7

Biological Effects of Carbon Dioxide Enrichment

Introduction

The Contribution of Group 1 to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) hardly mentions the beneficial effects of earth's rising atmospheric carbon dioxide (CO_2) concentration on the biosphere. In a chapter titled "Changes in Atmospheric Constituents and in Radiative Forcing" the authors say the following (IPCC, 2007–I, p. 186):

> Increased CO_2 concentrations can also "fertilize" plants by stimulating photosynthesis, which models suggest has contributed to increased vegetation cover and leaf area over the 20th century (Cramer *et al.,* 2001). Increases in the Normalized Difference Vegetation Index, a remote sensing product indicative of leaf area, biomass and potential photosynthesis, have been observed (Zhou *et al.,* 2001), although other causes including climate change itself are also likely to have contributed. Increased vegetative cover and leaf area would decrease surface albedo, which would act to oppose the increase in albedo due to deforestation. The RF due to this process has not been evaluated and there is a very low scientific understanding of these effects.

Later in that report, in a chapter titled "Couplings Between Changes in the Climate System and Biogeochemistry," a single paragraph is devoted to the "effects of elevated carbon dioxide" on plants. The paragraph concludes, "it is not yet clear how strong the CO_2 fertilization effect actually is" (p. 527).

Since CO_2 fertilization could affect crop yields and how efficiently plants use mineral nutritients and water, one would expect the subject to be addressed in the Contribution of Group 2, on "Impacts, Adaption and Vulnerability," and indeed it is, in a chapter titled "Food, Fibre and Forest Products" (IPCC, 2007-II). But that chapter belittles and largely ignores research on the benefits of enhanced CO_2 while exaggerating the possible negative effects of rapidly rising temperatures and extreme weather events predicted by computer models. The subject is not even mentioned in Chapter 8 of that report, on "Human Health," although even a modest effect on crops would have some effect on human health. (See Chapter 9 of the present report for our own, more complete, discussion of the health effects of climate change.)

The IPCC's failure to report the beneficial effects of rising CO_2 concentrations is surprising when literally thousands of peer-reviewed journal articles exist on the subject. It is also a major defect of the IPCC report and one reason why it is not a reliable summary of the science of climate change. In this chapter, we seek to provide the balance that eluded the IPCC.

The chapter begins with a survey of the scientific literature on the productivity responses of plants to higher CO_2 concentrations, and then reviews research on the effect of enhanced CO_2 on plant water-use efficiency, responsiveness to environmental stress, acclimation, competition among species (e.g., crops versus weeds), respiration, and other effects. We end with a survey of literature showing the general "greening of the Earth" that has occurred during the Current Warm Period.

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7.1. Plant Productivity Responses

Perhaps the best-known consequence of the rise in atmospheric CO_2 is the stimulation of plant productivity. This growth enhancement occurs because carbon dioxide is the primary raw material utilized by plants to produce the organic matter out of which they construct their tissues. Consequently, the more CO_2 there is in the air, the better plants grow. Over the past decade, the Center for the Study of Carbon Dioxide and Global Change, has archived thousands of results from hundreds of peer-reviewed research studies conducted by hundreds of researchers demonstrating this fact. The archive is available free of charge at http://www.co2science.org/data/plantgrowth/plantgrowth.php.

The Center's Web site lists the photosynthetic and dry weight responses of plants growing in CO_2-enriched air, arranged by scientific or common plant name. It also provides the full peer-reviewed journal references and experimental conditions in which each study was conducted for each record. We have summarized those results in two tables appearing in Appendix 2 and Appendix 3 to the current report. The first table, Table 7.1.1, indicates the mean biomass response of nearly 1,000 plants to a 300-ppm increase in atmospheric CO_2 concentration. The second table, Table 7.1.2, indicates the photosynthetic response to the same CO_2 enrichment for a largely similar list of plants.

In the rest of this section of Chapter 7, we provide a review of research on a representative sample of herbaceous and woody plants, chosen with an eye toward their importance to agriculture and the forestry and papermaking industries, followed by several acquatic plants.

7.1.1. Herbaceous Plants

A 300 ppm increase in the air's CO_2 content typically raises the productivity of most herbaceous plants by about one-third (Cure and Acock, 1986; Mortensen, 1987). This positive response occurs in plants that utilize all three of the major biochemical pathways (C_3, C_4, and crassulacean acid metabolism (CAM)) of photosynthesis (Poorter, 1993). Thus, with more CO_2 in the air, the productivity of nearly all crops rises, as they produce more branches and tillers, more and thicker leaves, more extensive root systems, and more flowers and fruit (Idso, 1989).

On average, a 300 ppm increase in atmospheric CO_2 enrichment leads to yield increases of 15 percent for CAM crops, 49 percent for C_3 cereals, 20 percent for C_4 cereals, 24 percent for fruits and melons, 44 percent for legumes, 48 percent for roots and tubers, and 37 percent for vegetables (Idso and Idso, 2000). It should come as no surprise, therefore, that the father of modern research in this area—Sylvan H. Wittwer—has said "it should be considered good fortune that we are living in a world of gradually increasing levels of atmospheric CO_2," and "the rising level of atmospheric CO_2 is a universally free premium, gaining in magnitude with time, on which we can all reckon for the future."

Additional information on this topic, including reviews of herbaceous plants not discussed here, can be found at http://www.co2science.org/subject/a/subject_a.php under the heading Agriculture.

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7.1.1.1. Alfalfa

Morgan *et al*. (2001) grew the C_3 legume alfalfa (*Medicago sativa* L.) for 20 days post-defoliation in growth chambers maintained at atmospheric CO_2 concentrations of 355 and 700 ppm and low or high levels of soil nitrogen to see how these factors affected plant regrowth. They determined that the plants in the elevated CO_2 treatment attained total dry weights over the 20-day regrowth period that were 62 percent greater than those reached by the plants grown in ambient air, irrespective of soil nitrogen concentration.

De Luis *et al*. (1999) grew alfalfa plants in controlled environment chambers in air of 400 and 700 ppm CO_2 for two weeks before imposing a two-week water treatment on them, wherein the soil in which half of the plants grew was maintained at a moisture content approaching field capacity while the soil in which the other half grew was maintained at a moisture content that was only 30 percent of field capacity. Under these conditions, the CO_2-enriched water-stressed plants displayed an average water-use efficiency that was 2.6 and 4.1 times greater than that of the water-stressed and well-watered plants, respectively, growing in ambient 400-ppm-CO_2 air. In addition, under ambient CO_2 conditions, the water stress treatment increased the mean plant root:shoot ratio by 108 percent, while in the elevated CO_2 treatment it increased it by 269 percent. As a result, the nodule biomass on the roots of the CO_2-enriched water-stressed plants was 40 and 100 percent greater than the nodule biomass on the roots of the well-watered and water-stressed plants, respectively, growing in ambient air. Hence, the CO_2-enriched water-stressed plants acquired 31 and 97 percent more total plant nitrogen than the well-watered and water-stressed plants, respectively, growing in ambient air. The CO_2-enriched water-stressed plants attained 2.6 and 2.3 times more total biomass than the water-stressed and well-watered plants, respectively, grown at 400 ppm CO_2.

Luscher *et al*. (2000) grew effectively and ineffectively nodulating (good nitrogen-fixing vs. poor nitrogen-fixing) alfalfa plants in large free-air CO_2 enrichment (FACE) plots for multiple growing seasons at atmospheric CO_2 concentrations of 350 and 600 ppm, while half of the plants in each treatment received a high supply of soil nitrogen and the other half received only minimal amounts of this essential nutrient. The extra CO_2 increased the yield of effectively nodulating plants by about 50 percent, regardless of soil nitrogen supply; caused a 25 percent yield reduction in ineffectively nodulating plants subjected to low soil nitrogen; and produced an intermediate yield stimulation of 11 percent for the same plants under conditions of high soil nitrogen, which suggests that the ability to symbiotically fix nitrogen is an important factor in eliciting strong positive growth responses to elevated CO_2 under conditions of low soil nitrogen supply.

Sgherri *et al*. (1998) grew alfalfa in open-top chambers at ambient (340 ppm) and enriched (600 ppm) CO_2 concentrations for 25 five days, after which water was withheld for five additional days so they could investigate the interactive effects of elevated CO_2 and water stress on plant water status, leaf soluble protein and carbohydrate content, and chloroplast thylakoid membrane composition. They found that the plants grown in elevated CO_2 exhibited the best water status during the moisture deficit part of the study, as indicated by leaf water potentials that were approximately 30 percent higher (less negative) than those observed in plants grown in ambient CO_2. This beneficial adjustment was achieved by partial closure of leaf stomata and by greater production of nonstructural carbohydrates (a CO_2-induced enhancement of 50 percent was observed), both of which phenomena can lead to decreases in transpirational water loss, the former by guard cells physically regulating stomatal apertures to directly control the exodus of water from leaves, and the latter by nonstructural carbohydrates influencing the amount of water available for transpiration. This latter phenomenon occurs because many nonstructural carbohydrates are osmotically active solutes that chemically associate with water through the formation of hydrogen bonds, thereby effectively reducing the amount of unbound water available for bulk flow during transpiration. Under water-stressed conditions, however, the CO_2-induced difference in total leaf nonstructural carbohydrates disappeared. This may have resulted from an increased mobilization of nonstructural carbohydrates to roots in the elevated CO_2 treatment, which would decrease the osmotic potential in that part of the plant, thereby causing an increased influx of soil moisture into the roots. If this did indeed occur, it would also contribute to a better overall water status of CO_2-enriched plants during drought conditions.

The plants grown at elevated CO_2 also maintained greater leaf chlorophyll contents and lipid to protein ratios, especially under conditions of water stress. Leaf chlorophyll content, for example, decreased by a mere 6 percent at 600 ppm CO_2, while it plummeted by approximately 30 percent at 340 ppm, when water was withheld. Moreover, leaf lipid contents in plants grown with atmospheric CO_2 enrichment were about 22 and 83 percent higher than those measured in plants grown at ambient CO_2 during periods of ample and insufficient soil moisture supply, respectively. Furthermore, at elevated CO_2 the average amounts of unsaturation for two of the most important lipids involved in thylakoid membrane composition were approximately 20 and 37 percent greater than what was measured in plants grown at 340 ppm during times of adequate and inadequate soil moisture, respectively. The greater lipid contents observed at elevated CO_2, and their increased amounts of unsaturation, may allow thylakoid membranes to maintain a more fluid and stable environment, which is critical during periods of water stress in enabling plants to continue photosynthetic carbon uptake.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/agriculturealfalfa.php.

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7.1.1.2. Cotton

As the CO_2 content of the air increases, cotton (*Gossypium hirsutum* L.) plants typically display enhanced rates of photosynthetic carbon uptake, as noted by Reddy *et al*. (1999), who reported that twice-ambient atmospheric CO_2 concentrations boosted photosynthetic rates of cotton by 137 to 190 percent at growth temperatures ranging from 2°C below ambient to 7°C above ambient.

Elevated CO_2 also enhances total plant biomass and harvestable yield. Reddy *et al*. (1998), for example, reported that plant biomass at 700 ppm CO_2 was enhanced by 31 to 78 percent at growth temperatures ranging from 20 to 40°C, while boll production was increased by 40 percent. Similarly, Tischler *et al*. (2000) found that a doubling of the atmospheric CO_2 concentration increased seedling biomass by at least 56 percent.

These results indicate that elevated CO_2 concentrations tend to ameliorate the negative effects of heat stress on productivity and growth in cotton. In addition, Booker (2000) discovered that elevated CO_2 reduced the deleterious effects of elevated ozone on leaf biomass and starch production.

Atmospheric CO_2 enrichment also can induce changes in cotton leaf chemistry that tend to increase carbon sequestration in plant biolitter and soils. Booker *et al*. (2000), for example, observed that biolitter produced from cotton plants grown at 720 ppm CO_2 decomposed at rates that were 10 to 14 percent slower than those displayed by ambiently grown plants; a after three years of exposure to air containing 550 ppm CO_2, Leavitt *et al*. (1994) reported that 10 percent of the organic carbon present in soils beneath CO_2-enriched FACE plots resulted from the extra CO_2 supplied to them.

In summary, as the CO_2 content of the air increases, cotton plants will display greater rates of photosynthesis and biomass production, which should lead to greater boll production in this important fiber crop, even under conditions of elevated air temperature and ozone concentration. In addition, carbon sequestration in fields planted to cotton should also increase with future increases in the air's CO_2 content.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/agriculturecotton.php.

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7.1.1.3. Maize

Maroco *et al*. (1999) grew corn (*Zea mays* L.), or maize as it is often called, for 30 days in plexiglass chambers maintained at either ambient or triple-ambient concentrations of atmospheric CO_2 to determine the effects of elevated CO_2 on the growth of this important agricultural C_4 species. This exercise revealed that elevated CO_2 (1,100 ppm) increased maize photosynthetic rates by about 15 percent relative to those measured in plants grown at 350 ppm CO_2, in spite of the fact that both rubisco and PEP-carboxylase were down-regulated. This increase in carbon fixation likely contributed to the 20 percent greater biomass accumulation observed in the CO_2-enriched plants. In addition, leaves of CO_2-enriched plants contained approximately 10 percent fewer stomates per unit leaf area than leaves of control plants, and atmospheric CO_2 enrichment reduced stomatal conductance by as much as 71 percent in elevated-CO_2-grown plants. As a result of these several different phenomena, the higher atmospheric CO_2 concentration greatly increased the intrinsic water-use efficiency of the CO_2-enriched plants.

In a study designed to examine the effects of elevated CO_2 under real-world field conditions, Leakey *et al*. (2004) grew maize out-of-doors at the SoyFACE facility in the heart of the United States Corn Belt, while exposing different sections of the field to atmospheric CO_2 concentrations of either 354 or 549 ppm. The crop was grown, in the words of the researchers, using cultural practices deemed "typical for this region of Illinois," during a year that turned out to have experienced summer rainfall that was "very close to the 50-year average for this site, indicating that the year was not atypical or a drought year." Then, on five different days during the growing season (11 and 22 July, 9 and 21 August, and 5 September), they measured diurnal patterns of photosynthesis, stomatal conductance, and microclimatic conditions.

Contrary to what many people had long assumed would be the case for a C_4 crop such as corn growing under even the best of natural conditions, Leakey *et al.* found that "growth at elevated CO_2 significantly increased leaf photosynthetic CO_2 uptake rate by up to 41 percent." The greatest whole-day increase was 21 percent (11 July) followed by 11 percent (22 July), during a period of low rainfall. Thereafter, however, during a period of greater rainfall, there were no significant differences between the photosynthetic rates of the plants in the two CO_2 treatments, so that over the entire growing season, the CO_2-induced increase in leaf photosynthetic rate averaged 10 percent.

Additionally, on all but the first day of measurements, stomatal conductance was significantly lower (-23 percent on average) under elevated CO_2 compared to ambient CO_2, which led to reduced transpiration rates in the CO_2-enriched plants on those days as well. Since "low soil water availability and high evaporative demand can both generate water stress and inhibit leaf net CO_2 assimilation in C_4 plants," they state that the lower stomatal conductance and transpiration rate they observed under elevated CO_2 "may have counteracted the development of water stress under elevated CO_2 and prevented the inhibition of leaf net CO_2 assimilation observed under ambient CO_2."

The implication of their research, in the words of Leakey *et al*., was that "contrary to expectations, this US Corn Belt summer climate appeared to cause sufficient water stress under ambient CO_2 to allow the ameliorating effects of elevated CO_2 to significantly enhance leaf net CO_2 assimilation." They concluded that "this response of *Z. mays* to elevated CO_2 indicates the potential for greater future crop biomass and harvestable yield across the US Corn Belt."

Also germane to this subject and supportive of the above conclusion are the effects of elevated CO_2 on weeds associated with corn. Conway and Toenniessen (2003), for example, speak of maize in Africa being attacked by the parasitic weed *Striga hermonthica*, which sucks vital nutrients from its roots, as well as from the roots of many other C_4 crops of the semi-arid tropics, including sorghum, sugar cane, and millet, plus the C_3 crop rice, particularly throughout much of Africa, where *Striga* is one of the region's most economically important parasitic weeds. Research shows how atmospheric CO_2 enrichment greatly reduces the damage done by this devastating weed (Watling and Press, 1997; Watling and Press, 2000).

Baczek-Kwinta and Koscielniak (2003) studied another phenomenon that is impacted by atmospheric CO_2 enrichment and that can affect the productivity of maize. Noting the tropical origin of maize and that the crop "is extremely sensitive to chill (temperatures 0-15°C)," they report that it is nevertheless often grown in cooler temperate zones. In such circumstances, however, maize can experience a variety of maladies associated with exposure to periods of low air temperature. To see if elevated CO_2 either exacerbates or ameliorates this problem, they grew two hybrid genotypes—KOC 9431 (chill-resistant) and K103xK85 (chill-sensitive)—from seed in air of either ambient (350 ppm) or elevated (700 ppm) CO_2 concentration (AC or EC, respectively), after which they exposed the plants to air of 7°C for eleven days, whereupon they let them recover for one day in ambient air of 20°C, all the while measuring several physiological and biochemical parameters pertaining to the plants' third fully expanded leaves.

The two researchers' protocol revealed that "EC inhibited chill-induced depression of net photosynthetic rate (PN), especially in leaves of chill-resistant genotype KOC 9431," which phenomenon "was distinct not only during chilling, but also during the recovery of plants at 20°C." In fact, they found that "seedlings subjected to EC showed 4-fold higher PN when compared to AC plants." They also determined that "EC diminished the rate of superoxide radical formation in leaves in comparison to the AC control." In addition, they found that leaf membrane injury "was significantly lower in samples of plants subjected to EC than AC." Last, they report that enrichment of the air with CO_2 successfully inhibited the decrease in the maximal quantum efficiency of photosystem 2, both after chilling and during the one-day recovery period. And in light of all of these positive effects of elevated CO_2, they concluded that "the increase in atmospheric CO_2 concentration seems to be one of the protective factors for maize grown in cold temperate regions."

But what about the effects of climate change, both past and possibly future, on corn production? For nine areas of contrasting environment within the Pampas region of Argentina, Magrin *et al.* (2005) evaluated changes in climate over the twentieth century along with changes in the yields of the region's chief crops. Then, after determining upward low-frequency trends in yield due to technological improvements in crop genetics and management techniques, plus the aerial fertilization effect of the historical increase in the air's CO_2 concentration, annual yield anomalies and concomitant climatic anomalies were calculated and used to develop relations describing the effects of changes in precipitation, temperature and solar radiation on crop yields, so that the effects of long-term changes in these climatic parameters on Argentina agriculture could be determined.

Noting that "technological improvements account for most of the observed changes in crop yields during the second part of the twentieth century," which totaled 110 percent for maize, Magrin *et al.* report that due to changes in climate between the periods 1950-70 and 1970-99, maize yields increased by 18 percent.

Much the same has been found to be true in Alberta, Canada, where Shen *et al*. (2005) derived and analyzed long-term (1901-2002) temporal trends in the agroclimate of the region. They report, for example, that "an earlier last spring frost, a later first fall frost, and a longer frost-free period are obvious all over the province." They also found that May-August precipitation in Alberta increased 14 percent from 1901 to 2002, and that annual precipitation exhibited a similar increasing trend, with most of the increase coming in the form of low-intensity events. In addition, the researchers note that "the area with sufficient corn heat units for corn production, calculated according to the 1973-2002 normal, has 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."

In light of these findings, Shen *et al*. conclude that "the changes of the agroclimatic parameters imply that Alberta agriculture has benefited from the last century's climate change," emphasizing that "the potential exists to grow crops and raise livestock in more regions of Alberta than was possible in the past." They also note that 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," and that the northward extension of the corn heat unit boundary that is sufficient for corn production "implies that Alberta farmers now have a larger variety of crops to choose from than were available previously." Hence, they say "there is no hesitation for us to conclude that the warming climate and increased precipitation benefit agriculture in Alberta."

