planet's most important crop plants, to identify which of their many varieties should be selected for additional crop breeding work. That is the only way to take full advantage of the significant increase in the atmosphere's CO_2 concentration that will occur over the next several decades.

In a standard paddy-culture FACE experiment conducted at Yangzhou, Jiangsu, China, during the years 2004–2006, Yang et al. (2009) grew a two-line inter-subspecific hybrid rice variety (Liangvoupeijiu) at ambient and elevated atmospheric CO₂ concentrations of 376 and 568 ppm, respectively, at two levels of field nitrogen (N) application-low N (12.5 g N m⁻²) and high N (25 g N m⁻²)—while measuring numerous aspects of crop growth, development, and final yield. The eight Chinese scientists found the 51% increase in atmospheric CO₂ concentration increased the final grain yield of the low N rice crop by 28% and that of the high N rice crop by 32%. As a result, and in light of the findings of two prior rice FACE experiments (Kim et al., 2003; Yang et al., 2006), they conclude "hybrid rice appears to profit much more from CO₂ enrichment than inbred rice cultivars (c. +13%)." Yang et al. describe Liangyoupeijiu as "one of the most popular 'super' hybrid rice varieties in China (Peng et al., 2004)."

Shimono *et al.* (2007) say lodging—the environmental beating down of a crop—"can occur under heavy rains and strong winds," and this phenomenon "decreases canopy photosynthesis due to self-shading (Setter *et al.*, 1997) and disturbs the translocation of carbon and nutrients to the rice grains (Hitaka and Kobayashi, 1961), resulting in lower yield and poor grain quality." They note Setter *et al.* (1997) found a moderate degree of lodging reduced canopy height by 35% and decreased yield by about 20%, whereas severe lodging reduced canopy height by 75% and decreased yield by up to 50%.

Shimono *et al.* designed a free-air CO_2 enrichment experiment to determine what effect the ongoing rise in the atmosphere's CO_2 content might have on lodging in rice plants, growing the cultivar Akitakomachi in paddy fields under three nitrogen (N) fertilization regimes—low N (6 g N m⁻²), medium N (9 g N m⁻²), and high N (15 g N m⁻²)—at two 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 $0 = 0^{\circ}$ from the vertical, $1 = 1^{\circ}-18^{\circ}$, $2 = 19^{\circ} 36^{\circ}$, $3 = 37^{\circ}-54^{\circ}$, $4 = 55^{\circ}-72^{\circ}$, and $5 = 73^{\circ}-90^{\circ}$.

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 CO_2 ," because the lowest internodes of the rice stems "became significantly shorter and thicker under elevated CO_2 ," which likely "strengthened the rice culms against the increased lodging that occurred under high N." They note the reduced lodging experienced under elevated CO_2 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 CO₂induced 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 threeyear 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 CO_2 /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 CO_2 /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 vield 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 CO_2 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, the 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 CO_2 , 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 CO_2 ." 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 CO_2 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 CO_2 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 CO_2 , 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 CO_2 plots.

Vanuytrecht et al. (2012) acquired peer-reviewed publications reporting the results of free-air CO₂enrichment (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 CO_2 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 CO_2 concentration.

Although "the FACE technique avoids the potential limitations of (semi-) closed systems by studying the influence of elevated CO_2 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 CO_2 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 CO_2 treatment at 27 days after planting, and wheat grain yields were 12% less in a fluctuating CO_2 treatment compared with a constant elevated CO_2 concentration treatment.

The results of the empirical studies described above suggest a future warming of the climate, coupled with rising atmospheric CO_2 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 highprotein-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 CO_2 , 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, CO_2 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 CO_2 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 processbased 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

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 CO_2 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 CO_2 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 CO_2 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 CO_2 fluxes using the High Resolution Biosphere Model of Esser *et al.* (1994) and real-world CO_2 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 CO_2 concentrations coincided with El Niño periods, and times of anomalous declining atmospheric CO_2 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 CO_2 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, LeOuere et al., 2000; Langenfelds et al., 2002)." At the other end of the spectrum, Reichenau and Esser report "volcanic eruptions with considerable aerosol may create disturbances production 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 CO_2 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 CO_2 fluxes between Earth's surface and atmosphere are likely to be short-lived and anomalous.