With respect to the future, Bootsma *et al*. (2005) derived relationships between agroclimatic indices and average yields of major grain crops, including corn, from field trials conducted in eastern Canada, after which they used them to estimate potential impacts of projected climate change scenarios on anticipated average yields for the period 2040 to 2069. Based on a range of available heat units projected by multiple General Circulation Model (GCM) experiments, they determined that average yields achievable in field trials could increase by 40 to 115 percent for corn, "not including the direct effect of increased atmospheric CO_2 concentrations." Adding expected CO_2 increases to the mix, along with gains in yield anticipated to be achieved through breeding and improved technology, these numbers rose to 114 to 186 percent.

In light of their findings, Bootsma *et al*. predict there will be a "switch to high-energy and high-protein-content crops (corn and soybeans) that are better adapted to the warmer climate."

In summary, as the air's CO_2 content continues to rise, and even if the climate of the world changes in the ways suggested by GCM and IPCC calculations, maize plants will likely display greater rates of photosynthesis and biomass production, as well as reduced transpirational water losses and increased water-use efficiencies, and more areas of the world will likely become suitable for growing this important crop.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/agriculturemaize.php.

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7.1.1.4. Peanut

Stanciel *et al*. (2000) grew peanuts (*Arachis hypogaea* L.) hydroponically for 110 days in controlled environment chambers maintained at atmospheric CO_2 concentrations of 400, 800 and 1200 ppm, finding that the net photosynthetic rates of plants grown at 800 ppm CO_2 were 29 percent greater than those of plants grown at 400 ppm CO_2, but that plants grown at 1200 ppm CO_2 displayed photosynthetic rates that were 24 percent *lower* than those exhibited by plants grown in 400-ppm CO_2 air. Nevertheless, the number of pods, pod weight and seed dry weight per unit area were all greater at 1200 ppm than at 400 ppm CO_2. Also, harvest index, which is the ratio of seed dry weight to pod dry weight, was 19 and 31 percent greater at 800 and 1200 ppm CO_2, respectively, than it was at 400 ppm CO_2. In addition, as the atmospheric CO_2 concentration increased, stomatal conductance decreased, becoming 44 and 50 percent lower at 800 and 1200 ppm than it was at 400 ppm CO_2. Thus, atmospheric CO_2 enrichment also reduced transpirational water loss, leading to a significant increase in plant water use efficiency.

Prasad *et al*. (2003) grew Virginia Runner (Georgia Green) peanuts from seed to maturity in sunlit growth chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm and daytime-maximum/nighttime-minimum air temperatures of 32/22, 36/26, 40/30 and 44/34°C, while they assessed various aspects of vegetative and reproductive growth. In doing so, they found that leaf photosynthetic rates were unaffected by air temperature over the range investigated, but they rose by 27 percent in response to the experimental doubling of the air's CO_2 content. Vegetative biomass, on the other hand, increased by 51 percent and 54 percent in the ambient and CO_2-enriched air, respectively, as air temperature rose from 32/22 to 40/30°C. A further air temperature increase to 44/34°C, however, caused moderate to slight decreases in vegetative biomass in both the ambient and CO_2-enriched air, so that the final biomass increase over the entire temperature range investigated was 27 percent in ambient air and 53 percent in CO_2-enriched air. When going from the lowest temperature ambient CO_2 treatment to the highest temperature elevated CO_2 treatment, however, there was a whopping 106 percent increase in vegetative biomass.

By contrast, seed yields in both the ambient and CO_2-enriched air dropped dramatically with each of the three temperature increases studied, declining at the highest temperature regime to but a small percentage of what they were at the lowest temperature regime. Nevertheless, Prasad *et al*. report that "seed yields at 36.4/26.4°C under elevated CO_2 were similar to those obtained at 32/22°C under ambient CO_2," the latter pair of which temperatures they describe as "present-day seasonal temperatures."

It would appear that a warming of 4.4°C above present-day seasonal temperatures for peanut production would have essentially no effect on peanut seed yields, as long as the atmosphere's CO_2 concentration rose concurrently, by something on the order of 350 ppm. It is also important to note, according to Prasad *et al*., that "maximum/minimum air temperatures of 32/22°C and higher are common in many peanut-producing countries across the globe." In fact, they note that "the Anantapur district in Andhra Pradesh, which is one of the largest peanut-producing regions in India, experiences season-long temperatures considerably greater than 32/22°C from planting to maturity."

In light of these real-world observations, i.e., that some of the best peanut-producing regions in the world currently experience air temperatures considerably greater than what Prasad *et al*. suggest is optimum for peanuts (something *less* than 32/22°C), it would appear that real-world declines in peanut seed yields in response to a degree or two of warming, even in air of ambient CO_2 concentration, must be very slight or even non-existent, for how else could the places that commonly experience these considerably higher temperatures remain some of the best peanut-producing areas in the world? This in turn suggests that for more realistic values of CO_2-induced global warming, i.e., temperature increases on the order of 0.4°C for a doubling of the air's CO_2 content (Idso, 1998), there would likely be a significant increase in real-world peanut production.

In another pertinent study, Vu (2005) grew peanut plants from seed to maturity in greenhouses maintained at atmospheric CO_2 concentrations of 360 and 720 ppm and at air temperatures that were 1.5 and 6.0°C above outdoor air temperatures, while he measured a number of parameters related to the plants' photosynthetic performance. His work revealed that although Rubisco protein content and activity were down-regulated by elevated CO_2, the Rubisco photosynthetic efficiency (the ratio of midday light-saturated carbon exchange rate to Rubisco initial or total activity) of the elevated-CO_2 plants "was 1.3- to 1.9-fold greater than that of the ambient-CO_2 plants at both growth temperatures." He also determined that "leaf soluble sugars and starch of plants grown at elevated CO_2 were 1.3- and 2-fold higher, respectively, than those of plants grown at ambient CO_2." In addition, he discovered that the leaf transpiration of the elevated-CO_2 plants relative to that of the ambient-CO_2 plants was 12 percent less at near-ambient temperatures and 17 percent less in the higher temperature regime, while the water use efficiency of the elevated-CO_2 plants relative to the ambient-CO_2 plants was 56 percent greater at near-ambient temperatures and 41 percent greater in the higher temperature environment.

In commenting on his findings, Vu notes that because less Rubisco protein was required by the elevated-CO_2 plants, the subsequent redistribution of excess leaf nitrogen "would increase the efficiency of nitrogen use for peanut under elevated CO_2," just as the optimization of inorganic carbon acquisition and greater accumulation of the primary photosynthetic products in the CO_2-enriched plants "would be beneficial for peanut growth at elevated CO_2." Indeed, in the absence of other stresses, Vu's conclusion was that "peanut photosynthesis would perform well under rising atmospheric CO_2 and temperature predicted for this century."

In a somewhat different type of study, Alexandrov and Hoogenboom (2000) studied how year-to-year changes in temperature, precipitation and solar radiation had influenced the yields of peanuts over a 30-year period in the southeastern United States, after which they used the results to predict future crop yields based on climate-change output from various global circulation models (GCMs) of the atmosphere. At ambient CO_2 concentrations, the GCM scenarios suggested a decrease in peanut yields by the year 2020, due in part to predicted changes in temperature and precipitation. However, when the yield-enhancing effects of a doubling of the atmospheric CO_2 concentration were included, a totally different result was obtained: a yield *increase*.

Although we have little faith in GCM scenarios, it is interesting to note that their climate change predictions often result in positive outcomes for agricultural productivity when the direct effects of elevated CO_2 on plant growth and development are included in the analyses. These results support the research reported later in this chapter describing the stress-ameliorating effects of atmospheric CO_2 enrichment on plant growth and development under unfavorable growing conditions characterized by high air temperatures and inadequate soil moisture.

In conclusion, it would appear that even if the climate changes that are typically predicted to result from anticipated increases in the air's CO_2 content were to materialize, the concurrent rise in the air's CO_2 concentration should more than compensate for any deleterious effects those changes in climate might otherwise have had on the growth and yield of peanuts.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/peanut.php.

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7.1.1.5. Potato

In the study of Sicher and Bunce (1999), exposure to twice-ambient atmospheric CO_2 concentrations enhanced rates of net photosynthesis in potato plants (*Solanum tuberosum* L.) by 49 percent; while in the study of Schapendonk *et al*. (2000), a doubling of the air's CO_2 content led to an 80 percent increase in net photosynthesis. In a study that additionally considered the role of the air's vapor pressure deficit (VPD), Bunce (2003) found that exposure to twice-ambient atmospheric CO_2 concentrations boosted net photosynthesis by 36 percent at a VPD of 0.5 kPa (moist air) but by 70 percent at a VPD of 3.5 kPa (dry air). Yet another complexity was investigated by Olivo *et al*. (2002), who assessed the effect of a doubling of the air's CO_2 content on the net photosynthetic rates of high-altitude (*Solanum curtilobum*) and low-altitude (*S. tuberosum*) and found the rate of the former to be enhanced by 56 percent and that of the latter by 53 percent. In addition, although they did not directly report photosynthetic rates, Louche-Tessandier *et al*. (1999) noted that photosynthetic acclimation was reduced in CO_2-enriched plants that were inoculated with a fungal symbiont, which consequently allowed them to produce greater amounts of biomass than non-inoculated control plants grown in ambient air.

Because elevated CO_2 concentrations stimulate photosynthesis in potatoes, it is to be expected they would also increase potato biomass production. Miglietta *et al*. (1998), for example, reported that potatoes grown at 660 ppm CO_2 produced 40 percent more tuber biomass than control plants grown in ambient air. Such reports are common, in fact, with twice-ambient atmospheric CO_2 concentrations having been reported to produce yield increases of 25 percent (Lawson *et al*., 2001), 36 percent (Chen and Setter, 2003), 37 percent (Schapendonk *et al*., 2000), 40 percent (Olivo *et al*., 2002), 44 percent (Sicher and Bunce, 1999), 85 percent (Olivo *et al*., 2002) and 100 percent (Ludewig *et al*., 1998).

A few studies have been conducted at even higher atmospheric CO_2 concentrations. Kauder *et al*. (2000), for example, grew plants for up to seven weeks in controlled environments receiving an extra 600 ppm CO_2, obtaining final tuber yields that were 30 percent greater than those of ambiently grown plants. Also, in a study of potato microcuttings grown for four weeks in environmental chambers maintained at ambient air and air enriched with an extra 1200 ppm CO_2, Pruski *et al*. (2002) found that the average number of nodes per stem was increased by 64 percent, the average stem dry weight by 92 percent, and the average shoot length by 131 percent.

Atmospheric CO_2 enrichment also leads to reductions in transpirational water loss by potato plants. Magliulo *et al*. (2003), for example, grew potatoes in the field within FACE rings maintained at either ambient (370 ppm) or enriched (550 ppm) atmospheric CO_2 concentrations for two consecutive years, finding that the CO_2-enriched plants used 12 percent less water than the ambient-treatment plants, while they produced 47 percent more tuber biomass. Hence, the CO_2-enriched plants experienced a 68 percent increase in water use efficienc*y*, or the amount of biomass produced per unit of water used in producing it. Likewise, Olivo *et al*. (2002) found that a doubling of the air's CO_2 content increased the instantaneous water-use efficiencies of high-altitude and low-altitude potato species by 90 percent and 80 percent, respectively.

In the final phenomenon considered here, we review the findings of three studies that evaluated the ability of atmospheric CO_2 enrichment to mitigate the deleterious effects of ozone pollution on potato growth. Fangmeier and Bender (2002) determined the mean tuber yield of potato as a function of atmospheric CO_2 concentration for conditions of ambient and high atmospheric O_3 concentrations, as derived from a trans-European set of experiments. At the mean ambient CO_2 concentration of 380 ppm, the high O_3 stress reduced mean tuber yield by approximately 9 percent. At CO_2 concentrations of 540 and 680 ppm, however, the high O_3 stress had no significant effect on tuber yield.

Much the same results were obtained by Wolf and van Oijen (2002, 2003), who used the validated potato model LPOTCO to project future European tuber yields. Under two climate change scenarios that incorporated the effects of increased greenhouse gases on climate (i.e., increased air temperature and reduced precipitation), the model generated increases in irrigated tuber production ranging from 2,000 to 4,000 kg of dry matter per hectare across Europe, with significant reductions in the negative effects of O_3 pollution.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/agriculturepotato.php.

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7.1.1.6. Rice

DeCosta *et al*. (2003a) grew two crops of rice (*Oryza sativa* L.) at the Rice Research and Development Institute of Sri Lanka from January to March (the maha season) and from May to August (the yala season) in open-top chambers in air of either ambient or ambient plus 200 pppm CO_2, determining that leaf net photosynthetic rates were significantly higher in the CO_2-enriched chambers than in the ambient-air chambers: 51-75 percent greater in the maha season and 22-33 percent greater in the yala season. Likewise, in the study of Gesch *et al*. (2002), where one-month-old plants were maintained at either 350 ppm CO_2 or switched to a concentration of 700 ppm for 10 additional days, the plants switched to CO_2-enriched air immediately displayed large increases in their photosynthetic rates that at the end of the experiment were still 31 percent greater than those exhibited by unswitched control plants.

With respect to the opposite of photosynthesis, Baker *et al*. (2000) reported that rates of carbon loss via dark respiration in rice plants decreased with increasing nocturnal CO_2 concentrations. As a result, it is not surprising that in the study of Weerakoon *et al*. (2000), rice plants exposed to an extra 300 ppm of atmospheric CO_2 exhibited a 35 percent increase in mean season-long radiation-use efficiency, defined as the amount of biomass produced per unit of solar radiation intercepted. In light of these several observations, therefore, one would logically expect rice plants to routinely produce more biomass at elevated levels of atmospheric CO_2.

In conjunction with the study of DeCosta *et al.* (2003a), DeCosta *et al.* (2003b) found that CO_2-enriched rice plants produced more leaves per hill, more tillers per hill, more total plant biomass, greater root dry weight, and more panicles per plant and had harvest indices that were increased by 4 percent and 2 percent, respectively, in the maha and yala seasons, which suite of benefits led to grain yield increases of 24 percent and 39 percent in those two periods. In another study, Kim *et al.* (2003) grew rice crops from the seedling stage to maturity at atmospheric CO_2 concentrations of ambient and ambient plus 200 ppm using FACE technology and three levels of applied nitrogen—low (LN, 4 g N m^{-2}), medium (MN, 8 and 9 g N m^{-2}), and high (HN, 15 g N m^{-2})—for three cropping seasons (1998-2000). They found that "the yield response to elevated CO_2 in crops supplied with MN (+14.6 percent) or HN (+15.2 percent) was about twice that of crops supplied with LN (+7.4 percent)," confirming the importance of N availability to the response of rice to atmospheric CO_2 enrichment that had previously been determined by Kim *et al.* (2001) and Kobaysahi *et al.* (2001).

Various environmental stresses can significantly alter the effect of elevated CO_2 on rice. In the study of Tako *et al.* (2001), rice plants grown at twice-ambient CO_2 concentrations and ambient temperatures displayed no significant increases in biomass production; but when air temperatures were raised by 2°C, the CO_2-enriched plants produced 22 percent more biomass than the plants grown in non-CO_2-enriched air. By contrast, Ziska *et al.* (1997) reported that CO_2-enriched rice plants grown at elevated air temperatures displayed no significant increases in biomass; but when the plants were grown at ambient air temperatures, the additional 300 ppm of CO_2 boosted their rate of biomass production by 40 percent. In light of these observations, rice growers should select cultivars that are most responsive to elevated CO_2 concentrations at the air temperatures likely to prevail in their locality in order to maximize their yield production in a future high-CO_2 world.

Water stress can also severely reduce rice production. As an example, Widodo *et al.* (2003) grew rice plants in eight outdoor, sunlit, controlled-environment chambers at daytime atmospheric CO_2 concentrations of 350 and 700 ppm for an entire season. In one set of chambers, the plants were continuously flooded. In another set, drought stress was imposed during panicle initiation. In another, it was imposed during anthesis; and in the last set, drought stress was imposed at both stages. The resultant drought-induced effects, according to the scientists, "were more severe for plants grown at ambient than at elevated CO_2." They report, for example, that "plants grown under elevated CO_2 were able to maintain midday leaf photosynthesis, and to some extent other photosynthetic-related parameters, longer into the drought period than plants grown at ambient CO_2."

Recovery from the drought-induced water stress was also more rapid in the elevated CO_2 treatment. At panicle initiation, for example, Widodo *et al.* observed that "as water was added back following a drought induction, it took more than 24 days for the ambient CO_2 [water]-stressed plants to recuperate in midday leaf CER, compared with only 6-8 days for the elevated CO_2 [water]-stressed plants." Similarly, they report that "for the drought imposed during anthesis, midday leaf CER of the elevated CO_2 [water]-stressed plants were fully recovered after 16 days of re-watering, whereas those of the ambient CO_2 [water]-stressed plants were still 21 percent lagging behind their unstressed controls at that date." Hence, they concluded that "rice grown under future rising atmospheric CO_2 should be better able to tolerate drought situations."

In a somewhat different type of study, Watling and Press (2000) found that rice plants growing in ambient air and infected with a root hemiparasitic angiosperm obtained final biomass values that were only 35 percent of those obtained by uninfected plants. In air of 700 ppm CO_2, however, the infected plants obtained biomass values that were 73 percent of those obtained by uninfected plants. Thus, atmospheric CO_2 enrichment significantly reduced the negative impact of this parasite on biomass production in rice.

In summary, as the CO_2 concentration of the air continues to rise, rice plants will likely experience greater photosynthetic rates, produce more biomass, be less affected by root parasites, and better deal with environmental stresses, all of which effects should lead to greater grain yields.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/agriculturerice.php.

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7.1.1.7. Sorghum

Many laboratory and field experiments have demonstrated a significant positive impact of elevated levels of atmospheric CO_2 on total biomass and grain production in the C_4 crop sorghum (*Sorghum bicolor* (L.) Moench).

Ottman *et al*. (2001) grew sorghum plants in a FACE experiment conducted near Phoenix, Arizona, USA, where plants were fumigated with air containing either 360 or 560 ppm CO_2 and where they were further subjected to irrigation regimes resulting in both adequate and inadequate levels of soil moisture. Averaged over the two years of their study, the extra CO_2 increased grain yield by only 4 percent in the plots receiving adequate levels of soil moisture but by 16 percent in the dry soil moisture plots.

Prior *et al*. (2005) grew sorghum in two different years in 7-meter-wide x 76-meter-long x 2-m-deep bins filled with a silt loam soil, upon which they constructed a number of clear-plastic-wall open-top chambers they maintained at ambient CO_2 concentrations and ambient concentrations plus 300 ppm. In the first of the two years, the extra CO_2 increased sorghum residue production by 14 percent, while in the second year it increased crop residue production by 24 percent and grain production by 22 percent. For a CO_2 increase of 200 ppm comparable to that employed in the study of Ottman *et al*., these figures translate to crop residue increases of 9 percent and 16 percent and a grain increase of 15 percent.

In a review of primary research papers describing results obtained from large-scale FACE experiments conducted over the prior 15 years, Ainsworth and Long (2005) determined that, in the mean, sorghum grain yield was increased by approximately 7 percent in response to a 200-ppm increase in the atmosphere's CO_2 concentration.

An experiment with a bit more complexity was carried out several years earlier by Watling and Press (1997), who grew sorghum with and without infection by the parasitic C_3 weeds *Striga hermonthica* and *S. asiatica*. The study lasted for about two months and was conducted in controlled environment cabinets fumigated with air of either 350 or 700 ppm CO_2. In the absence of parasite infection, the extra 350 ppm of CO_2 boosted plant biomass production by 35 percent, which adjusted downward to make it compatible with the 200-ppm increase employed in most FACE studies corresponds to an increase of just under 21 percent. When infected with *S. asiatica*, the biomass stimulation provided by the extra CO_2 was about the same; but when infected with *S. hermonthica*, it was almost 80 percent, which corresponds to a similarly downward adjusted biomass increase of 45 percent.

In light of these several observations, it would appear that although the CO_2-induced increase in total biomass and grain yield of sorghum is rather modest, ranging from 4 to 16 percent under well-watered conditions, it can be on the high end of this range when the plants are stressed by a shortage of water (16 percent has been observed) and by parasitic infection (45 percent has been observed). Consequently, elevated levels of atmospheric CO_2 seem to help sorghum most when help is most needed.

Additional information on this topic, including reviews on sorghum not discussed here, can be found at http://www.co2science.org/subject/a/subject_a.php under the main heading Agriculture, sub heading Sorghum.

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7.1.1.8. Soybean

Wittwer (1995) reports that the common soybean (*Glycine max* L.) "provides about two-thirds of the world's protein concentrate for livestock feeding, and is a valuable ingredient in formulated feeds for poultry and fish." Bernacchi *et al*. (2005) characterize the soybean as "the world's most important seed legume." Consequently, it is important to determine how soybeans will likely respond to rising atmospheric CO_2 concentrations with and without concomitant increases in air temperature and under both well-watered and water-stressed conditions.

Rogers *et al*. (2004) grew soybeans from emergence to grain maturity in ambient and CO_2-enriched air (372 and 552 ppm CO_2, respectively) at the SoyFACE facility of the University of Illinois at Urbana-Champaign, Illinois, USA, while CO_2 uptake and transpiration measurements were made from pre-dawn to post-sunset on seven days representative of different developmental stages of the crop. Across the growing season, they found that the mean daily integral of leaf net photosynthesis rose by 24.6 percent in the elevated CO_2 treatment, while mid-day stomatal conductance dropped by 21.9 percent, in response to the 48 percent increase in atmospheric CO_2 employed in their study. With respect to photosynthesis, they additionally report "there was no evidence of any loss of stimulation toward the end of the growing season," noting that the largest stimulation actually occurred during late seed filling. Nevertheless, they say that the photosynthetic stimulation they observed was only "about half the 44.5 percent theoretical maximum increase calculated from Rubisco kinetics." Thus, there is an opportunity for soybeans to perhaps become even more responsive to atmospheric CO_2 enrichment than they are currently, which potential could well be realized via future developments in the field of genetic engineering.

Bunce (2005) grew soybeans in the field in open-top chambers maintained at atmospheric CO_2 concentrations of ambient and ambient +350 ppm at the Beltsville Agricultural Research Center in Maryland, USA, where net CO_2 exchange rate measurements were performed on a total of 16 days between 18 July and 11 September of 2000 and 2003, during flowering to early pod-filling. Over the course of this study, daytime net photosynthesis per unit leaf area was 48 percent greater in the plants growing in the CO_2-enriched air, while nighttime respiration per unit leaf area was not affected by elevated CO_2.

However, because the elevated CO_2 increased leaf dry mass per unit area by an average of 23 percent, respiration per unit mass was significantly lower for the leaves of the soybeans growing in the CO_2-enriched air, producing a sure recipe for accelerated growth and higher soybean seed yields.

Working in Australia, Japan, and the United States, Ziska *et al.* (2001b) observed a recurrent diurnal pattern of atmospheric CO_2 concentration, whereby maximum values of 440-540 ppm occurred during a three-hour pre-dawn period that was followed by a decrease to values of 350-400 ppm by mid-morning, after which there was a slow but steady increase in the late afternoon and early evening that brought the air's CO_2 concentration back to its pre-dawn maximum value. In an attempt to see if the pre-dawn CO_2 spikes they observed affected plant growth, they grew soybeans for one month in controlled-environment chambers under three different sets of conditions: a constant 24-hour exposure to 370 ppm CO_2, a constant 370 ppm CO_2 exposure during the day followed by a constant 500 ppm CO_2 exposure at night, and a CO_2 exposure of 500 ppm from 2200 to 0900 followed by a decrease to 370 ppm by 1000, which was maintained until 2200, somewhat mimicking the CO_2 cycle they observed in nature. This program revealed that the 24-hour exposure to 370 ppm CO_2 and the 370-ppm-day/500-ppm-night treatments produced essentially the same results in terms of biomass production after 29 days. However, the CO_2 treatment that mimicked the observed atmospheric CO_2 pattern resulted in a plant biomass increase of 20 percent.

In a study that evaluated a whole range of atmospheric CO_2 concentrations, from far below ambient levels to high above them, Allen *et al.* (1998) grew soybeans for an entire season in growth chambers maintained at atmospheric CO_2 concentrations of 160, 220, 280, 330, 660, and 990 ppm. In doing so, they observed a consistent increase in total nonstructural carbohydrates in all vegetative components including roots, stems, petioles, and especially the leaves, as CO_2 concentrations rose. There was, however, no overall significant effect of treatment CO_2 concentration on nonstructural carbohydrate accumulation in soybean reproductive components, including podwalls and seeds, which observations indicate that the higher yields reported in the literature for soybeans exposed to elevated CO_2 most likely result from increases in the number of pods produced per plant, and not from the production of larger individual pods or seeds.

The increasing amounts of total nonstructural carbohydrates that were produced with each additional increment of CO_2 provided the raw materials to support greater biomass production at each CO_2 level. Although final biomass and yield data were not reported in this paper, the authors did present biomass data obtained at 66 days into the experiment. Relative to above-ground biomass measured at 330 ppm CO_2, the plants that were grown in sub-ambient CO_2 concentrations of 280, 220, and 160 ppm exhibited 12, 33, and 60 percent *less* biomass, respectively, while plants grown in atmospheric CO_2 concentrations of 660 and 990 ppm displayed 46 and 66 percent more biomass.

In a study of two contrasting soybean cultivars, Ziska and Bunce (2000) grew *Ripley*, which is semi-dwarf and determinate in growth, and *Spencer*, which is standard-size and indeterminate in growth, for two growing seasons in open-top chambers maintained at atmospheric CO_2 concentrations of ambient and ambient plus 300 ppm. Averaged over both years, the elevated CO_2 treatment increased photosynthetic rates in the Ripley and Spencer varieties by 76 and 60 percent, respectively. However, Spencer showed a greater CO_2-induced increase in vegetative biomass than Ripley (132 vs. 65 percent). Likewise, elevated CO_2 enhanced seed yield in Spencer by 60 percent but by only 35 percent in Ripley, suggesting that cultivar selection for favorable yield responses to atmospheric CO_2 enrichment could have a big impact on future farm productivity.

In another study of contrasting types of soybeans, Nakamura *et al.* (1999) grew nodulated and non-nodulated plants in pots within controlled-environmental cabinets maintained at atmospheric CO_2 concentrations of 360 and 700 ppm in combination with low and high soil nitrogen supply for three weeks. They found that at low nitrogen, elevated CO_2 increased total plant dry mass by approximately 40 and 80 percent in nodulated soybeans grown at low and high nitrogen supply, respectively, while non-nodulated plants exhibited no CO_2-induced growth response at low nitrogen but an approximate 60 percent growth enhancement at high nitrogen supply. Hence, it would appear that as the air's CO_2 content continues to rise, non-nodulated soybeans will display increases in biomass only if they are grown in nitrogen-rich soils. Nodulated soybeans, however, should display increased growth in both nitrogen-rich and nitrogen-poor soils, with their responses being about twice as large in high as in low soil nitrogen conditions.

In yet another study of soybeans with different genetic characteristics, Ziska *et al*. (2001a) grew one modern and eight ancestral soybean genotypes in glasshouses maintained at atmospheric CO_2 concentrations of 400 and 710 ppm, finding that the elevated CO_2 increased photosynthetic rates in all cultivars by an average of 75 percent. This photosynthetic enhancement led to CO_2-induced increases in seed yield that averaged 40 percent, except for one of the ancestral varieties that exhibited an 80 percent increase in seed yield.

To get a glimpse of what might happen if future temperatures also continue to rise, Ziska (1998) grew soybeans for 21 days in controlled environments having atmospheric CO_2 concentrations of approximately 360 (ambient) or 720 ppm and soil temperatures of 25° (ambient) or 30°C. He found that elevated CO_2 significantly increased whole plant net photosynthesis at both temperatures, with the greatest effect occurring at 30°C. As time progressed, however, this photosynthetic stimulation dropped from 50 percent at 13 days into the experiment to 30 percent at its conclusion eight days later; in spite of this partial acclimation, which was far from complete, atmospheric CO_2 enrichment significantly enhanced total plant dry weight at final harvest by 36 and 42 percent at 25° and 30°C, respectively.

Studying the complicating effects of water stress were Serraj *et al*. (1999), who grew soybeans from seed in pots within a glasshouse until they were four weeks old, after which half of the plants were subjected to an atmospheric CO_2 concentration of 360 ppm, while the other half were exposed to an elevated concentration of 700 ppm. In addition, half of the plants at each CO_2 concentration were well-watered and half of them were allowed to experience water stress for a period of 18 days. This protocol revealed that short-term (18-day) exposure of soybeans to elevated CO_2 significantly decreased daily and cumulative transpirational water losses compared to plants grown at 360 ppm CO_2, regardless of water treatment. In fact, elevated CO_2 reduced total water loss by 25 and 10 percent in well-watered and water-stressed plants, respectively. Also, drought stress significantly reduced rates of net photosynthesis among plants of both CO_2 treatments. However, plants grown in elevated CO_2 consistently exhibited higher photosynthetic rates than plants grown at ambient CO_2, regardless of soil water status.

At final harvest, the elevated CO_2 treatment had little effect on the total dry weight of plants grown at optimal soil moisture, but it increased the total dry weight of water-stressed plants by about 33 percent. Also, while root dry weight declined for plants grown under conditions of water stress and ambient CO_2 concentration, no such decline was exhibited by plants subjected to atmospheric CO_2 enrichment and water stress.

Studying *both* water and high-temperature stress were Ferris *et al*. (1999), who grew soybeans in glasshouses maintained at atmospheric CO_2 concentrations of 360 and 700 ppm for 52 days, before having various environmental stresses imposed on them for eight days during early seed filling. For the eight-day stress period, some plants were subjected to air temperatures that were 15°C higher than those to which the control plants were exposed, while some were subjected to a water stress treatment in which their soil moisture contents were maintained at 40 percent of that experienced by the control plants. Averaged across all stress treatments and harvests, this protocol revealed that the high CO_2 treatment increased total plant biomass by 41 percent. Both high-temperature and water-deficit treatments, singly or in combination, reduced overall biomass by approximately the same degree, regardless of CO_2 treatment. Thus, even when the greatest biomass reductions of 17 percent occurred in the CO_2-enriched and ambiently grown plants, in response to the combined stresses of high temperature and low soil moisture, plants grown in elevated CO_2 still exhibited an average biomass that was 24 percent greater than that displayed by plants grown in ambient CO_2.

Averaged across all stress treatments and harvests, elevated CO_2 increased seed yield by 32 percent. In addition, it tended to ameliorate the negative effects of environmental stresses. CO_2-enriched plants that were water stressed, for example, had an average seed yield that was 34 percent greater than that displayed by water-stressed controls grown at ambient CO_2, while CO_2-enriched plants exposed to high temperatures produced 38 percent more seed than their respectively stressed counterparts. In fact, the greatest relative impact of elevated CO_2 on seed yield occurred in response to the combined stresses of high temperature and low soil moisture, with CO_2-enriched plants exhibiting a seed yield that was 50 percent larger than that of similarly stressed plants grown in ambient CO_2.

In a predictive application of this type of knowledge, but based on a different means of obtaining it, Alexandrov and Hoogenboom (2000) studied how temperature, precipitation, and solar radiation influenced soybean yields over a 30-year period in the southeastern United States, after which they used the results they obtained to predict future crop yields based on climate output from various global circulation models of the atmosphere. At ambient CO_2 concentrations, the model-derived scenarios pointed to a decrease in soybean yields by the year 2020, due in part to predicted changes in temperature and precipitation. However, when the yield-enhancing effects of a doubling of the air's CO_2 concentration were included in the simulations, a completely different projection was obtained: a yield *increase*.

Shifting to the subject of soybean seed *quality*, Caldwell *et al*. (2005) write that "the beneficial effects of isoflavone-rich foods have been the subject of numerous studies (Birt *et al*., 2001; Messina, 1999)," and that "foods derived from soybeans are generally considered to provide both specific and general health benefits," presumably via these substances. Hence, it is only natural they would wonder how the isoflavone content of soybean seeds may be affected by the ongoing rise in the air's CO_2 content, and that they would conduct a set of experiments to find the answer.

The scientists grew well-watered and fertilized soybean plants from seed to maturity in pots within two controlled-environment chambers, one maintained at an atmospheric CO_2 concentration of 400 ppm and one at 700 ppm. The chambers were initially kept at a constant air temperature of 25°C. At the onset of seed fill, however, air temperature was reduced to 18°C until seed development was complete, in order to simulate average outdoor temperatures at this stage of plant development. In a second experiment, this protocol was repeated, except the temperature during seed fill was maintained at 23°C, with and without drought (a third treatment), while in a third experiment, seed-fill temperature was maintained at 28°C, with or without drought.

In the first experiment, where air temperature during seed fill was 18°C, the elevated CO_2 treatment increased the total isoflavone content of the soybean seeds by 8 percent. In the second experiment, where air temperature during seed fill was 23°C, the extra CO_2 increased total seed isoflavone content by 104 percent, while in the third experiment, where air temperature during seed fill was 28°C, the CO_2-induced isoflavone increase was 101 percent. Finally, when drought-stress was added as a third environmental variable, the extra CO_2 boosted total seed isoflavone content by 186 percent when seed-fill air temperature was 23°C, while at a seed-fill temperature of 28°C, it increased isoflavone content by 38 percent.

Under all environmental circumstances studied, enriching the air with an extra 300 ppm of CO_2 increased the total isoflavone content of soybean seeds. In addition, the percent increases measured under the stress situations investigated were always greater than the percent increase measured under optimal growing conditions.

Also writing on the subject of soybean seed quality, Thomas *et al*. (2003) say "the unique chemical composition of soybean has made it one of the most valuable agronomic crops worldwide," noting that "oil and protein comprise ~20 and 40%, respectively, of the dry weight of soybean seed." Consequently, they explored the effects of elevated CO_2 plus temperature on soybeans that were grown to maturity in sunlit controlled-environment chambers with sinusoidally varying day/night max/min temperatures of 28/18°, 32/22°, 36/26°, 40/30°, and 44/34°C and atmospheric CO_2 concentrations of 350 and 700 ppm. This work revealed that the effect of temperature on seed composition and gene expression was "pronounced," but that "there was no effect of CO_2." In this regard, however, they note that "Heagle *et al*. (1998) observed a positive significant effect of CO_2 enrichment on soybean seed oil and oleic acid concentration," the latter of which parameters their own study found to rise with increasing temperature all the way from 28/18° to 44/34°C. In addition, they determined that "32/22°C is optimum for producing the highest oil concentration in soybean seed," that "the degree of fatty acid saturation in soybean oil was significantly increased by increasing temperature," and that crude protein concentration increased with temperature to 40/30°C.

In commenting on these observations, Thomas *et al*. note that "the intrinsic value of soybean seed is in its supply of essential fatty acids and amino acids in the oil and protein, respectively." Hence, we conclude that the temperature-driven changes they identified in these parameters, as well as the CO_2 effect observed by Heagle *et al*., bode well for the future production of this important crop and its value to society in a CO_2-enriched and warming world. Thomas *et al*. note, however, that "temperatures during the soybean-growing season in the southern USA are at, or slightly higher than, 32/22°C," and that warming could negatively impact the soybean oil industry in this region. For the world as a whole, however, warming would be a positive development for soybean production; while in the southern United States, shifts in planting zones could readily accommodate changing weather patterns associated with this phenomenon.

In conclusion, as the air's CO_2 content continues to rise, soybeans will likely respond by displaying significant increases in growth and yield, with possible improvements in seed quality; these beneficial effects will likely persist even if temperatures rise or soil moisture levels decline, regardless of their cause.

Additional information on this topic, including reviews on sorghum not discussed here, can be found at http://www.co2science.org/subject/a/subject_a.php under the main heading Agriculture, sub heading Soybean.

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7.1.1.9. Strawberry

In the open-top chamber study of Bunce (2001), strawberry plants (*Fragaria* x *ananassa*) exposed to air containing an extra 300 and 600 ppm CO_2

displayed photosynthetic rates that were 77 and 106 percent greater, respectively, than rates displayed by plants grown in ambient air containing 350 ppm CO_2. Similarly, Bushway and Pritts (2002) reported that strawberry plants grown at atmospheric CO_2 concentrations between 700 and 1,000 ppm exhibited photosynthetic rates that were consistently more than 50 percent greater than rates displayed by control plants.

Because elevated CO_2 stimulates rates of photosynthesis in strawberry plants, it is expected that it would also increase biomass production in this important agricultural species. After growing plants in air containing an additional 170 ppm CO_2 above ambient concentrations, Deng and Woodward (1998) reported that total fresh fruit weights were 42 and 17 percent greater than weights displayed by control plants receiving high and low soil nitrogen inputs, respectively. In addition, Bushway and Pritts (2002) reported that a two- to three-fold increase in the air's CO_2 content boosted strawberry fruit yield by 62 percent.

As the air's CO_2 content continues to rise, strawberry plants will likely exhibit enhanced rates of photosynthesis and biomass production, which should lead to greater fruit yields.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/agriculturestraw.php.

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7.1.1.10. Sunflower

As the CO_2 content of the air increases, sunflower plants (*Helianthus annus* L.) will likely display enhanced rates of photosynthetic carbon uptake. In the study of Sims *et al*. (1999), exposure to twice-ambient atmospheric CO_2 concentrations enhanced rates of net photosynthesis in individual upper-canopy sunflower leaves by approximately 50 percent. Similarly, Luo *et al*. (2000) reported that sunflowers grown at 750 ppm CO_2 displayed canopy carbon uptake rates that were fully 53 percent greater than those exhibited by plants grown at 400 ppm CO_2.

The study of Zerihun *et al*. (2000) reported that twice-ambient CO_2 concentrations increased whole plant biomass in sunflowers by 44, 13, and 115 percent when the plants were simultaneously exposed to low, medium, and high levels of soil nitrogen, respectively.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/agriculturesun.php.

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7.1.1.11. Tomato

In the study of Ziska *et al*. (2001), tomato plants (*Lycopersicon esculentum* Mill.) grown at a nocturnal atmospheric CO_2 concentration of 500 ppm displayed total plant biomass values that were 10 percent greater than those exhibited by control plants growing in air containing 370 ppm CO_2. This result was likely the consequence of the elevated CO_2 reducing the rate of nocturnal respiration in the plants, which would have allowed them to utilize the retained carbon to produce more biomass.

This CO_2-induced benefit, as well as a host of other positive effects of atmospheric CO_2 enrichment, are also manifest under unfavorable growing conditions. Jwa and Walling (2001), for example, reported that fungal infection reduced plant biomass in tomatoes growing in normal air by about 30 percent. However, in fungal-infected plants grown at twice-ambient atmospheric CO_2 concentrations, the elevated CO_2 completely ameliorated the growth-reducing effects of the pathogen.

In another stressful situation, Maggio *et al.* (2002) reported that a 500-ppm increase in the air's CO_2 concentration increased the average value of the root-zone salinity threshold in tomato plants by about 60 percent. In addition, they reported that the water-use efficiency of the CO_2-enriched plants was about twice that of the ambiently grown plants.