Langenfelds *et al.* (1999) analyzed O_2/N_2 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 Langenfelds *et al.* those years. necessarily acknowledge the existence of a terrestrial carbon sink of like magnitude. They suggest this "compensating growth of the [terrestrial] biosphere" is due to "reforestation, 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 CO_2 -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 belowground.

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 CO_2 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 CO_2 can be the deciding factor in determining whether a plant lives or dies.

These benefits of atmospheric CO_2 enrichment apply to both agricultural and natural ecosystems. As Wittwer (1995) has noted, "the rising level of atmospheric CO_2 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 CO_2 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 CO_2 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 CO_2 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 " CO_2 seems to be the only environ-mental 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 highaltitude long-lived bristlecone, foxtail, and limber pine trees in Arizona, California, Colo-rado, 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 the trees' enhancing growth rates, strongly implicating the historical rise in atmospheric CO₂ content as the factor responsible for their everincreasing productivity over the prior century and a half.

Phillips and Gentry (1994) provided perhaps the most striking evidence for the significant twentiethcentury 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 CO_2 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 vears 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.*, 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

climate and atmospheric CO_2 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 CO_2 - and temperatureinduced 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 CO_2 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 CO₂induced 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 compares well with result estimates of up to 1.1 Pg C vr⁻¹ derived from independent

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).

empirical observations of same-period anthropogenic CO_2 emissions, changes in land use, CO_2 uptake by the world's oceans, and increases in the air's CO_2 concentration.

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." Llovd (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 CO_2 emissions, to calculate the residual fluxes of carbon (in the form of CO_2) 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 CO_2 -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 CO_2 -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 CO_2 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 CO_2 enrichment is most pronounced at higher tem-



Figure 4.2.1.4. Interannual variations in global Net Primary Productivity (NPP) in relation to atmospheric CO_2 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 satellitederived 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, utiliza-tion, 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 bv increases in atmospheric dioxide carbon and precipitation.

Cao *et al.* (2005) used the CEVSA (Carbon Exchanges in the Vegetation-Soil-Atmosphere sys-tem) 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 CO_2 is greater in warmer conditions, so the CO_2 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 CO_2 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 CO_2 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 ($50-90^{\circ}N$, $30-50^{\circ}N$, $10-30^{\circ}N$, $10^{\circ}N-10^{\circ}S$, $10-30^{\circ}S$, and $30-63^{\circ}S$) 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

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 CO_2 accumulating in the atmosphere to the CO_2 flux into the atmosphere due to human activitiesknown 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 CO_2 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 CO_2 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 Niñoinduced 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,"

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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 1σ (dark shaded bands) and 2σ (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 halfcentury. 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 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 CO_2 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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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,



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."

Seaguist 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, eastwest band of NPP increase (>10 g C m⁻² year⁻¹). The band extends up to about 17°N and includes several hotspots (>20 g C m⁻² 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 g C m⁻² year⁻¹, yielding a total mean rate of change of 51.0 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 submodels 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 CO_2 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 CO_2 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 CO_2 concentration and its antitranspiration 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 vears 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 vield."

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 CO_2 , 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 CO_2 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: $1.6\%/day \ge 5$ 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 CO_2 concentration (Idso and Idso, 1994), so the 1°C increase in temperature experienced in China between 1982 and 1999 could easily boost the initial CO_2 -induced 7.3% NPP enhancement to 10.7%. That, when combined with the 8.0% enhancement caused by the warminginduced 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

peak NPP has advanced," which "may indirectly explain the enhanced amplitude and advanced timing of the seasonal cycle of atmospheric CO_2 concentration (Keeling *et al.*, 1996)." They further suggest the enhanced amplitude of the seasonal CO_2 cycle "was probably due to the rise in atmospheric CO_2 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 CO_2 and O_2 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 CO_2 ."

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 temperaturelimited 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 18vear 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 15day 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 R^2 value of 0.40 and P < 0.001 (see Figure 4.2.2.2.1.1.1). They also found increasing trends for all three subsets of the growing season: April–May, June–August, and September–October.



Figure 4.2.2.2.1.1.1. 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 CO_2 concentration between 1901 and 2000. They report their modeling exercise indicates "during the past

100 years a combination of increasing CO_2 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 CO_2 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 spatiotemporal 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-winderosion 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 CO_2 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 (O_3) 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 O_3 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 O_3 pollution had consistent negative effects on forest production, reducing total NPP by 0.2 to 1.6% from the 1960s to 2000–2005; without O_3 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 O_3 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

additive, but that the synergy between the effects of climate change and doubled CO_2 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 CO_2 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 with temperature, precipitation, results 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 CO_2 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 satellitebased 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 CO_2 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 4.2.2.1.4.1. Interannual variations in aboveground biomass for China's grassland during the years 1982–1999. Adapted from Piao *et al.* (2007).