As the CO_2 content of the air increases, tomato plants will likely display greater rates of photosynthesis and biomass production, which should consequently lead to greater fruit yields, even under stressful conditions of fungal infection and high soil salinity.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/agriculturetomato.php.

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7.1.1.12. Wheat

In one study, Dijkstra *et al.* (1999) grew winter wheat (*Triticum aestivum* L.) in open-top chambers and field-tracking sun-lit climatized enclosures maintained at atmospheric CO_2 concentrations of ambient and ambient plus 350 ppm CO_2 for two years, determining that the elevated CO_2 increased both final grain yield and total above-ground biomass by 19 percent. In another study, Masle (2000) grew two varieties of wheat for close to a month in greenhouses maintained at atmospheric CO_2 concentrations of 350 and 900 ppm, finding that the CO_2-enriched plants exhibited biomass increases of 52 to 93 percent, depending upon variety and vernalization treatment.

Based on a plethora of experimental observations of this nature, many scientists have developed yield prediction models for wheat. Using the output of several such models, Alexandrov and Hoogenboom (2000) estimated the impact of typically predicted climate changes on wheat production in Bulgaria in the twenty-first century, finding that a doubling of the air's CO_2 concentration would likely enhance wheat yields there between 12 and 49 percent in spite of a predicted 2.9° to 4.1°C increase in air temperature. Likewise, Eitzinger *et al.* (2001) employed the WOFOST crop model to estimate wheat production in northeastern Austria in the year 2080. For a doubled atmospheric CO_2 concentration with concomitant climate changes derived from five different general circulation models of the atmosphere, they obtained simulated yield increases of 30 to 55 percent, even in the face of predicted changes in both temperature and precipitation.

Southworth *et al.* (2002) used the CERES-Wheat growth model to calculate winter wheat production during the period 2050-2059 for 10 representative farm locations in Indiana, Illinois, Ohio, Michigan, and Wisconsin, USA, for six future climate scenarios. They report that some of the southern portions of this group of states would have exhibited climate-induced yield decreases had the aerial fertilization effect of the CO_2 increase that drove the predicted changes in climate not been included in the model. When they did include the increase in the air's CO_2 concentration (to a value of 555 ppm), however, they note that "wheat yields increased 60 to 100% above current yields across the central and northern areas of the study region," while in the southern areas "small increases and small decreases were found." The few minor decreases, however, were associated with the more extreme Hadley Center greenhouse run that presumed a 1 percent increase in greenhouse gases per year and a doubled climate variability; hence, they would have to be considered highly unlikely.

In discussing their findings, Southworth *et al.* note that other modeling studies have obtained similar results for other areas. They report, for example, that Brown and Rosenberg (1999) found winter wheat yields across other parts of the United States to increase "under all climate change scenarios modeled (1, 2.5, and 5°C temperature increases)," and that

Cuculeanu *et al*. (1999) found modeled yields of winter wheat in southern Romania to increase by 15 to 21 percent across five sites. Also, they note that Harrison and Butterfield (1996) "found increased yields of winter wheat across Europe under all the climate change scenarios they modeled."

Van Ittersum *et al*. (2003) performed a number of simulation experiments with the Agricultural Production Systems Simulator (APSIM)-Nwheat model in which they explored the implications of possible increases in atmospheric CO_2 concentration and near-surface air temperature for wheat production and deep drainage at three sites in Western Australia differing in precipitation, soil characteristics, nitrogenous fertilizer application rates, and wheat cultivars. They first assessed the impact of the ongoing rise in the air's CO_2 content, finding that wheat grain yield increased linearly at a rate of 10-16 percent for each 100-ppm increase in atmospheric CO_2 concentration, with only a slight concomitant increase in deep drainage (a big win, small loss outcome). For a likely future CO_2 increase of 200 ppm, increases in grain yield varied between 3 and 17 percent for low nitrogen fertilizer application rates and between 21 and 34 percent for high rates of nitrogen application, with the greatest relative yield response being found for the driest site studied.

When potential warming was factored into the picture, the results proved even better. The positive effects of the CO_2 increase on wheat grain yield were enhanced an extra 3-8 percent when temperatures were increased by 3°C in the model simulations. These yield increases were determined to result in an increased financial return to the typical Western Australian wheat farmer of 15-35 percent. In addition, the imposition of the simultaneous temperature increase led to a significant decline in deep drainage, producing a truly win-win situation that enhanced the average farmer's net income by an additional 10-20 percent. Consequently, it was determined that the CO_2-induced increase in temperature predicted by the IPCC could well increase the net profitability of Western Australian wheat farmers by anywhere from 25-55 percent, while at the same time mitigating what van Ittersum *et al*. refer to as "one of Australia's most severe land degradation problems."

In a wide variety of circumstances, atmospheric CO_2 enrichment significantly increases the biomass production and yield of wheat plants, thereby benefiting both wheat producers and consumers alike.

Additional information on this topic, including reviews on sorghum not discussed here, can be found at http://www.co2science.org/subject/a/subject_a.php under the main heading Agriculture, sub heading Wheat.

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7.1.2. Woody Plants

The growth response of woody plants to atmospheric CO_2 enrichment has also been extensively studied. Ceulemans and Mousseau (1994), for example, tabulated the results of 95 separate experimental investigations related to this topic. The review of Poorter (1993) includes 41 additional sets of pertinent results, and the two reviews of Wullschleger et al. (1995, 1997) contain 40 other sets of applicable data. When averaged together, these 176 individual woody plant experiments reveal a mean growth enhancement on the order of 50 percent for an approximate doubling of the air's CO_2 content, which is about one-and-a-half times as much as the response of non-woody herbaceous plants.

It is possible, however, that this larger result is still an underestimate of the capacity of trees and shrubs to respond to atmospheric CO_2 enrichment; for the mean duration of the 176 woody plant experiments described above was only five months, which may not have been sufficient for the long-term equilibrium effects of the CO_2 enrichment of the air to be manifest. In the world's longest such experiment, for example, Kimball *et al.* (2007) observed a 70 percent sustained increase in biomass production over the entire last decade of a 17-year study in response to a 75 percent increase in the air's CO_2 content employed throughout the experiment. Likewise, studies of Eldarica pine trees conducted at the same location have revealed a similarly increasing growth response over the same length of time (Idso and Kimball, 1994).

In the subsections that follow, we highlight the results of studies that have examined the growth response of several woody plants to atmospheric CO_2 enrichment. We end the section with discussions of the effect of CO_2 enhancement on wood density and forest productivity and carbon sequestration. For more information on this topic, see http://www.co2science.org/data/plant_growth/plantgrowth.php.

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7.1.2.1. Aspen-Poplar

Several studies have documented the effects of elevated levels of atmospheric CO_2 on photosynthesis in various aspen clones (*Populus tremuloides*). In the short-term study of Kruger *et al.* (1998), aspen seedlings grown for 70 days at atmospheric CO_2 concentrations of 650 ppm exhibited photosynthetic rates that were approximately 10 percent greater than those displayed by seedlings maintained at ambient CO_2 concentrations. In the longer five-month study of Kubiske *et al.* (1998), atmospheric CO_2 enrichment significantly increased photosynthetic rates in four aspen genotypes, regardless of soil nitrogen status.

In an even longer 2.5-year study, Wang and Curtis (2001) also observed significant CO_2-induced photosynthetic increases in two male and two female aspen clones; when six aspen genotypes were grown in open-top chambers for 2.5 years at atmospheric CO_2 concentrations of 350 and 700 ppm, Curtis *et al.* (2000) reported that the elevated CO_2 concentrations increased rates of net photosynthesis by 128 and 31 percent at high and low soil nitrogen contents, respectively. In addition, in a study that looked only at air temperature effects that was conducted at ambient CO_2 concentrations, King *et al.* (1999) determined that increasing the air temperature from 13° to 29°C enhanced photosynthetic rates in four different aspen clones by an average of 35 percent.

In a FACE study, where O_3-sensitive and O_3-tolerant clones were grown for six months in field plots receiving 360 and 560 ppm CO_2 in combination with ambient and enriched (1.5 times ambient) O_3 levels, Noormets *et al*. (2001) reported that CO_2-induced increases in photosynthetic rates were at least maintained, and sometimes even increased, when clones were simultaneously exposed to elevated O_3. After an entire year of treatment exposure, in fact, Karnosky *et al*. (1999) noted that the powerful ameliorating effect of elevated CO_2 on ozone-induced damage was still operating strongly in this system. O_3-induced foliar damages in O_3-sensitive and O_3-tolerant clones were reduced from 55 and 17 percent, respectively, at ambient CO_2, to 38 and 3 percent, respectively, at elevated CO_2.

With respect to biomass production, Pregitzer *et al*. (2000) reported that 2.5 years of exposure to twice-ambient concentrations of atmospheric CO_2 increased fine-root biomass in six aspen genotypes by an average of 65 and 17 percent on nitrogen-rich and nitrogen-poor soils, respectively. Using this same experimental system, Zak *et al*. (2000) determined that elevated CO_2 enhanced total seedling biomass by 38 percent at high soil nitrogen and by 16 percent at low soil nitrogen. Similar results were reported in the two-year open-top chamber study of Mikan *et al*. (2000), who observed 50 and 25 percent CO_2-induced increases in total seedling biomass at high and low soil nitrogen levels, respectively.

As the air's CO_2 content continues to increase, aspen seedlings will likely display enhanced rates of photosynthesis and biomass production, regardless of genotype, gender, O_3-sensitvity, and soil nitrogen status. Consequently, greater amounts of carbon will likely be sequestered in the tissues of this most abundant of North American tree species and in the soils in which they are rooted in the years and decades ahead.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/treesaspen.php.

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7.1.2.2. Beech

Egli and Korner (1997) rooted eight beech saplings (genus *Fagus*) directly into calcareous or acidic soils in open-top chambers and exposed them to atmospheric CO_2 concentrations of either 370 or 570 ppm. Over the first year of their study, the saplings growing on calcareous soil in CO_2-enriched air exhibited a 9 percent increase in stem diameter; they speculated that this initial small difference may "cumulate to higher 'final' tree biomass through compounding interest." At the end of three years of differential CO_2 exposure, the trees in the CO_2-enriched chambers were experiencing net ecosystem carbon exchange rates that were 58 percent greater than the rates of the trees in the ambient CO_2 chambers, regardless of soil type; the stem dry mass of the CO_2-enriched trees was increased by about 13 percent over that observed in the ambient-air chambers (Maurer *et al*., 1999).

In a similar but much shorter experiment, Dyckmans *et al*. (2000) grew three-year-old seedlings of beech for six weeks in controlled environment chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm, finding that the doubling of the air's CO_2 content increased seedling carbon uptake by 63 percent. They also noted that the majority of the assimilated carbon was allocated to the early development of leaves, which would be expected to subsequently lead to greater absolute amounts of photosynthetic carbon fixation.

In the two-year study of Grams *et al*. (1999), beech seedlings grown at ambient CO_2 concentrations displayed large reductions in photosynthetic rates when simultaneously exposed to twice-ambient levels of ozone. However, at twice-ambient CO_2 concentrations, twice-ambient ozone concentrations had no negative effects on the trees' photosynthetic rates. Thus, atmospheric CO_2 enrichment completely ameliorated the negative effects of ozone on photosynthesis in this species.

Similarly, Polle *et al*. (1997) reported that beech seedlings grown at 700 ppm CO_2 for two years displayed significantly reduced activities of catalase and superoxide dismutase, which are antioxidative enzymes responsible for detoxifying highly reactive oxygenated compounds within cells. Their data imply that CO_2-enriched atmospheres are conducive to less oxidative stress and, therefore, less production of harmful oxygenated compounds than typically occurs in ambient air. Consequently, the seedlings growing in the CO_2-enriched air were likely able to remobilize a portion of some of their valuable raw materials away from the production of detoxifying enzymes and reinvest them into other processes required for facilitating optimal plant development and growth.

With respect to this concept of resource optimization, Duquesnay *et al*. (1998) studied the relative amounts of ^{12}C and ^{13}C in tree rings of beech growing for the past century in northeastern France and determined that the intrinsic water-use efficiency of the trees had increased by approximately 33 percent over that time period, no doubt in response to the concomitant rise in the air's CO_2 concentration over the past 100 years.

In conclusion, as the CO_2 content of the air increases, beech trees will likely display enhanced rates of photosynthesis and decreased damage resulting from oxidative stress. Together, these phenomena should allow greater optimization of raw materials within beech, allowing them to produce greater amounts of biomass ever more efficiently as the atmospheric CO_2 concentration increases.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/treesbeech.php.

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7.1.2.3. Birch

In the relatively short-term study of Wayne *et al.* (1998), yellow birch seedlings (*Betula pendula*) grown for two months at atmospheric CO_2 concentrations of 800 ppm exhibited photosynthetic rates that were about 50 percent greater than those displayed by control seedlings fumigated with air containing 400 ppm CO_2. Similarly, in the three-month study of Tjoelker *et al.* (1998a), paper birch seedlings grown at 580 ppm CO_2 displayed photosynthetic rates that were approximately 30 percent greater than those exhibited by seedlings exposed to 370 ppm CO_2. Likewise, Kellomaki and Wang (2001) reported that birch seedlings exposed to an atmospheric CO_2 concentration of 700 ppm for five months displayed photosynthetic rates that were about 25 percent greater than seedlings grown at 350 ppm CO_2. Finally, in the much longer four-year study conducted by Wang *et al.* (1998), silver birch seedlings grown in open-top chambers receiving twice-ambient concentrations of atmospheric CO_2 displayed photosynthetic rates that were fully 110 percent greater than rates displayed by their ambiently grown counterparts. Thus, short-term photosynthetic enhancements resulting from atmospheric CO_2 enrichment appear to persist for several years or longer.

Because elevated CO_2 enhances photosynthetic rates in birch trees, it likely will also lead to increased biomass production in these important deciduous trees, as it has in several experiments. In the three-month study of Tjoelker *et al.* (1998b), for example, a 57 percent increase in the air's CO_2 content increased the biomass of paper birch seedlings by 50 percent. When similar seedlings were grown at 700 ppm CO_2 for four months, Catovsky and Bazzaz (1999) reported that elevated CO_2 increased total seedling biomass by 27 and 130 percent under wet and dry soil moisture regimes, respectively. In the interesting study of Godbold *et al.* (1997), paper birch seedlings grown at 700 ppm for six months not only increased their total biomass, but also increased the number of root tips per plant by more than 50 percent. In the longer two-year study of Berntson and Bazzaz (1998), twice-ambient levels of CO_2 increased the biomass of a mixed yellow and white birch mesocosm by 31 percent; and in another two-year study, Wayne *et al.* (1998) reported that yellow birch seedlings grown at 800 ppm CO_2 produced 60 and 227 percent more biomass than seedlings grown at 400 ppm CO_2 at ambient and elevated air temperatures, respectively. Finally, after exposing silver birch seedlings to twice-ambient CO_2 concentrations for four years, Wang *et al.* (1998) noted that CO_2-enriched seedlings produced 60 percent more biomass than ambiently grown seedlings. Hence, atmospheric CO_2 enrichment clearly enhances birch biomass in both short- and medium-term experiments.

In some studies, elevated CO_2 also reduced stomatal conductances in birch trees, thereby boosting their water-use efficiencies. Tjoelker *et al.* (1998a), for example, reported that paper birch seedlings grown at 580 ppm CO_2 for three months experienced 10-25 percent reductions in stomatal conductance, which contributed to 40-80 percent increases in water-use efficiency. Similar CO_2-induced reductions in stomatal conductance (21 percent) were reported in silver birch seedlings grown for four years at 700 ppm CO_2 by Rey and Jarvis (1998).

The results of these several studies suggest that the ongoing rise in the air's CO_2 content will likely increase rates of photosynthesis and biomass production in birch trees, as well as improve their water use efficiencies, irrespective of any concomitant changes in air temperature and/or soil moisture status that might occur. Consequently, rates of carbon sequestration by this abundant temperate forest species should also increase in the years and decades ahead.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/treesbirch.php.

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7.1.2.4. Citrus Trees

How does atmospheric CO_2 enrichment affect the growth and development of citrus trees and the fruit they produce?

In the study of Keutgen and Chen (2001), cuttings of *Citrus madurensis* grown for three months at 600 ppm CO_2 displayed rates of photosynthesis that were more than 300 percent greater than those measured on control cuttings grown at 300 ppm CO_2. In addition, elevated CO_2 concentrations have been shown to increase photosynthetic rates in mango (Schaffer *et al.*, 1997), mangosteen (Schaffer *et al.*, 1999), and sweet orange (Jifon *et al.*, 2002). In the study of Jifon *et al.*, it was further reported that twice-ambient CO_2 concentrations increased photosynthetic rates in mycorrhizal- and non-mycorrhizal-treated sour orange seedlings by 118 and 18 percent, respectively.

Such CO_2-induced increases in photosynthesis should lead to enhanced biomass production; and so they do. Idso and Kimball (2001), for example, have documented how a 75 percent increase in the air's CO_2 content has boosted the long-term production of above-ground wood and fruit biomass in sour orange trees by 80 percent in a study that has been ongoing since November 1987. Furthermore, Idso *et al.* (2002) have additionally demonstrated that the 300-ppm increase in the air's CO_2 content has increased the fresh weight of individual oranges by an average of 4 percent and the vitamin C content of their juice by an average of 5 percent.

In summary, these peer-reviewed studies suggest that as the air's CO_2 content slowly but steadily rises, citrus trees will respond by increasing their rates of photosynthesis and biomass production. In addition, they may also increase the vitamin C content of their fruit, which may help to prevent an array of human health problems brought about by insufficient intake of vitamin C.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/treescitrus.php.

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7.1.2.5. Eucalyptus

In the eight-month study of Roden *et al.* (1999), *Eucalyptus pauciflora* seedlings growing at 700 ppm CO_2 displayed seasonal rates of net photosynthesis that were approximately 30 percent greater than those exhibited by their ambiently grown counterparts. In another eight-month study, Palanisamy (1999) reported that well-watered *Eucalyptus cladocalyx* seedlings exposed to 800 ppm CO_2 exhibited photosynthetic rates that were 120 percent higher than those observed in control plants growing at 380 ppm CO_2. Moreover, after a one-month period of water stress, photosynthetic rates of CO_2-enriched seedlings were still 12 percent greater than rates displayed by ambiently grown water-stressed seedlings.

Because elevated CO_2 enhances photosynthetic rates in eucalyptus species, this phenomenon should lead to increased biomass production in these rapidly growing trees. And so it does. In the eight-month experiment of Gleadow *et al*. (1998), for example, *Eucalyptus cladocalyx* seedlings growing at 800 ppm CO_2 displayed 134 and 98 percent more biomass than seedlings growing at 400 ppm CO_2 at low and high soil nitrogen concentrations, respectively. Similarly, *Eucalyptus pauciflora* seedlings growing at twice-ambient CO_2 concentrations for eight months produced 53 percent more biomass than control seedlings (Roden *et al*., 1999).

In summary, as the CO_2 content of the air increases, eucalyptus seedlings will likely display enhanced rates of photosynthesis and biomass production, regardless of soil moisture and nutrient status. Consequently, greater amounts of carbon will likely be sequestered by this rapidly growing tree species.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/treeseuc.php.

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7.1.2.6. Fruit-Bearing

Several studies have recently documented the effects of elevated atmospheric CO_2 concentrations on photosynthesis in various fruiting trees. In an eight-day experiment, Pan *et al*. (1998) found that twice-ambient CO_2 concentrations increased rates of net photosynthesis in one-year-old apple seedlings by 90 percent. In a longer three-month study, Keutgen and Chen (2001) noted that cuttings of *Citrus madurensis* exposed to 600 ppm CO_2 displayed rates of photosynthesis that were more than 300 percent greater than rates observed in control cuttings exposed to 300 ppm CO_2. Likewise, in the review paper of Schaffer *et al*. (1997), it was noted that atmospheric CO_2 enrichment had previously been shown to enhance rates of net photosynthesis in various tropical and sub-tropical fruit trees, including avocado, banana, citrus, mango, and mangosteen. Finally in the two-year study of Centritto *et al*. (1999a), cherry seedlings grown at 700 ppm CO_2 exhibited photosynthetic rates that were 44 percent greater than those displayed by seedlings grown in ambient air, independent of a concomitant soil moisture treatment.