(2010)Peng al. used snow-depth et 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 CO_2 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 CO_2 changes due to lowered CO_2 partial pressure"; (2) "water conservation of steppe vegetation in response to experimental CO_2 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 CO_2 increase," even in spite of "increasing land-use by herding"; and (4) "experimental CO_2 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 CO_2 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 CO_2 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 CO_2 concentration that has occurred since pre-industrial times should have improved water use efficiency (WUE) in most plants by increasing the ratio of CO_2 fixed to water lost via evapotranspiration. That this hypothesis is correct has been demonstrated by Leavitt *et al.* (2003) in the context of the longterm atmospheric CO_2 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 CO_2 ," 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 waterlimited environments."

Singh et al. (2011) used U.S. National Oceanic and Atmospheric Administration (NOAA) satellitederived 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-ofincrease 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 $72^{\circ}02$ 'N to $72^{\circ}40$ 'N and from $101^{\circ}15$ 'E to $102^{\circ}06$ ' 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 satellitebased 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 latu)-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 $1-2^{\circ}$ 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 CO_2 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 CO_2 ," 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 CO_2 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 cvanobacteria": 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 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 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 vears 1901 to 2002, using observed values of monthly climatology and annual global atmospheric CO₂ concentrations (Figure 4.2.2.2.2).

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



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, ORCIDEE, 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 CO_2 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 CO_2 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 CO_2 ." 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



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 CO_2 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 CO_2 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 CO_2 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 CO_2 .

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 CO_2 emissions that pushes the air's CO_2 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 significantly 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 CO_2 ." They also note, "under a high CO_2 stomata will be much less open which will lead to a reduced evapotranspiration and lower water loss, both for C_3 and C_4 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 CO_2 , 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 'forwardlooking 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



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 CO_2 , 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 vears. 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 δ^{13} 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 halfcentury (1930 to 1980), when the atmosphere's CO_2 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 CO_2 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 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 nitrogenenriching effect." Hence, they considered "the enriching effect of increasing CO_2 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 CO_2 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 CO_2 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 CO_2 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 fullscale '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 forestline 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; Hendenas et al., 2011)." They state the change in shrubs and small trees thev 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 $68^{\circ}20$ 'N, $18^{\circ}50$ '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 CO_2 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 $C/m^2/year$) 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 sitespecific ring-width-derived productivity histories with same-site NDVI time series, and used the resulting relationship to establish six regional forest productivity 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 determinants of changes in forest primary 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 semiarid 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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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 CO_2 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 CO₂induced 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, " δCO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 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 newbranch 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 longterm 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 CO_2 to the atmosphere declined, and they became CO_2 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 CO_2 content and its aerial fertilization and antitranspirant effects? Although these well-documented consequences of atmospheric CO_2 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 CO_2 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 1-2decades 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 vears, 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 realworld 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 localwarming. 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 groundbased 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
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 CO_2 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 CO_2 concentration averaged 299 ppm, and during the second it averaged 346 ppm. The mean rate of rise of the atmosphere's CO_2 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 ringwidth residuals for the later period (when the air's CO_2 concentration was 15% greater and its rate-ofrise 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 CO_2 concentration and the rate of atmospheric CO_2 increase were both relatively high." They note, "these results are consistent with expectations for CO_2 -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 CO_2 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 (CO_2 , O_3 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

(-40%), $CO_2 + O_3$ (+60%), $CO_2 + N$ deposition (+184%), and $CO_2 + N$ deposition + O_3 (+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 CO_2 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 CO_2 , 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 and ground amounts mean 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 CO_2 -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 that was ultimately agriculture 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 aboveground 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 CO_2 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 microhabitats," 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 2×2 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 CO_2 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 twentiethcentury increases in air temperature and atmospheric CO_2 concentration did not negatively affect plant communities in the eastern United States. Rather, the temperature and CO_2 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 "coincidently 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 "longterm increases in radial growth appear unrelated to historical disturbance levels for the region, to longterm 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 CO_2 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 from historical increase results 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 CO_2 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 twentiethcentury 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 48year record derived from an average of 17 measurements per year, Raymond and Cole (2003) demonstrated 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 CO_2 , an increase [in] rainwater throughput, or an increase in plant and microbial production of CO_2 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 CO_2 content, which also leads to an increase in plant and microbial production of CO_2 and organic acids in soils.