Because elevated CO_2 enhances the photosynthetic rates of fruiting trees, it should also lead to increased biomass production in them. In the two-year study of Centritto *et al*. (1999b), for example, well-watered and water-stressed seedlings growing at twice-ambient CO_2 concentrations displayed basal trunk areas that were 47 and 51 percent larger than their respective ambient controls. Similarly, in a study spanning more than 13 years, Idso and Kimball (2001) demonstrated that the above-ground wood biomass of mature sour orange trees growing in air enriched with an additional 300 ppm of CO_2 was 80 percent greater than that attained by control trees growing in ambient air.

As the CO_2 content of the air increases, fruit trees will likely display enhanced rates of photosynthesis and biomass production, regardless of soil moisture conditions. Consequently, greater amounts of carbon will likely be sequestered in the woody trunks and branches of such species. Moreover, fruit yields may increase as well. In the study of Idso and Kimball, for example, fruit yields were stimulated to essentially the same degree as above-ground wood biomass; i.e., by 80 percent in response to a 75 percent increase in the air's CO_2 content.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/treesfruit.php.

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7.1.2.7. Nitrogen-Fixing Trees

In the six-week study of Schortemeyer *et al.* (1999), seedlings of Australian blackwood (*Acacia melanoxylon*) grown at twice-ambient atmospheric CO_2 concentrations displayed photosynthetic rates that were 22 percent greater than those of ambiently grown seedlings. In addition, the CO_2-enriched seedlings exhibited biomass values that were twice as large as those displayed by control seedlings grown in air of 350 ppm CO_2. Likewise, Polley *et al.* (1999) reported that a doubling of the atmospheric CO_2 concentration for three months increased honey mesquite (*Prosopis glandulosa*) seedling root and shoot biomass by 37 and 46 percent, respectively.

Several studies have investigated the effects of elevated CO_2 on black locust (*Robinia pseudoacacia*) seedlings. Uselman *et al*. (2000), grew seedlings for three months at 700 ppm CO_2 and reported that this treatment increased the root exudation of organic carbon compounds by 20 percent, while Uselman *et al*. (1999) reported no CO_2-induced increases in the root exudation of organic nitrogen compounds. Nonetheless, elevated CO_2 enhanced total seedling biomass by 14 percent (Uselman *et al*., 2000).

In the study of Olesniewicz and Thomas (1999), black locust seedlings grown at twice-ambient CO_2 concentrations for two months exhibited a 69 percent increase in their average rate of nitrogen-fixation when they were not inoculated with an arbuscular mycorrhizal fungal species. It was further determined that the amount of seedling nitrogen derived from nitrogen-fixation increased in CO_2-enriched plants by 212 and 90 percent in non-inoculated and inoculated seedlings, respectively. Elevated CO_2 enhanced total plant biomass by 180 and 51 percent in non-inoculated and inoculated seedlings, respectively.

As the CO_2 content of the air increases, nitrogen-fixing trees respond by exhibiting enhanced rates of photosynthesis and biomass production, as well as enhanced rates of nitrogen fixation.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/treesnitrofix.php.

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7.1.2.8. Oak

How do oak (genus *Quercus*) trees respond to atmospheric CO_2 enrichment? In the two-month study of Anderson and Tomlinson (1998), northern red oak seedlings exposed to 700 ppm CO_2 displayed photosynthetic rates that were 34 and 69 percent greater than those displayed by control plants growing under well-watered and water-stressed conditions, respectively. Similarly, in the four-month study of Li *et al*. (2000), *Quercus myrtifolia* seedlings growing at twice-ambient CO_2 concentrations exhibited rates of photosynthesis at the onset of senescence that were 97 percent greater than those displayed by ambiently growing seedlings.

In the year-long study of Staudt *et al*. (2001), *Quercus ilex* seedlings grown at 700 ppm CO_2 displayed trunk and branch biomasses that were 90 percent greater than those measured on seedlings growing at 350 ppm CO_2. Also, in the eight-month inter-generational study performed by Polle *et al.* (2001), seedlings produced from acorns collected from ambient and CO_2-enriched mother trees and germinated in air of either ambient or twice-ambient atmospheric CO_2 concentration displayed whole-plant biomass values that were 158 and 246 percent greater, respectively, than those exhibited by their respective control seedlings growing in ambient air.

In another study, Schulte *et al*. (1998) grew oak seedlings for 15 weeks at twice-ambient CO_2 concentrations, finding that elevated CO_2 enhanced seedling biomass by 92 and 128 percent under well-watered and water-stressed conditions, respectively. In a similar study conducted by Tomlinson and Anderson (1998), water-stressed seedlings growing at 700 ppm CO_2 displayed biomass values that were similar to those exhibited by well-watered plants growing in ambient air. Thus, atmospheric CO_2 enrichment continues to benefit oak trees even under water-stressed conditions.

Additional studies have demonstrated that oak seedlings also respond positively to atmospheric CO_2 enrichment when they are faced with other environmental stresses and resource limitations. When pedunculate oak seedlings were subjected to two different soil nutrient regimes, for example, Maillard *et al*. (2001) reported that a doubling of the atmospheric CO_2 concentration enhanced seedling biomass by 140 and 30 percent under high and low soil nitrogen conditions, respectively. And in the study of Usami *et al*. (2001), saplings of *Quercus myrsinaefolia* that were grown at 700 ppm CO_2 displayed biomass increases that were 110 and 140 percent greater than their ambiently grown counterparts when they were simultaneously subjected to air temperatures that were 3° and 5°C greater than ambient temperature, respectively. Thus, elevated CO_2 concentrations tend to ameliorate some of the negative effects caused by growth-reducing stresses in oaks. In fact, when Schwanz and Polle (1998) reported that elevated CO_2 exposure caused reductions in the amounts of several foliar antioxidative enzymes in mature oak trees, they suggested that this phenomenon was the result of atmospheric CO_2 enrichment causing the trees to experience less oxidative stress and, therefore, they had less need for antioxidative enzymes.

In some studies, elevated CO_2 has been shown to reduce stomatal conductances in oak trees, thus contributing to greater tree water-use efficiencies. Tognetti *et al*. (1998a), for example, reported that oak seedlings growing near a natural CO_2-emitting spring exhibited less water loss and more favorable turgor pressures than trees growing further away from the spring. The resulting improvement in water-use efficiency was so significant that Tognetti *et al.* (1998b) stated, "such marked increases in water-use efficiency under elevated CO_2 might be of great importance in Mediterranean environments in the perspective of global climate change."

In summary, it is clear that as the CO_2 content of the air increases, oak seedlings will likely display enhanced rates of photosynthesis and biomass production, regardless of air temperature, soil moisture, and soil nutrient status. Consequently, greater amounts of carbon will likely be removed from the atmosphere by the trees of this abundant genus and stored in their tissues and the soils in which they are rooted.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/treesoak.php.

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7.1.2.9. Pine

7.1.2.9.1. Loblolly

Tissue *et al*. (1997) grew seedlings of loblolly pine trees (*Pinus taeda* L.) for a period of four years in open-top chambers maintained at atmospheric CO_2 concentrations of either 350 or 650 ppm in a study of the long-term effects of elevated CO_2 on the growth of this abundant pine species. This experiment indicated there was a mean biomass accumulation in the seedlings grown in CO_2-enriched air that was 90 percent greater than that attained by the seedlings grown in ambient air.

Johnson *et al*. (1998) reviewed 11 of their previously published papers, describing the results of a series of greenhouse and open-top chamber studies of the growth responses of loblolly pine seedlings to a range of atmospheric CO_2 and soil nitrogen concentrations. This work indicated that when soil nitrogen levels were so low as to be extremely deficient, or so high as to be toxic, growth responses to atmospheric CO_2 enrichment were negligible. For moderate soil nitrogen deficiencies, however, a doubling of the air's CO_2 content sometimes boosted growth by as much as 1,000 percent. Consequently, since the nitrogen status of most of earth's ecosystems falls somewhere between extreme deficiency and toxicity, these results suggest that loblolly pine trees may experience large increases in growth as the air's CO_2 content continues to climb.

Naidu and DeLucia (1999) described the results of working one full year in 30-meter-diameter circular FACE plots maintained at atmospheric CO_2 concentrations of either 350 or 560 ppm in an originally 13-year-old loblolly pine plantation in North Carolina, USA, where they determined the effects of the elevated CO_2 treatment on the productivity of the trees, which were growing in soil that was characteristically low in nitrogen and phosphorus. After the first year of atmospheric CO_2 enrichment in this Duke Forest Face Study, the growth rate of the CO_2-enriched trees was about 24 percent greater than that of the trees exposed to ambient CO_2, in spite of the likelihood of soil nutrient limitations and a severe summer drought (rainfall in August 1997 was about 90 percent below the 50-year average).

After four years of work at the Duke Forest Face Site, Finzi *et al*. (2002) reported that the extra 200 or so ppm of CO_2 had increased the average yearly dry matter production of the CO_2-enriched trees by 32 percent, while at the eight-year point of the experiment Moore *et al*. (2006) reported there had been a sustained increase in trunk basal area increment that varied between 13 and 27 percent with variations in weather and the timing of growth. What is more, they say "there was no evidence of a decline in the relative enhancement of tree growth by elevated CO_2 as might be expected if soil nutrients were becoming progressively more limiting," which many people had expected would occur in light of the site's low soil nitrogen and phosphorus content. In addition, at the six-year point of the study Pritchard *et al*. (2008) determined that the extra CO_2 had increased the average standing crop of fine roots by 23 percent.

Gavazzi *et al*. (2000) grew one-year-old loblolly pine seedlings for about four months in pots placed within growth chambers maintained at atmospheric CO_2 concentrations of either 360 or 660 ppm and adequate or inadequate levels of soil moisture, while the pots were seeded with a variety of C_3 and C_4 weeds. In the course of this experiment, they found that total seedling biomass was always greater under well-watered as opposed to water-stressed conditions, and that elevated CO_2 increased total seedling biomass by 22 percent in both water treatments. In the elevated CO_2 and water-stressed treatment, however, they also found that seedling root-to-shoot ratios were about 80 percent greater than they were in the elevated CO_2 and well-watered treatment, due to a 63 percent increase in root biomass. In the case of the weeds, total biomass was also always greater under well-watered compared to water-stressed conditions. However, the elevated CO_2 did *not* increase weed biomass; in fact, it reduced it by approximately 22 percent. Consequently, in assessing the effects of elevated CO_2 on competition between loblolly pine seedlings and weeds, the seedlings were definitely the winners, with the researchers concluding that the CO_2-induced increase in root-to-shoot ratio under water-stressed conditions may "contribute to an improved ability of loblolly pine to compete against weeds on dry sites."

Working with data obtained from stands of loblolly pine plantations at 94 locations scattered throughout the southeastern United States, Westfall and Amateis (2003) employed mean height measurements made at three-year intervals over a period of 15 years to calculate a site index related to mean growth rate for each of the five three-year periods, which index would be expected to increase monotonically if growth rates were being enhanced above "normal" by some monotonically increasing growth-promoting factor. This protocol indicated, in their words, that "mean site index over the 94 plots consistently increased at each remeasurement period," which would suggest, as they phrase it, that "loblolly pine plantations are realizing greater than expected growth rates," and, we would add, that the growth rate increases are growing larger and larger with each succeeding three-year period.

As for what might be causing the monotonically increasing growth rates of loblolly pine trees over the entire southeastern region of the United States, the two researchers say that in addition to rising atmospheric CO_2 concentrations, "two other likely factors that could affect growth are temperature and precipitation." However, they report that a review of annual precipitation amounts and mean ground surface temperatures showed no trends in these factors over the period of their study. They also suggest that 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 are partial to the aerial fertilization effect of atmospheric CO_2 enrichment as the explanation. What is more, they note that "similar results were reported by Boyer (2001) for natural stands of longleaf pine, where increases in dominant stand height are occurring over generations on the same site."

The studies reported here indicate that as the CO_2 content of the air continues to rise, loblolly pine trees will likely experience significant increases in biomass production, even on nutrient-poor soils, during times of drought, and in competition with weeds.

Additional information on this topic, including reviews loblolly pine trees not discussed here, can be found at http://www.co2science.org/subject/t/subject_t.php, under the heading Trees, Types, Pine, Loblolly.

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7.1.2.9.2. Ponderosa

Walker *et al*. (1998b) grew seedlings of Ponderosa pine (*Pinus ponderosa* Dougl. ex P. Laws & C. Laws) for an entire year in controlled environment chambers with atmospheric CO_2 concentrations of either 350 (ambient), 525, or 700 ppm. In addition, low or high levels of nitrogen and phosphorus were supplied to determine the main and interactive effects of atmospheric CO_2 enrichment and soil nutrition on seedling growth and fungal colonization of the seedlings' roots. After 12 months, they found that phosphorus supply had little impact on overall seedling growth, while high nitrogen increased nearly every parameter measured, including root, shoot, and total biomass, as did atmospheric CO_2 enrichment. Averaged over all nitrogen and phosphate treatments, total root dry weights at 525 and 700 ppm CO_2 were 92 and 49 percent greater, respectively, than those observed at ambient CO_2, while shoot dry weights were 83 and 26 percent greater. Consequently, seedlings grown at 525 and 700 ppm CO_2 had total dry weights that were 86 and 35 percent greater, respectively, than those measured at ambient CO_2. In addition, elevated CO_2 increased the total number of ectomycorrhizal fungi on roots by 170 percent at 525 ppm CO_2 and 85 percent at 700 ppm CO_2 relative to the number observed at ambient CO_2.

Walker *et al*. (1998a) grew Ponderosa pine seedlings for two growing seasons out-of-doors in open-top chambers having atmospheric CO_2 concentrations of 350, 525, and 700 ppm on soils of low, medium, and high nitrogen content to determine the interactive effects of these variables on juvenile tree growth. The elevated CO_2 concentrations had little effect on most growth parameters after the first growing season, with the one exception of below-ground biomass, which increased with both CO_2 and soil nitrogen. After two growing seasons, however, elevated CO_2 significantly increased all growth parameters, including tree height, stem diameter, shoot weight, stem volume, and root volume, with the greatest responses typically occurring at the highest CO_2 concentration in the highest soil nitrogen treatment. Root volume at 700 ppm CO_2 and high soil nitrogen, for example, exceeded that of all other treatments by at least 45 percent, as did shoot volume by 42 percent. Similarly, at high CO_2 and soil nitrogen coarse root and shoot weights exceeded those at ambient CO_2 and high nitrogen by 80 and 88 percent, respectively.

Johnson *et al*. (1998) reviewed 11 of their previously published papers (including the two discussed above) in which they describe the results of a series of greenhouse and open-top chamber studies of the growth responses of Ponderosa pine seedlings to a range of atmospheric CO_2 and soil nitrogen concentrations. These studies indicated that when soil nitrogen levels were so low as to be extremely deficient, or so high as to be toxic, growth responses to atmospheric CO_2 enrichment were negligible. For moderate soil nitrogen deficiencies, however, a doubling of the air's CO_2 content sometimes boosted growth by as much as 1,000 percent. In addition, atmospheric CO_2 enrichment mitigated the negative growth response of ponderosa pine to extremely high soil nitrogen in two separate studies.

Maherali and DeLucia (2000) grew Ponderosa pine seedlings for six months in controlled environment chambers maintained at atmospheric CO_2 concentrations ranging from 350 to 1,100 ppm, while they were subjected to either low (15/25°C night/day) or high (20/30°C night/day) temperatures. This study revealed that although elevated CO_2 had no significant effect on stomatal conductance, seedlings grown in the high temperature treatment exhibited a 15 percent increase in this parameter relative to seedlings grown in the low temperature treatment. Similarly, specific hydraulic conductivity, which is a measure of the amount of water moving through a plant relative to its leaf or needle area, also increased in the seedlings exposed to the high temperature treatment. In addition, biomass production rose by 42 percent in the low temperature treatment and 62 percent in the high temperature treatment when the atmospheric CO_2 concentration was raised from 350 to 1,100 ppm.

Tingey *et al*. (2005) studied the effects of atmospheric CO_2 enrichment (to approximately 350 ppm above ambient) on the fine-root architecture of Ponderosa pine seedlings growing in open-top chambers via minirhizotron tubes over a period of four years. This experiment showed that "elevated CO_2 increased both fine root extensity (degree of soil exploration) and intensity (extent that roots use explored areas) but had no effect on mycorrhizae," the latter of which observations was presumed to be due to the fact that soil nitrogen was not limiting to growth in this study. More specifically, they report that "extensity increased 1.5- to 2-fold in elevated CO_2 while intensity increased only 20 percent or less," noting that similar extensity results had been obtained over shorter periods of four months to two years by Arnone (1997), Berntson and Bazzaz (1998), DeLucia *et al*. (1997) and Runion *et al*. (1997), while similar intensity results had been obtained by Berntson (1994).

Last, Soule and Knapp (2006) studied Ponderosa pine trees growing naturally at eight sites within the Pacific Northwest of the United States, in order to see how they may have responded to the increase in the atmosphere's CO_2 concentration that occurred after 1950. In selecting these sites, they chose locations that "fit several criteria designed to limit potential confounding influences associated with anthropogenic disturbance." They also say they selected locations with "a variety of climatic and topoedaphic conditions, ranging from extremely water-limiting environments ... to areas where soil moisture should be a limiting factor for growth only during extreme drought years," additionally noting that all sites were located in areas "where ozone concentrations and nitrogen deposition are typically low."

At each of the eight sites that met all of these criteria, Soule and Knapp obtained core samples from about 40 mature trees that included "the potentially oldest trees on each site," so that their results would indicate, as they put it, "the response of mature, naturally occurring ponderosa pine trees that germinated before anthropogenically elevated CO_2 levels, but where growth, particularly post-1950, has occurred under increasing and substantially higher atmospheric CO_2 concentrations." Utilizing meteorological evaluations of the Palmer Drought Severity Index, they thus compared ponderosa pine radial growth rates during matched wet and dry years pre- and post-1950.

So what did they find? Overall, the two researchers report finding a post-1950 radial growth enhancement that was "more pronounced during drought years compared with wet years, and the greatest response occurred at the most stressed site." As for the magnitude of the response, they determined that "the relative change in growth [was] upward at seven of our [eight] sites, ranging from 11 to 133%."

With respect to the meaning and significance of their observations, Soule and Knapp say their results "showing that radial growth has increased in the post-1950s period ... while climatic conditions have generally been unchanged, suggest that nonclimatic driving forces are operative." In addition, they say that "these radial growth responses are generally consistent with what has been shown in long-term open-top chamber (Idso and Kimball, 2001) and FACE studies (Ainsworth and Long, 2005)." Hence, they say their findings suggest that "elevated levels of atmospheric CO_2 are acting as a driving force for increased radial growth of ponderosa pine, but that the overall influence of this effect may be enhanced, reduced or obviated by site-specific conditions."

Summarizing their findings Soule and Knapp recount how they had "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 state in their very next sentence that their results "support these hypotheses." Hence, they conclude their paper by stating it is likely that "an atmospheric CO_2-driven growth-enhancement effect exists for ponderosa pine growing under specific natural conditions within the [USA's] interior Pacific Northwest."

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/treesponderosa.php.

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7.1.2.9.3. Scots

Rouhier and Read (1998) grew seedlings of Scots pine (*Pinus sylvestris* L.) for four months in growth cabinets maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm. In addition, one-third of the seedlings were inoculated with one species of mycorrhizal fungi, one-third were inoculated with another species, and one-third were not inoculated at all, in order to determine the effects of elevated CO_2 on mycorrhizal fungi and their interactive effects on seedling growth. These procedures resulted in the doubled atmospheric CO_2 content increasing seedling dry mass by an average of 45 percent regardless of fungal inoculation. In addition, the extra CO_2 increased the number of hyphal tips associated with seedling roots by about 62 percent for both fungal species. Hyphal growth was also accelerated by elevated CO_2; after 55 days of treatment, the mycorrhizal network produced by one of the fungal symbionts occupied 444 percent more area than its counterpart exposed to ambient CO_2.

These results suggest that as the air's CO_2 content continues to rise, fungal symbionts of Scots pine will likely receive greater allocations of carbon from their host. This carbon can be used to increase their mycorrhizal networks, which would enable the fungi to explore greater volumes of soil in search of minerals and nutrients to benefit the growth of its host. In addition, by receiving greater allocations of carbon, fungal symbionts may keep photosynthetic down regulation from occurring, as they provide an additional sink for leaf-produced carbohydrates.

Janssens *et al*. (1998) grew three-year-old Scots pine seedlings in open-top chambers kept at ambient and 700 ppm atmospheric CO_2 concentrations for six months while they studied the effects of elevated CO_2 on root growth and respiration. In doing so, they learned that the elevated CO_2 treatment significantly increased total root length by 122 percent and dry mass by 135 percent relative to the roots of seedlings grown in ambient-CO_2 air. In addition, although starch accumulation in the CO_2-enriched roots was nearly 90 percent greater than that observed in the roots produced in the ambient-CO_2 treatment, the carbon-to-nitrogen ratio of the CO_2-enriched roots was significantly *lower* than that of the control-plant roots, indicative of the fact that they contained an even greater relative abundance of nitrogen. The most important implication of this study, therefore, was that Scots pine seedlings will likely be able to find the nitrogen they need to sustain large growth responses to atmospheric CO_2 enrichment with the huge root systems they typically produce in CO_2-enriched air.

Kainulainen *et al*. (1998) constructed open-top chambers around Scots pine trees that were about 20 years old and fumigated them with combinations of ambient or CO_2-enriched air (645 ppm) and ambient or twice-ambient (20 to 40 ppb) ozone-enriched air for three growing seasons to study the interactive effects of these gases on starch and secondary metabolite production. In doing so, they determined that elevated CO_2 and O_3 (ozone) had no significant impact on starch production in Scots pine, even after two years of treatment exposure. However, near the end of the third year, the elevated CO_2 alone significantly enhanced starch production in current-year needles, although neither extra CO_2, extra O_3, nor combinations thereof had any significant effects on the concentrations of secondary metabolites they investigated.

Kellomaki and Wang (1998) constructed closed-top chambers around 30-year-old Scots pine trees, which they fumigated with air containing either 350 or 700 ppm CO_2 at ambient and elevated (ambient plus 4°C) air temperatures for one full year, after which they assessed tree water-use by measuring cumulative sap flow for 32 additional days. This protocol revealed that the CO_2-enriched air reduced cumulative sap flow by 14 percent at ambient air temperatures, but that sap flow was unaffected by atmospheric CO_2 concentration in the trees growing at the elevated air temperatures. These findings suggest that cumulative water-use by Scotts pine trees in a CO_2-enriched world of the future will likely be less than or equal to—but no more than—what it is today.

Seven years later, Wang *et al*. (2005) published a report of a study in which they measured sap flow, crown structure, and microclimatic parameters in order to calculate the transpiration rates of individual 30-year-old Scots pine trees that were maintained for a period of *three* years in ambient air and air enriched with an extra 350 ppm of CO_2 and/or warmed by 2° to 6°C in closed-top chambers constructed within a naturally seeded stand of the trees. As they describe it, the results of this experiment indicated that "(i) elevated CO_2 significantly enhanced whole-tree transpiration rate during the first measuring year [by 14%] due to a large increase in whole-tree foliage area, 1998, but reduced it in the subsequent years of 1999 and 2000 [by 13% and 16%, respectively] as a consequence of a greater decrease in crown conductance which off-set the increase in foliage area per tree; (ii) trees growing in elevated temperature always had higher sap flow rates throughout three measuring years [by 54%, 45% and 57%, respectively]; and (iii) the response of sap flow to the combination of elevated temperature and CO_2 was similar to that of elevated temperature alone, indicating a dominant role for temperature and a lack of interaction between elevated CO_2 and temperature." These observations suggest that as the air's CO_2 content continues to rise, we probably can expect to see a decrease in evaporative water loss rates from naturally occurring stands of Scots pine trees ... unless there is a large concurrent increase in air temperature.

Also working with closed-top chambers that were constructed around 20-year-old Scots pines and fumigated with air containing 350 and 700 ppm CO_2 at ambient and elevated (ambient plus 4°C) air temperatures for a period of three years were Peltola *et al*. (2002), who studied the effects of elevated CO_2 and air temperature on stem growth in this coniferous species when it was growing on a soil low in nitrogen. After three years of treatment, they found that cumulative stem diameter growth in the CO_2-enriched trees growing at ambient air temperatures was 57 percent greater than that displayed by control trees growing at ambient CO_2 and ambient air temperatures, while the trees exposed to elevated CO_2 *and* elevated air temperature exhibited cumulative stem-diameter growth that was 67 percent greater than that displayed by trees exposed to ambient-CO_2 air and ambient air temperatures. Consequently, as the air's CO_2 content continues to rise, Scots pine trees will likely respond by increasing stem-diameter growth, even if growing on soils low in nitrogen, and even if air temperatures rise by as much as 4°C.

In a somewhat different type of study, Kainulainen *et al*. (2003) collected needle litter beneath 22-year-old Scots pines that had been growing for the prior three years in open-top chambers that had been maintained at atmospheric CO_2 concentrations of 350 and 600 ppm in combination with ambient and elevated (approximately 1.4 x ambient) ozone concentrations to determine the impacts of these variables on the subsequent decomposition of senesced needles. This they did by enclosing the needles in litterbags and placing the bags within a native litter layer in a Scots pine forest, where decomposition rates were assessed by measuring accumulated litterbag mass loss over a period of 19 months. Interestingly, the three researchers found that exposure to elevated CO_2 during growth did *not* affect subsequent rates of needle decomposition, nor did elevated O_3 exposure affect decomposition, nor did exposure to elevated concentrations of the two gases together affect it.

Finally, Bergh *et al*. (2003) used a boreal version of the process-based BIOMASS simulation model to quantify the individual and combined effects of elevated air temperature (2° and 4°C above ambient) and CO_2 concentration (350 ppm above ambient) on the net primary production (NPP) of Scots pine forests growing in Denmark, Finland, Iceland, Norway, and Sweden. This work revealed that air temperature increases of 2° and 4°C led to mean NPP increases of 11 and 20 percent, respectively. However, when the air's CO_2 concentration was simultaneously increased from 350 to 700 ppm, the corresponding mean NPP increases rose to 41 and 55 percent. Last, when the air's CO_2 content was doubled at the prevailing ambient temperature, the mean value of the NPP rose by 27 percent. Consequently, as the air's CO_2 content continues to rise, Ponderosa pines of Denmark, Finland, Iceland, Norway, and Sweden should grow ever more productively; and if air temperature also rises, they will likely grow better still.

Given the above results, as the air's CO_2 content continues to rise, we can expect to see the root systems of Scots pines significantly enhanced, together with the mycorrhizal fungal networks that live in close association with them and help secure the nutrients the trees need to sustain large CO_2-induced increases in biomass production. Concurrently, we can expect to see much smaller changes in total evaporative water loss, which means that whole-tree water use efficiency should also be significantly enhanced.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/treesscots.php.

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7.1.2.10. Spruce

Several studies have recently documented the effects of elevated CO_2 on photosynthesis in various varieties of spruce (genus *Picea*). In the relatively short-term study of Tjoelker *et al*. (1998a), black spruce (*Picea mariana*) seedlings grown for three months at atmospheric CO_2 concentrations of 580 ppm exhibited photosynthetic rates that were about 28 percent greater than those displayed by control seedlings fumigated with air containing 370 ppm CO_2. Similarly, Egli *et al*. (1998) reported that Norway spruce (*Picea abies*) seedlings grown at 570 ppm CO_2 displayed photosynthetic rates that were 35 percent greater than those exhibited by seedlings grown at 370 ppm. In two branch bag studies conducted on mature trees, it was demonstrated that twice-ambient levels of atmospheric CO_2 enhanced rates of photosynthesis in current-year needles by 50 percent in Norway spruce (Roberntz and Stockfors, 1998) and 100 percent in Sitka spruce (*Picea sitchensis*) (Barton and Jarvis, 1999). Finally, in the four-year open-top chamber study of Murray *et al*. (2000), the authors reported that Sitka spruce seedlings growing at 700 ppm CO_2 exhibited photosynthetic rates that were 19 and 33 percent greater than those observed in control trees growing in ambient air and receiving low and high amounts of nitrogen fertilization, respectively.

Because elevated CO_2 enhances photosynthetic rates in spruce species, this phenomenon should lead to increased biomass production in these important coniferous trees. In the short-term three-month study of Tjoelker *et al*. (1998b), for example, black spruce seedlings receiving an extra 210 ppm CO_2 displayed final dry weights that were about 20 percent greater than those of seedlings growing at ambient CO_2. Similarly, after growing Sitka spruce for three years in open-top chambers, Centritto *et al*. (1999) reported that a doubling of the atmospheric CO_2 concentration enhanced sapling dry mass by 42 percent.

In summary, it is clear that as the CO_2 content of the air increases, spruce trees will likely display enhanced rates of photosynthesis and biomass production, regardless of soil nutrient status. Consequently, rates of carbon sequestration by this abundant coniferous forest species will likely be enhanced.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/treesspruce.php.

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7.1.2.11. Tropical

Several studies have recently documented the effects of elevated atmospheric CO_2 concentrations on photosynthesis in various tropical and sub-tropical trees. In the relatively short-term study of Lovelock *et al*. (1999a), for example, seedlings of the tropical tree *Copaifera aromatica* that were grown for two months at an atmospheric CO_2 concentration of 860 ppm exhibited photosynthetic rates that were consistently 50-100 percent greater than those displayed by control seedlings fumigated with air containing 390 ppm CO_2. Similarly, Lovelock *et al*. (1999b) reported that a 10-month 390-ppm increase in the air's CO_2 content boosted rates of net photosynthesis in 30-m tall *Luehea seemannii* trees by 30 percent. Likewise, in the review paper of Schaffer *et al*. (1999), it was noted that atmospheric CO_2 enrichment had previously been shown to enhance rates of net photosynthesis in a number of tropical and sub-tropical fruit trees, including avocado, banana, citrus, mango, and mangosteen. Even at the ecosystem level, Lin *et al*. (1998) found that a 1,700-m^2 synthetic rainforest mesocosm displayed a 79 percent enhancement in net ecosystem carbon exchange rate in response to a 72 percent increase in the air's CO_2 content.

Because elevated CO_2 enhances photosynthetic rates in tropical and sub-tropical trees, it should also lead to increased carbohydrate and biomass production in these species. At a tropical forest research site in Panama, twice-ambient CO_2 concentrations enhanced foliar sugar concentrations by up to 30 percent (Wurth *et al*., 1998), while doubling the foliar concentrations of starch (Lovelock *et al*., 1998) in a number of tree species. Also, in the study of Hoffmann *et al*. (2000), elevated CO_2 (700 ppm) enhanced dry weights of an "uncut" Brazilian savannah tree species (*Keilmeyera coriacea*) by about 50 percent, while it enhanced the dry weight of the same "cut" species by nearly 300 percent. Although not specifically quantified, Schaffer *et al*. (1997) noted that twice-ambient CO_2 exposure for one year obviously enhanced dry mass production in two mango ecotypes. Finally, in the six-month study of Sheu *et al*. (1999), a doubling of the atmospheric CO_2 concentration increased seedling dry weight in *Schima superba* by 14 and 49 percent when grown at ambient and elevated (5°C above ambient) air temperatures, respectively.

It is clear that as the air's CO_2 content rises, tropical and sub-tropical trees will likely display enhanced rates of photosynthesis and biomass production, even under conditions of herbivory and elevated air temperature. Consequently, greater carbon sequestration will also likely occur within earth's tropical and sub-tropical forests as ever more CO_2 accumulates in the atmosphere.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/treestropical.php.

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7.1.2.12. Wood Density

Numerous experiments have demonstrated that trees grown in air enriched with CO_2 nearly always sequester more biomass in their trunks and branches than do trees grown in ambient air. Several studies also have looked at the effects of elevated CO_2 on the *density* of that sequestered biomass.

Rogers *et al*. (1983) observed no difference in the wood density of loblolly pine (*Pinus taeda*) trees grown at 340 and 718 ppm CO_2 for 10 weeks; but they found a 33 percent CO_2-induced increase in the wood density of sweetgum (*Liquidambar styraciflua*) trees that were grown at these concentrations for only eight weeks. Doyle (1987) and Telewski and Strain

(1987) studied the same two tree species over three growing seasons in air of 350 and 650 ppm CO_2, finding no effect of atmospheric CO_2 enrichment on the stem density of sweetgum, but a mean increase of 9 percent in the stem density of loblolly pine.

Conroy *et al*. (1990) grew seedlings of two *Pinus radiata* families at 340 and 660 ppm CO_2 for 114 weeks, finding CO_2-induced trunk density increases for the two families of 5.4 and 5.6 percent when soil phosphorus was less than adequate and increases of 5.6 and 1.2 percent when it was non-limiting. In a similar study, Hattenschwiler *et al*. (1996) grew six genotypes of clonally propagated four-year-old Norway spruce (*Picea abies*) for three years at CO_2 concentrations of 280, 420, and 560 ppm at three different rates of wet nitrogen deposition. On average, they found that wood density was 12 percent greater in the trees grown at the two higher CO_2 concentrations than it was in the trees grown at 280 ppm.

Norby *et al*. (1996) grew yellow poplar or "tulip" trees (*Liriodendron tulipifera*) at ambient and ambient plus 300 ppm CO_2 for three years, during which time the wood density of the trees increased by approximately 7 percent. Tognetti *et al*. (1998) studied two species of oak tree—one deciduous (*Quercus pubescens*) and one evergreen (*Quercus ilex*)—growing in the vicinity of CO_2 springs in central Italy that raised the CO_2 concentration of the surrounding air by approximately 385 ppm. This increase in the air's CO_2 content increased the wood density of the deciduous oaks by 4.2 percent and that of the evergreen oaks by 6.4 percent.

Telewski *et al*. (1999) grew loblolly pine trees for four years at ambient and ambient plus 300 ppm CO_2. In their study, wood density determined directly from mass and volume measurements was increased by 15 percent by the extra CO_2; average ring density determined by X-ray densitometry was increased by 4.5 percent.

Beismann *et al*. (2002) grew different genotypes of spruce and beech (*Fagus sylvatica*) seedlings for four years in open-top chambers maintained at atmospheric CO_2 concentrations of 370 and 590 ppm in combination with low and high levels of wet nitrogen application on both rich calcareous and poor acidic soils to study the effects of these factors on seedling toughness (fracture characteristics) and rigidity (bending characteristics such as modulus of elasticity). They found that some genotypes of each species were sensitive to elevated CO_2, while others were not. Similarly, some were responsive to elevated nitrogen deposition, while others were not. Moreover, such responses were often dependent upon soil type. Averaged across all tested genotypes, however, atmospheric CO_2 enrichment increased wood toughness in spruce seedlings grown on acidic soils by 12 and 18 percent at low and high levels of nitrogen deposition, respectively. In addition, atmospheric CO_2 enrichment increased this same wood property in spruce seedlings grown on calcareous soils by about 17 and 14 percent with low and high levels of nitrogen deposition, respectively. By contrast, elevated CO2 had no significant effects on the mechanical wood properties of beech seedlings, regardless of soil type.

Finally, Kilpelainen *et al*. (2003) erected 16 open-top chambers within a 15-year-old stand of Scots pines growing on a nutrient-poor sandy soil of low nitrogen content near the Mekrijarvi Research Station of the University of Joensuu, Finland. Over the next three years they maintained the trees within these chambers in a well-watered condition, while they enriched the air in half of the chambers to a mean daytime CO_2 concentration of approximately 580 ppm and maintained the air in half of each of the two CO_2 treatments at 2°C above ambient. In the ambient temperature treatment the 60 percent increase in the air's CO_2 concentration increased latewood density by 27 percent and maximum wood density by 11 percent, while in the elevated-temperature treatment it increased latewood density by 25 percent and maximum wood density by 15 percent. These changes led to mean overall CO_2-induced wood density increases of 2.8 percent in the ambient-temperature treatment and 5.6 percent in the elevated-temperature treatment.

In light of these several observations, it is clear that different species of trees respond differently to atmospheric CO_2 enrichment, and that they respond with still greater variety under different sets of environmental conditions. In general, however, atmospheric CO_2 enrichment tends to increase wood density in both seedlings and mature trees more often than not, thereby also increasing a number of strength properties of their branches and trunks.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/w/wooddensity.php.

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7.1.2.13. Forests

Forests contain perennial trees that remove CO_2 from the atmosphere during photosynthesis and store its carbon within their woody tissues for decades to periods sometimes in excess of a thousand years. Thus, it is important to understand how increases in the air's CO_2 content affect forest productivity and carbon sequestration, which has a great effect on the rate of rise of the air's CO_2 concentration. In this summary, we review several recent scientific publications pertaining to these subjects.

By examining various properties of tree rings, researchers can deduce how historical increases in the air's CO_2 concentration have already affected tree productivity and water use efficiency. Duquesnay *et al.* (1998), for example, analyzed the relative amounts of ^{12}C and ^{13}C present in yearly growth rings of beech trees raised in silviculture regimes in northeastern France, determining that their intrinsic water use efficiencies rose by approximately 33 percent during the past century, as the air's CO_2 concentration rose from approximately 280 to 360 ppm. In another case, Rathgeber *et al.* (2000) used tree-ring density data to create a historical productivity baseline for forest stands of *Pinus halepensis* in southeastern France, from which they determined that the net productivity of such forests would increase by 8 to 55 percent with a doubling of the air's CO_2 content. Finally, when running a forest growth model based on empirical observations reported in the literature, Lloyd (1999) determined that the rise in the atmospheric CO_2 concentration since the onset of the Industrial Revolution likely increased the net primary productivity of mature temperate deciduous forests by about 7 percent. In addition, he determined that a proportional increase in anthropogenic nitrogen deposition likely increased forest net primary productivity by 25 percent. And when he combined the two effects, the net primary productivity stimulation rose to 40 percent, which is more than the sum of the individual growth enhancements resulting from the increases in CO_2 and nitrogen.

The results of these studies demonstrate that historic increases in the air's CO_2 content have already conferred great benefits upon earth's forests. But will future increases in the air's CO_2 concentration continue to do so? Several research teams have embarked on long-term studies of various forest communities in an attempt to address this important question. What follows are some important observations that have been made from their mostly ongoing CO_2-enrichment studies.