The findings presented above indicate the late twentieth-century rise in temperature and CO_2 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 hydroecological 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 highlevel 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) processbased 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 CO_2 , 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 CO_2 , 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 vegetationmediated 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 CO_2 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 CO_2 content, with plant intrinsic water-use efficiency rising by 10 to 25% from 1750 to 1970, during which time the air's CO_2 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 CO_2 " 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 CO_2 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 germinated pine trees that 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 preand 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 CO_2 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 CO_2 -driven growthenhancement 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 CO_2 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 CO_2 concentration and climate, the real-world change in CO_2 with a constant preindustrial climate, and the real-world change in climate with a constant preindustrial CO_2 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 droughtadapted 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 CO_2 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 bv 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 oldgrowth 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

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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 CO_2 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 CO_2 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 oldgrowth 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 longterm 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, $\delta^{13}C$ leaf, and discrimination, $\Delta^{13}C$ leaf, oxygen isotope composition, $\delta^{18}O$ 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 Ca 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 Ca appear to be "simply related to the availability of CO₂ 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 CO₂ assimilation by the trees' stomatal conductance-with needles to their concomitant historical changes in temperature, precipitation, and atmospheric CO₂ 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 CO₂ in the atmosphere." Over the latter period, tree growth remained rather stable because of lower-than-normal precipitation and higher-thannormal 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 CO₂ content rises.

Lloyd and Farquhar (2008) provide additional support for this attribution, concluding, "the magnitude and pattern of increases in forest dynamics across Amazonia observed over the last few decades are consistent with a CO₂-induced stimulation of tree growth." Phillips et al. (2008) 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 CO₂," because of "the undisputed long-term increase in [its] concentration, the key role of CO₂ in photosynthesis, and the demonstrated effects of CO₂ fertilization on plant growth rates."

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 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.

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 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.

Jurik *et al.* (1984) exposed bigtooth aspen leaves to atmospheric CO_2 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. where the net photosynthetic rate of the leaves exposed to 1,935 ppm CO_2 is maximal, the extra CO_2 boosts the net photosynthetic rate of the foliage by 450%. The extra CO_2 increases the optimum temperature for net photosynthesis in this species by about 11°C: from 25°C in air of 325 ppm CO_2 to 36°C in air of 1935 ppm CO_2 .

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 CO_2 but somewhere in the vicinity of 50°C in air of 1935 ppm CO_2 . Thus not only was the optimum temperature for the growth of bigtooth aspen greatly increased by the extra CO_2 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

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 CO_2 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-

have



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,

induced plant stress caused by the worst-case scenario of climate-model-predicted CO_2 -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 CO_2 .

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 CO_2 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 transpirationreducing 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 wellprepared 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 C_3 crops."