In 1996, circular FACE plots (30-m diameter) receiving atmospheric CO_2 concentrations of 360 and 560 ppm were established in a 15-year-old loblolly pine (*Pinus taeda*) plantation in North Carolina, USA, to study the effects of elevated CO_2 on the growth and productivity of this particular forest community, which also had several hardwood species present in the understory beneath the primary coniferous canopy. Using this experimental set-up as a platform for several experiments, Hymus *et al*. (1999) reported that net photosynthetic rates of CO_2-enriched loblolly pines trees were 65 percent greater than rates observed in control trees exposed to ambient air. These greater rates of carbon fixation contributed to the 24 percent greater growth rates observed in the CO_2-enriched pine trees in the first year of this long-term study (Naidu and DeLucia 1999). In addition, DeLucia and Thomas (2000) reported that the elevated CO_2 increased rates of net photosynthesis by 50 to 160 percent in four subdominant hardwood species present in the forest understory. Moreover, for one species—sweetgum (*Liquidambar styraciflua*)—the extra CO_2 enhanced rates of net photosynthesis in sun and shade leaves by 166 and 68 percent, respectively, even when the trees were naturally subjected to summer seasonal stresses imposed by high temperature and low soil water availability. Consequently, after two years of atmospheric CO_2 enrichment, total ecosystem net primary productivity in the CO_2-enriched plots was 25 percent greater than that measured in control plots fumigated with ambient air.

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

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

It is clear that as the air's CO_2 concentration continues to rise, forests will likely respond by exhibiting significant increases in total primary productivity and biomass production. Consequently, forests will likely grow much more robustly and significantly expand their ranges, as has already been documented in many parts of the world, including gallery forest in Kansas, USA (Knight *et al*., 1994) and the Budal and Sjodal valleys in Norway (Olsson *et al*., 2000). Such CO_2-induced increases in growth and range expansion should result in large increases in global carbon sequestration within forests.

Additional information on this topic, including reviews on forests not discussed here, can be found at http://www.co2science.org/subject/f/subject_f.php under the heading Forests.

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7.1.3. Aquatic Plants

We have shown how atmospheric CO_2 enrichment typically enhances the growth and productivity of nearly all terrestrial plants. But what about *aquatic* plants? In this section we seek to answer that question.

7.1.3.1. Freshwater Algae

How do freshwater algae respond to increases in the air's CO_2 content? The subject has not been thoroughly researched, but the results of the studies discussed below provide a glimpse of what the future may hold as the atmosphere's CO_2 concentration continues its upward course.

Working with cells of the freshwater alga *Chlorella pyrenoidosa*, Xia and Gao (2003) cultured them in Bristol's solution within controlled environment chambers maintained at low and high light levels (50 and 200 μmol/m²/s) during 12-hour light periods that were followed by 12-hour dark periods for a total of 13 days, while the solutions in which the cells grew were continuously aerated with air of either 350 or 700 ppm CO_2. When the cells were harvested (in the exponential growth phase) at the conclusion of this period, the biomass (cell density) of the twice-ambient CO_2 treatment was found to be 10.9 percent and 8.3 percent greater than that of the ambient-air treatment in the low- and high-light regimes, respectively, although only the high-light result was statistically significant. The two scientists concluded from these observations that a "doubled atmospheric CO_2 concentration would affect the growth of *C. pyrenoidosa* when it grows under bright solar radiation, and such an effect would increase by a great extent when the cell density becomes high." Their data also suggest the same may well be true when the alga grows under *not*-so-bright conditions.

Working on a much larger scale "in the field" with six 1.5-m-diameter flexible plastic cylinders placed in the littoral zone of Lake Hampen in central Jutland, Denmark (three maintained at the ambient CO_2 concentration of the air and three enriched to 10 times the ambient CO_2 concentration), Andersen and Andersen (2006) measured the CO_2-induced growth response of a mixture of several species of filamentous freshwater algae dominated by *Zygnema* species, but containing some *Mougeotia* and *Spirogyra*. After one full growing season (May to November), they determined that the biomass of the microalgal mixture in the CO_2-enriched cylinders was increased by 220 percent in early July, by 90 percent in mid-August, and by a whopping 3,750 percent in mid-November.

In another study of the subject, Schippers *et al.* (2004a) say "it is usually thought that unlike terrestrial plants, phytoplankton will not show a significant response to an increase of atmospheric

CO_2," but they note, in this regard, that "most analyses have not examined the full dynamic interaction between phytoplankton production and assimilation, carbon-chemistry and the air-water flux of CO_2," and that "the effect of photosynthesis on pH and the dissociation of carbon (C) species have been neglected in most studies."

In an attempt to rectify this situation, Schippers *et al.* developed "an integrated model of phytoplankton growth, air-water exchange and C chemistry to analyze the potential increase of phytoplankton productivity due to an atmospheric CO_2 elevation," and as a test of their model, they let the freshwater alga *Chlamydomonas reinhardtii* grow in 300-ml bottles filled with 150 ml of a nutrient-rich medium at enclosed atmospheric CO_2 concentrations of 350 and 700 ppm that they maintained at two air-water exchange rates characterized by CO_2 exchange coefficients of 2.1 and 5.1 m day^{-1}, as described by Shippers *et al.* (2004b), while periodically measuring the biovolume of the solutions by means of an electronic particle counter. The results of this effort, as they describe it, "confirm the theoretical prediction that if algal effects on C chemistry are strong, increased phytoplankton productivity because of atmospheric CO_2 elevation should become proportional to the increased atmospheric CO_2," which suggests that algal productivity "would double at the predicted increase of atmospheric CO_2 to 700 ppm." Although they note that "strong algal effects (resulting in high pH levels) at which this occurs are rare under natural conditions," they still predict that effects on algal production in freshwater systems could be such that a "doubling of atmospheric CO_2 may result in an increase of the productivity of more than 50%."

In the last of the few papers we have reviewed in this area, Logothetis *et al.* (2004) note that "the function and structure of the photosynthetic apparatus of many algal species resembles that of higher plants (Plumley and Smidt, 1984; Brown, 1988; Plumley *et al.*, 1993)," and that "unicellular green algae demonstrate responses to increased CO_2 similar to those of higher plants in terms of biomass increases (Muller *et al.*, 1993)." However, they also note that "little is known about the changes to their photosynthetic apparatus during exposure to high CO_2," which deficiency they began to correct via a new experiment, wherein batches of the unicellular green alga *Scenedesmus obliquus* (wild type strain D3) were grown autotrophically in liquid culture medium for several days in a temperature-controlled water bath of 30°C at low (55 µmol m^{-2} s^{-1}) and high (235 µmol m^{-2} s^{-1}) light intensity while they were continuously aerated with air of either 300 or 100,000 ppm CO_2. This protocol revealed that exposure to the latter high CO_2 concentration produces, in their words, a "reorganization of the photosynthetic apparatus" that "leads to enhanced photosynthetic rates, which ... leads to an immense increase of biomass." After five days under low light conditions, for example, the CO_2-induced increase in biomass was approximately 300 percent, while under high light conditions it was approximately 600 percent.

Based on these few observations, it is not possible to draw any sweeping conclusions about the subject. However, they do indicate there may be a real potential for the ongoing rise in the air's CO_2 content to significantly stimulate the productivity of this freshwater contingent of earth's plants.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/aquaticplants.php.

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7.1.3.2. Freshwater Macrophytes

In this section we discuss the findings of papers that investigate the influence of CO_2 concentrations as it applies to submersed, floating, and emergent freshwater macrophytes, beginning with studies of aquatic plants that live their lives totally submersed in freshwater environments.

For several multi-week periods, Idso (1997) grew specimens of corkscrew vallisneria (*Vallisneria tortifolia*) in several 10- and 29-gallon glass tanks (containing 10-cm bottom-layers of common aquarium gravel) that were filled with tap water maintained within 0.5°C of either 18.2°C or 24.5°C, while the semi-sealed air spaces above these "Poor Man's Biospheres," as he christened them, were maintained at a number of different CO_2 concentrations. With the harvesting of plants at the end of the study, this protocol revealed that the CO_2-induced growth enhancement of the plants was *linear* (in contrast to the gradually declining CO_2-induced growth enhancements typically exhibited by most terrestrial plants as the air's CO_2 content climbs ever higher), and that the linear relationship extended to the highest atmospheric CO_2 concentration studied: 2,100 ppm. In addition, he found that the CO_2-induced growth increase experienced by the plants in the higher of the two water temperature treatments (a 128 percent increase in going from an atmospheric CO_2 concentration of 365 ppm to one of 2,100 ppm) was 3.5 times greater than that of the plants in the lower water temperature treatment. Although this response may seem rather dramatic, it is not unique; Idso reports that Titus *et al*. (1990), who studied the closely related *Vallisneria americana*, "observed that the biomass of their experimental plants also rose linearly with the CO_2 content of the air above the water within which they grew, and that [it] did so from the value of the [then] current global mean (365 ppm) to a concentration fully ten times larger."

In another study of a closely allied species, Yan *et al*. (2006) collected turions of *Vallisneria spinulosa* from Liangzi Lake, Hubei Province, China, and planted them in tanks containing 15-cm-deep layers of fertile lake sediments, topped with 40 cm of lake water, that were placed in two glasshouses—one maintained at the ambient atmospheric CO_2 concentration of 390 ppm and the other maintained at an elevated concentration of 1,000 ppm—where the plants grew for a period of 120 days, after which they were harvested and the dry weights of their various organs determined. As they describe it, this work indicated that the "total biomass accumulation of plants grown in the elevated CO_2 was 2.3 times that of plants grown in ambient CO_2, with biomass of leaves, roots and rhizomes increasing by 106%, 183% and 67%, respectively." Most spectacularly of all, they report that "turion biomass increased 4.5-fold," because "the mean turion numbers per ramet and mean biomass per turion in elevated CO_2 were 1.7-4.3 and 1.9-3.4 times those in ambient CO_2."

In Denmark, in a study of small slow-growing evergreen perennials called *isoetids* that live submersed along the shores of numerous freshwater lakes, Andersen *et al*. (2006) grew specimens of *Littorella uniflora* in sediment cores removed from Lake Hampen in 75-liter tanks with 10-cm overburdens of filtered lake water for a period of 53 days, while measuring various plant, water, and sediment properties, after which they destructively harvested the plants and measured their biomass. Throughout this period, half of the tanks had ambient air bubbled through their waters, while the other half were similarly exposed to a mixture of ambient air and pure CO_2 that produced a 10-fold increase in the air's CO_2 concentration. This ultra-CO_2-enrichment led to a 30 percent increase in plant biomass, as well as "higher O_2 release to the sediment which is important for the cycling and retention of nutrients in sediments of oligotrophic softwater lakes." And when the ultra-CO_2-enrichment was maintained for an entire growing season (May-November), Andersen and Andersen (2006) report that the 10-fold increase in aquatic CO_2 concentration enhanced the biomass production of *Littorella uniflora* by a much larger 78 percent.

In a study of an "in-between" type of plant that has submersed roots and rhizomes that are anchored in water-body sediments, but which has floating leaves on the surface of the water and emergent flowers that protrude above the water surface, Idso *et al*. (1990) grew water lilies (*Nymphaea marliac*) for two consecutive years in sunken metal stock tanks located out-of-doors at Phoenix, Arizona (USA) and enclosed within clear-plastic-wall open-top chambers through which air of either 350 or 650 ppm CO_2 was continuously circulated. This work revealed that in addition to the leaves of the plants being larger in the CO_2-enriched treatment, there were 75 percent more of them than there were in the ambient-air tanks at the conclusion of the initial five-month-long growing season. Each of the plants in the high-CO_2 tanks also produced twice as many flowers as the plants growing in ambient air; and the flowers that blossomed in the CO_2-enriched air were more substantial than those that bloomed in the air of ambient CO_2 concentration: they had more petals, the petals were longer, and they had a greater percent dry matter content, such that each flower consequently weighed about 50 percent more than each flower in the ambient-air treatment. In addition, the stems that supported the flowers were slightly longer in the CO_2-enriched tanks, and the percent dry matter contents of both the flower and leaf stems were greater, so that the total dry matter in the flower and leaf stems in the CO_2-enriched tanks exceeded that of the flower and leaf stems in the ambient-air tanks by approximately 60 percent.

Just above the surface of the soil that covered the bottoms of the tanks, there were also noticeable differences. Plants in the CO_2-enriched tanks had more and bigger basal rosette leaves, which were attached to longer stems of greater percent dry matter content, which led to the total biomass of these portions of the plants being 2.9 times greater than the total biomass of the corresponding portions of the plants in the ambient-air tanks. In addition, plants in the CO_2-enriched tanks had more than twice as many unopened basal rosette leaves.

The greatest differences of all, however, were hidden within the soil that covered the bottoms of the stock tanks. When half of the plants were harvested at the conclusion of the first growing season, for example, the number of new rhizomes produced over that period was discovered to be 2.4 times greater in the CO_2-enriched tanks than it was in the ambient-air tanks; the number of major roots produced there was found to be 3.2 times greater. As with all other plant parts, the percent dry matter contents of the new roots and rhizomes were also greater in the CO_2-enriched tanks. Overall, therefore, the total dry matter production within the submerged soils of the water lily ecosystems was 4.3 times greater in the CO_2-enriched tanks than it was in the ambient-air tanks; the total dry matter production of all plant parts—those in the submerged soil, those in the free water, and those in the air above—was 3.7 times greater in the high-CO_2 enclosures.

Over the second growing season, the growth enhancement in the high-CO_2 tanks was somewhat less; but the plants in those tanks were so far ahead of the plants in the ambient-air tanks that in their first five months of growth, they produced what it took the plants in the ambient-air tanks fully 21 months to produce.

Moving on to plants that are exclusively floating freshwater macrophytes, Idso (1997) grew many batches of the common water fern (*Azolla pinnata*) over a wide range of atmospheric CO_2 concentrations at two different water temperatures (18.2°C and 24.5°C) in Poor Man's Biospheres for periods of several weeks. This work revealed that a 900-ppm increase in the CO_2 concentration of the air above the tanks led to only a 19 percent increase in the biomass production of the plants floating in the cooler water, but that it led to a 66 percent biomass increase in the plants floating in the warmer water.

In an earlier study of *Azolla pinnata*, Idso *et al*. (1989) conducted three separate two- to three-month experiments wherein they grew batches of the floating fern out-of-doors in adequately fertilized water contained in sunken metal stock tanks located within clear-plastic-wall open-top chambers that were continuously maintained at atmospheric CO_2 concentrations of either 340 or 640 ppm, during which time the plants were briefly removed from the water and weighed at weekly intervals, while their photosynthetic rates were measured at hourly intervals from dawn to dusk on selected cloudless days. As a result of this protocol, they found the photosynthetic and growth rates of the plants growing in ambient air "first decreased, then stagnated, and finally became negative when mean air temperature rose above 30°C." In the high CO_2 treatment, on the other hand, they found that "the debilitating effects of high temperatures were reduced: in one case to a much less severe negative growth rate, in another case to merely a short period of zero growth rate, and in a third case to no discernible ill effects whatsoever—in spite of the fact that the ambient treatment plants in this instance all died."

Last, in a study of an emergent freshwater macrophyte, Ojala *et al*. (2002) grew water horsetail (*Equisetum fluviatile*) plants at ambient and double-ambient atmospheric CO_2 concentrations and ambient and ambient + 3°C air temperatures for three years, although the plants were subjected to the double-ambient CO_2 condition for only approximately five months of each year. This work revealed that the increase in air temperature boosted maximum shoot biomass by 60 percent, but the elevated CO_2 had no effect on this aspect of plant growth. However, elevated CO_2 and temperature—both singly and in combination—positively affected *root* growth, which was enhanced by 10, 15, and 25 percent by elevated air temperature, CO_2, and the two factors together, respectively.

In light of the several experimental findings discussed above, we conclude that the ongoing rise in the air's CO_2 content will likely have significant positive impacts on most freshwater macrophytes, including submersed, floating, and emergent species.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/aquaticmacrophytes.php.

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7.1.3.3. Marine Macroaglae

How do marine macroalgae respond to increases in the air's CO_2 content? The results of the studies discussed below provide a glimpse of what the future may hold in this regard, as the atmosphere's CO_2 concentration continues its upward climb.

Gao *et al*. (1993) grew cultures of the red macroalgae *Gracilaria* sp. and *G. chilensis* in vessels enriched with nitrogen and phosphorus that were continuously aerated with normal air containing 350 ppm CO_2, air enriched with an extra 650 ppm CO_2, and air enriched with an extra 1,250 ppm CO_2 for a period of 19 days. Compared to the control treatments, the relative growth enhancements in the + 650-ppm and +1250-ppm CO_2 treatments were 20 percent and 60 percent, respectively, for *G. chilensis*, and 130 percent and 190 percent, respectively, for the *Gracilaria* sp.

With respect to these findings, the researchers comment that "in their natural habitats, photosynthesis and growth of *Gracilaria* species are likely to be CO_2-limited, especially when the population density is high and water movement is slow." Hence, as the air's CO_2 content continues to rise, these marine macroalgae should grow ever better in the years ahead. Such should also be the case with many other macroalgae, for Gao *et al*. note that "photosynthesis by most macroalgae is probably limited by inorganic carbon sources in natural seawater," citing the studies of Surif and Raven (1989), Maberly (1990), Gao *et al*. (1991), and Levavasseur *et al*. (1991) as evidence for this statement.

In a subsequent study, Kubler *et al*. (1999) grew *Lomentaria articulata*, a red seaweed common to the Northeast Atlantic intertidal zone, for three weeks in hydroponic cultures subjected to various atmospheric CO_2 and O_2 concentrations. In doing so, they found that oxygen concentrations ranging from 10 to 200 percent of ambient had no significant effect on either the seaweed's daily net carbon gain or its total wet biomass production rate. By contrast, CO_2 concentrations ranging from 67 to 500 percent of ambient had highly significant effects on these parameters. At twice the ambient CO_2 concentration, for example, daily net carbon gain and total wet biomass production rates were 52 and 314 percent greater than they were at ambient CO_2.

More recently, Zou (2005) collected specimens of the brown seaweed *Hizikia fusiforme* from intertidal rocks along the coast of Nanao Island, Shantou, China, and maintained them in glass aquariums that contained filtered seawater enriched with 60 µM $NaNO_3$ and 6.0 µM NaH_2PO_4, while continuously aerating the aquariums with air of either 360 or 700 ppm CO_2 and periodically measuring seaweed growth and nitrogen assimilation rates, as well as nitrate reductase activities. By these means they determined that the slightly less than a doubling of the air's CO_2 concentration increased the seaweed's mean relative growth rate by about 50 percent, its mean rate of nitrate uptake during the study's 12-hour light periods by some 200 percent, and its nitrate reductase activity by approximately 20 percent over a wide range of substrate nitrate concentrations.

As a subsidiary aspect of the study, Zou notes that "the extract of *H. fusiforme* has an immunomodulating activity on humans and this ability might be used for clinical application to treat several diseases such as tumors (Suetsuna, 1998; Shan *et al*., 1999)." He also reports that the alga "has been used as a food delicacy and an herbal ingredient in China, Japan and Korea." In fact, he says that it "is now becoming one of the most important species for seaweed mariculture in China, owing to its high commercial value and increasing market demand." The ongoing rise in the air's CO_2 content bodes well for all of these applications. In addition, Zou notes that "the intensive cultivation of *H. fusiforme* would remove nutrients more efficiently with the future elevation of CO_2 levels in seawater, which could be a possible solution to the problem of ongoing coastal eutrophication," suggesting that rising CO_2 levels may also assist in the amelioration of this environmental problem.

In light of these several observations, the ongoing rise in the air's CO_2 content should help marine macroalgae to become more productive with the passage of time.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/aquaticmacroalgae.php.

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7.1.3.4. Marine Microalgae

How do marine microalgae respond to increases in the air's CO_2 content? Based on the late twentieth century work of Riebesell *et al*. (1993), Hein and Sand-Jensen (1997), and Wolf-Gladrow *et al*., (1999), it would appear that the productivity of earth's marine microalgae may be significantly enhanced by elevated concentrations of atmospheric CO_2. More recent work by other researchers suggests the same.