The scientists point out "only a fraction of available germplasm of crops has been tested for CO_2 responsiveness" and "further research is needed to elucidate the mechanisms of yield response to CO_2 , to assess the genetic diversity available for improving responsiveness and to devise efficient schemes for selection for adaptation to rising ambient CO_2 , 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 wellfertilized 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 CO_2 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 CO_2 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 CO_2 . That endeavor, Ziska *et al.* write, "could maximize productivity as CO_2 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 destroying 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 CO_2 in the CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 concentrations: ambient (~370 ppm) and elevated (~570 ppm). They found the extra 200 ppm of CO_2 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 threeyear 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% CO₂induced 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 CO_2 than inbred japonica cultivars." Both the Japanese and Chinese FACE studies of inbred japonica cultivars found CO_2 induced grain yield enhancements on the order of only 13% for a 200 ppm increase in the air's CO_2 concentration. Noting "there is a pressing need to identify genotypes which could optimize harvestable yield as atmospheric CO_2 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 wellwatered 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 CO_2 as a percentage of that at ambient CO_2 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 CO_2 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 sizerelated 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 CO_2 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 CO_2 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. Realworld 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 CO_2 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 CO_2 -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 CO_2 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 $4^{\circ}-5^{\circ}$ 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 highaltitude 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 impoverish-ment, 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 $1.1-2.0^{\circ}$ 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, pinyonjuniper woodland, chaparral shrubland, and conifer forest." They found "the average elevation of the dominant plant species rose by ~65 meters," The 30year mean temperature measured at seven stations around Deep Canvon 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 CO_2 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 withinpopulation 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 microrefugia 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 CO_2 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 coarsescale 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 Rafaelli, 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 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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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 (C₄ 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-ofdoors 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 CO₂-induced biomass increase of 70%. They also found the extra CO₂ "reduced the coefficients of variation for all aspects of plant growth, especially reproductive biomass," so the CO₂-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 "CO₂-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 nonconspecifics." 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 CO_2 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 CO_2 ," suggesting it was likely the interior-forest lianas were limited by the enhanced tree growth provided by the CO_2 increase, which likely resulted in the trees becoming more competitive with the vines because of CO_2 -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 CO_2 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 CO₂induced 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 CO_2 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 CO_2 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, compilation 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 CO_2 . 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. magellan-icum*—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 CO_2 exchange rates did not vary among species nor with altitude. Net CO_2 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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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 CO_2 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 CO_2 -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 CO_2 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 CO_2 concentrations tended to be approximately 180 ppm. This value, according to Sage and Coleman, might not be much above the "critical CO_2 threshold at which catastrophic interactions occur." Thus they speculated plants of the late Pleistocene "might have been adapted to lower CO_2 concentrations than currently exist." And in light of the short period of evolutionary time that has elapsed since the last of these low- CO_2 conditions prevailed, the two researchers suggest "many if not most plants might still be adapted to CO_2 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 CO_2 enrichment far above what is characteristic of the CO_2 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 CO_2 content continues to rise, there may be additional "substantial room for natural selection and bioengineering to remove the constraints [of low CO_2 adaptation], thereby creating novel genotypes able to exploit high CO_2 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 CO_2 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 CO_2 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 microevolution as the air's CO₂ concentration continues to rise in the years and decades ahead.

The ongoing rise in atmospheric CO_2 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 CO_2 -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 CO_2 -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 threegeneration Populus pedigree generated by the hybridization of two contrasting Populus specieswhere 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 OTL 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 CO_2 ," 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 CO_2 , while an additional three areas of the genome on linkage groups IV, XVI and XIX appeared important in determining root growth response to elevated CO_2 ." Consequently, stating their results "quantify and identify genetic variation in response to elevated CO_2 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 CO_2 ," as subsequent studies have further demonstrated.

Springer et al. (2008) grew well-watered and well-fertilized plants of two closely related outcrossed 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 CO_2 to alter the expression of plant genes in ways that may enable plants to take better advantage of the ongoing rise in atmospheric CO_2 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) CO_2 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 CO_2 treatments during the daylight hours of each

growing season. They found disease incidence was lower in the elevated CO_2 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 CO_2 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 CO_2 ... reduced disease incidence on *Solidago rigida*."

Kaligaric 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 (Moller 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 CO_2 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 CO_2 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 CO_2 springs, where they "have been exposed to a CO_2 -enriched atmosphere over many generations," providing what the researchers call "a unique opportunity to explore the micro-evolutionary response of wild plants to elevated CO_2 ."

Onoda et al. write, "the adaptation of leaf photosynthesis to elevated CO₂ was tested by a common experiment with herbaceous garden 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 CO_2 -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 CO2responsive 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 CO_2 concentration to their advantage.

Nakamura *et al.* (2011) suggest "evolutionary responses to elevated CO_2 in wild plants are, in general, difficult to detect using growth experiments, because the duration of experiments is often too short

compared to the time required for evolution." They note areas around natural CO_2 springs—and locations nearby but beyond the influence of the additional CO_2 —provide ideal sources of plants for such studies, as the plants near the springs have "been exposed to high CO_2 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 C_3 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 CO_2 , some of which were heritable," indicating "an evolutionary differentiation occurred in the *P*. *asiatica* population across a CO_2 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 CO_2 , suggesting that plants from higher- CO_2 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 CO_2 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 CO_2 populations."

The scientific findings described above indicate the ongoing rise in atmospheric CO_2 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 CO_2 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 populationlevel 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 halfcentury." 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 CO_2 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 dendrochronological 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 'preadapted' genes in F. svlvatica," 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 CO_2 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 belowaverage 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 lifehistory 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 selfincompatible 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 "climatically demonstrates 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 agroecosystems 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 microevolutionary 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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