In a study of the unicellular marine diatom *Skeletonema costatus*, which is widely distributed in coastal waters throughout the world and is a major component of most natural assemblages of marine phytoplankton, Chen and Gao (2004) grew cell cultures of the species in filtered nutrient-enriched seawater maintained at 20°C under a light/dark cycle of 12/12 hours at a light intensity of 200 µmol m^{-2} s^{-1}, while continuously aerating the culture solutions with air of either 350 or 1,000 ppm CO_2 and measuring a number of physiological parameters related to the diatom's photosynthetic activity. They report that cell numbers of the alga "increased steadily throughout the light period and they were 1.6 and 2.1 times higher after the 12 h light period for the alga grown at 350 and 1000 ppm CO_2, respectively." They also say that chlorophyll *a* concentrations "increased 4.4- and 5.4-fold during the middle 8 h of the light period for the alga grown at 350 and 1000 ppm CO_2, respectively," and that "the contents of cellular chlorophyll a were higher for the alga grown at 1000 ppm CO_2 than that at 350 ppm CO_2." In addition, they note that the initial slope of the light saturation curve of photosynthesis and the photochemical efficiency of photosystem II "increased with increasing CO_2, indicating that the efficiency of light-harvesting and energy conversion in photosynthesis were increased." The end result of these several responses, in the words of Chen and Gao, was that "*S. costatum* benefited from CO_2 enrichment."

In another report of a study of marine microalgae that would appear to have enormous implications, Gordillo *et al*. (2003) begin by noting that "one of the main queries for depicting future scenarios of evolution of atmospheric composition and temperature is whether an atmospheric CO_2 increase stimulates primary production, especially in aquatic plants." Why do they say that? They say it because, as they put it, "aquatic primary producers account for about 50 percent of the total carbon fixation in the biosphere (Falkowski and Raven, 1997)."

Although the question addressed by Gordillo *et al*. sounds simple enough, its answer is not straightforward. In many phytoplankton, both freshwater and marine, photosynthesis appears to be saturated under current environmental conditions. Raven (1991), however, has suggested that those very same species, many of which employ carbon-concentrating mechanisms, could well decrease the amount of energy they expend in this latter activity in a CO_2-enriched world, which metabolic readjustment would leave a larger proportion of their captured energy available for fueling enhanced growth.

To explore this possibility, the four researchers studied various aspects of the growth response of the microalgal chlorophyte *Dunaliella viridis* (which possesses a carbon concentrating mechanism and has been used as a model species for the study of inorganic carbon uptake) to atmospheric CO_2 enrichment. Specifically, they batch-cultured the chlorophyte, which is one of the most ubiquitous eukaryotic organisms in hypersaline environments, in 250-ml Perspex cylinders under controlled laboratory conditions at high (5 m*M*) and low (0.5 m*M*) nitrate concentrations, while continuously aerating half of the cultures with ambient air of approximately 350 ppm CO_2 and the other half with air of approximately 10,000 ppm CO_2. In doing so, they discovered that atmospheric CO_2 enrichment had little effect on dark respiration in both N treatments. Likewise, it had little effect on photosynthesis in the low-N treatment. In the high-N treatment, the extra CO_2 increased photosynthesis by 114 percent. In the case of biomass production, the results were even more extreme: in the low-N treatment elevated CO_2 had no effect at all, while in the high-N treatment it nearly tripled the cell density of the culture solution.

In discussing their findings, Gordillo *et al*. note that "it has long been debated whether phytoplankton species are growth-limited by current levels of CO_2 in aquatic systems, i.e. whether an increase in atmospheric CO_2 could stimulate growth (Riebesell *et al*., 1993)." Their results clearly indicate that it can, as long as sufficient nitrogen is available. But that was not all that Gordillo *et al*. learned. In the high-N treatment, where elevated CO_2 greatly stimulated photosynthesis and biomass production, once the logarithmic growth phase had run its course and equilibrium growth was attained, approximately 70 percent of the carbon assimilated by the chlorophyte was released to the water, while in the low-CO_2 treatment only 35 percent was released.

With respect to this suite of observations, Gordillo *et al*. say "the release of organic carbon to the external medium has been proposed as a mechanism for maintaining the metabolic integrity of the cell (Ormerod, 1983)," and that "according to Wood and Van Valen (1990), organic carbon release would be a sink mechanism protecting the photosynthetic apparatus from an overload of products that cannot be invested in growth or stored." They additionally state that stores of photosynthetic products "are reduced to avoid overload and produce a high demand for photosynthates." Under these conditions, they conclude that "the process would then divert assimilated C to either the production of new biomass, or the release to the external medium once the culture conditions do not allow further exponential growth."

A second consequence of enhanced organic carbon release in the face of atmospheric CO_2 enrichment and sufficient N availability is that the internal C:N balance of the phytoplankton is maintained within a rather tight range. This phenomenon has also been observed in the green seaweed *Ulva rigida* (Gordillo *et al*., 2001) and the cyanobacterium *Spirulina platensis* (Gordillo *et al*., 1999). Hence, what the study of Gordillo *et al*. implies about the response of *Dunaliella viridis* to atmospheric CO_2 enrichment may well be widely applicable to many, if not most, aquatic plants, not the least of which may be the zooxanthellae that by this means (enhanced organic carbon release) could provide their coral hosts with the source of extra energy they need to continue building their skeletons at a non-reduced rate in the face of the negative calcification pressure produced by the changes in seawater chemistry that have been predicted to result from the ongoing rise in the air's CO_2 concentration.

In light of these several observations, there would appear to be ample reason to be optimistic about the response of earth's marine macroalgae to the ongoing rise in the air's CO_2 content.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/aquaticmicroalgae.php.

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7.2. Water Use Efficiency

Another major consequence of atmospheric CO_2 enrichment is that plants exposed to elevated levels of atmospheric CO_2 generally do not open their leaf stomatal pores—through which they take in carbon dioxide and give off water vapor—as wide as they do at lower CO_2 concentrations and tend to produce fewer of these pores per unit area of leaf surface. Both changes tend to reduce most plants' rates of water loss by transpiration. The amount of carbon they gain per unit of water lost—or water-use efficiency—therefore typically rises, increasing their ability to withstand drought. In this section, we explore the phenomena of water use efficiency as it pertains to agricultural, grassland, and woody species.

Additional information on this topic, including reviews water use efficiency not discussed here, can be found at http://www.co2science.org/subject/w/subject_w.php under the heading Water Use Efficiency.

7.2.1. Agricultural Species

In the study of Serraj *et al*. (1999), soybeans grown at 700 ppm CO_2 displayed 10 to 25 percent reductions in total water loss while simultaneously exhibiting increases in dry weight of as much as 33 percent. Thus, elevated CO_2 significantly increased the water-use efficiencies of the studied plants. Likewise, Garcia *et al*. (1998) determined that spring wheat grown at 550 ppm CO_2 exhibited a water-use efficiency that was about one-third greater than that exhibited by plants grown at 370 ppm CO_2. Similarly, Hakala *et al*. (1999) reported that twice-ambient CO_2 concentrations increased the water-use efficiency of spring wheat by 70 to 100 percent, depending on experimental air temperature. In addition, Hunsaker *et al*. (2000) reported CO_2-induced increases in water-use efficiency for field-grown wheat that were 20 and 10 percent higher than those displayed by ambiently grown wheat subjected to high and low soil nitrogen regimes, respectively. Also, pea plants grown for two months in growth chambers receiving atmospheric CO_2 concentrations of 700 ppm displayed an average water-use efficiency that was 27 percent greater than that exhibited by ambiently grown control plants (Gavito *et al*., 2000).

In some cases, the water-use efficiency increases caused by atmospheric CO_2 enrichment are spectacularly high. De Luis *et al*. (1999), for example, demonstrated that alfalfa plants subjected to atmospheric CO_2 concentrations of 700 ppm had water-use efficiencies that were 2.6 and 4.1 times greater than those displayed by control plants growing at 400 ppm CO_2 under water-stressed and well-watered conditions, respectively. Also, when grown at an atmospheric CO_2 concentration of 700 ppm, a 2.7-fold increase in water-use efficiency was reported by Malmstrom and Field (1997) for oats infected with the barley yellow dwarf virus.

In addition to enhancing the water-use efficiencies of agricultural C_3 crops, as reported in the preceding paragraphs, elevated CO_2 also enhances the water-use efficiencies of crops possessing alternate carbon fixation pathways. Maroco *et al*. (1999), for example, demonstrated that maize—a C_4 crop—grown for 30 days at an atmospheric CO_2 concentration of 1,100 ppm exhibited an intrinsic water-use efficiency that was 225 percent higher than that of plants grown at 350 ppm CO_2. In addition, Conley *et al*. (2001) reported that a 200-ppm increase in the air's CO_2 content boosted the water-use efficiency of field-grown sorghum by 9 and 19 percent under well-watered and water-stressed conditions, respectively. Also, Zhu *et al*. (1999) reported that pineapple—a CAM plant—grown at 700 ppm CO_2 exhibited water-use efficiencies that were always significantly greater than those displayed by control plants grown at 350 ppm CO_2 over a range of growth temperatures.

It is clear from the studies above that as the CO_2 content of the air continues to rise, earth's agricultural species will respond favorably by exhibiting increases in water-use efficiency. It is likely that food and fiber production will increase on a worldwide basis, even in areas where productivity is severely restricted due to limited availability of soil moisture.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/w/wateruseag.php.

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7.2.2. Grassland Species

In the study of Grunzweig and Korner (2001), model grasslands representative of the semi-arid Negev of Israel, which were grown for five months at atmospheric CO_2 concentrations of 440 and 600 ppm, exhibited cumulative water-use efficiencies that were 17 and 28 percent greater, respectively, than control communities grown at 280 ppm CO_2. Similarly, Szente *et al.* (1998) reported a doubling of the atmospheric CO_2 concentration increased the water-use efficiency of two C_3 grasses and two broad-leaved species common to the loess grasslands of Budapest by 72 and 266 percent, respectively. In addition, Leymarie *et al.* (1999) calculated that twice-ambient CO_2 concentrations increased the water-use efficiency of the herbaceous weedy species *Arabidopsis thaliana* by 41 and 120 percent under well-watered and water-stressed conditions, respectively. Other CO_2-induced increases in C_3 plant water-use efficiency have been documented by Clark *et al.* (1999) for several New Zealand pasture species and Roumet *et al.* (2000) for various Mediterranean herbs.

Elevated CO_2 also has been shown to substantially increase the water-use efficiency of C_4 grassland species. Adams *et al.* (2000), for example, reported that twice-ambient CO_2 concentrations enhanced the daily water-use efficiency of a C_4 tallgrass prairie in Kansas, USA, dominated by *Andropogon gerardii*. LeCain and Morgan (1998) also documented enhanced water-use efficiencies for six different C_4 grasses grown with twice-ambient CO_2 concentrations. Likewise, Seneweera *et al.* (1998) reported that a 650-ppm increase in the air's CO_2 content dramatically increased the water-use efficiency of the perennial C_4 grass *Panicum coloratum*.

As the air's CO_2 content continues to rise, nearly all of earth's grassland species—including both C_3 and C_4 plants—will likely experience increases in water-use efficiency. Concomitantly, the productivity of the world's grasslands should increase, even if available moisture decreases in certain areas. Moreover, such CO_2-induced increases in water-use efficiency will likely allow grassland species to expand their ranges into desert areas where they previously could not survive due to lack of sufficient moisture.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/w/waterusegrass.php.

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7.2.3. Woody Species

The effect of elevated atmospheric CO_2 concentrations on the water-use efficiencies of trees is clearly positive, having been documented in a number of different single-species studies of longleaf pine (Runion *et al*., 1999), red oak (Anderson and Tomlinson, 1998), scrub oak (Lodge *et al*., 2001), silver birch (Rey and Jarvis, 1998), beech (Bucher-Wallin *et al*., 2000; Egli *et al*., 1998), sweetgum (Gunderson *et al*., 2002; Wullschleger and Norby, 2001), and spruce (Roberntz and Stockfors, 1998). Likewise, in a multi-species study performed by Tjoelker *et al*. (1998), seedlings of quaking aspen, paper birch, tamarack, black spruce, and jack pine, which were grown at 580 ppm CO_2 for three months, displayed water-use efficiencies that were 40 to 80 percent larger than those exhibited by their respective controls grown at 370 ppm CO_2.

Similar results are also obtained when trees are exposed to different environmental stresses. In a study conducted by Centritto *et al*. (1999), for example, cherry seedlings grown at twice-ambient levels of atmospheric CO_2 displayed water-use efficiencies that were 50 percent greater than their ambient controls, regardless of soil moisture status. And in the study of Wayne *et al*. (1998), yellow birch seedlings grown at 800 ppm CO_2 had water-use efficiencies that were 52 and 94 percent greater than their respective controls, while simultaneously subjected to uncharacteristically low and high air temperature regimes.

In some parts of the world, perennial woody species have been exposed to elevated atmospheric CO_2 concentrations for decades, due to their proximity to CO_2-emitting springs and vents in the earth, allowing scientists to assess the long-term effects of this phenomenon. In Venezuela, for example, the water-use efficiency of a common tree exposed to a lifetime atmospheric CO_2 concentration of approximately 1,000 ppm rose 2-fold and 19-fold during the local wet and dry seasons, respectively (Fernandez *et al*., 1998). Similarly, Bartak *et al*. (1999) reported that 30-year-old *Arbutus unedo* trees growing in central Italy at a lifetime atmospheric CO_2 concentration around 465 ppm exhibited water-use efficiencies that were 100 percent greater than control trees growing at a lifetime CO_2 concentration of 355 ppm. In addition, two species of oaks in central Italy that had been growing for 15 to 25 years at an atmospheric CO_2 concentration ranging from 500 to 1,000 ppm displayed "such marked increases in water-use efficiency under elevated CO_2," in the words of the scientists who studied them, that this phenomenon "might be of great importance in Mediterranean environments in the perspective of global climate change" (Blaschke *et al*., 2001; Tognetti *et al*., 1998). Thus, the long-term effects of elevated CO_2 concentrations on water-use efficiency are likely to persist and increase with increasing atmospheric CO_2 concentrations.

In some cases, scientists have looked to the past and determined the positive impact the historic rise in the air's CO_2 content has already had on plant water-use efficiency. Duquesnay *et al*. (1998), for example, used tree-ring data derived from beech trees to determine that over the past century the water-use efficiency of such trees in north-eastern France increased by approximately 33 percent. Similarly, Feng (1999) used tree-ring chronologies derived from a number of trees in western North America to calculate a 10 to 25 percent increase in tree water-use efficiency from 1750 to 1970, during which time the atmospheric CO_2 concentration rose by approximately 16 percent. In another study, Knapp *et al*. (2001) developed tree-ring chronologies from western juniper stands located in Oregon, USA, for the past century, determining that growth recovery from drought was much greater in the latter third of their chronologies (1964-1998) than it was in the first third (1896-1930). In this case, the authors suggested that the greater atmospheric CO_2 concentrations of the latter period allowed the trees to more quickly recover from water stress. Finally, Beerling *et al*. (1998) grew *Gingko* saplings at 350 and 650 ppm CO_2 for three years, finding that elevated atmospheric CO_2 concentrations reduced leaf stomatal densities to values comparable to those measured on fossilized *Gingko* leaves dating back to the Triassic and Jurassic periods, implying greater water-use efficiencies for those times too.

On another note, Prince *et al*. (1998) demonstrated that rain-use efficiency, which is similar to water-use efficiency, slowly increased in the African Sahel from 1982 to 1990, while Nicholson *et* *al*. (1998) observed neither an increase nor a decrease in this parameter from 1980 to 1995 for the central and western Sahel.

In summary, it is clear that as the CO_2 content of the air continues to rise, nearly all of earth's trees will respond favorably by exhibiting increases in water-use efficiency. It is thus likely that as time progresses, earth's woody species will expand into areas where they previously could not exist due to limiting amounts of available moisture. Therefore, one can expect the earth to become a greener biospheric body with greater carbon sequestering capacity as the atmospheric CO_2 concentration continues to rise.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/w/waterusetrees.php.

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7.3. Amelioration of Environmental Stresses

Atmospheric CO_2 enrichment has been shown to help ameliorate the detrimental effects of several environmental stresses on plant growth and development, including disease, herbivory (predation by insects), shade (caused by increased cloudiness), ozone (a common air pollutant), low temperatures, nitrogen deficiency, UV-B radiation, and water stress. In this section we survey research on each of these types of stress.

Additional information on this topic, including reviews on stresses not discussed here, can be found at http://www.co2science.org/subject/g/subject_g.php under the heading Growth Response to CO_2 with Other Variables.

7.3.1. Disease

According to the IPCC, CO_2-induced global warming will increase the risk of plant disease outbreaks, resulting in negative consequences for food, fiber, and forestry across all world regions (IPCC, 2007-II). But it appears the IPCC has omitted the results of real-world observations that contradict this forecast.

Chakraborty and Datta (2003) note there are a number of CO_2-induced changes in plant physiology, anatomy and morphology that have been implicated in increased plant resistance to disease and that "can potentially enhance host resistance at elevated CO_2." Among these phenomena they list "increased net photosynthesis allowing mobilization of resources into host resistance (Hibberd *et al*., 1996a.); reduced stomatal density and conductance (Hibberd *et al*., 1996b); greater accumulation of carbohydrates in leaves; more waxes, extra layers of epidermal cells and increased fibre content (Owensby, 1994); production of papillae and accumulation of silicon at penetration sites (Hibberd *et al*., 1996a); greater number of mesophyll cells (Bowes, 1993); and increased biosynthesis of phenolics (Hartley *et al*., 2000), among others."

Malmstrom and Field (1997) grew individual oat plants for two months in pots placed within phytocells maintained at atmospheric CO_2 concentrations of 350 and 700 ppm, while they infected one-third of the plants with the barley yellow dwarf virus (BYDV), which plagues more than 150 plant species worldwide, including all major cereal crops. Over the course of their study, they found that elevated CO_2 stimulated rates of net photosynthesis in all plants, regardless of pathogen infection. However, the greatest percentage increase occurred in diseased individuals (48 percent vs. 34 percent). Moreover, atmospheric CO_2 enrichment decreased stomatal conductance by 50 percent in infected plants but by only 34 percent in healthy ones, which led to a CO_2-induced doubling of the instantaneous water-use efficiency of the healthy plants, but an increase of fully 2.7-fold in the diseased plants. Last, after 60 days of growth under these conditions, they determined that the extra CO_2 increased total plant biomass by 36 percent in infected plants, but by only 12 percent in healthy plants. In addition, while elevated CO_2 had little effect on root growth in the healthy plants, it increased root biomass in the infected plants by up to 60 percent. Consequently, it can be appreciated that as the CO_2 content of the air continues to rise, its many positive effects will likely offset some, if not most, of the negative effects of the destructive BYDV. Quoting Malmstrom and Field with respect to two specific examples, they say in their concluding remarks that CO_2 enrichment "may reduce losses of infected plants to drought" and "may enable diseased plants to compete better with healthy neighbors."

Tiedemann and Firsching (2000) grew spring wheat plants from germination to maturity in controlled-environment chambers maintained at ambient (377 ppm) and elevated (612 ppm) concentrations of atmospheric CO_2 and at ambient (20 ppb) and elevated (61 ppb) concentrations of ozone (and combinations thereof), the latter of which gases is typically toxic to most plants. In addition, half of the plants in each treatment were inoculated with a leaf rust-causing fungus. Under these conditions, the elevated CO_2 increased the photosynthetic rates of the diseased plants by 20 and 42 percent at the ambient and elevated ozone concentrations, respectively. It also enhanced the yield of the infected plants, increasing it by 57 percent, even in the presence of high ozone concentrations.

Jwa and Walling (2001) grew tomato plants hydroponically for eight weeks in controlled-environment chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm. In addition, at week five of the study, half of all plants growing in each CO_2 concentration were infected with a fungal pathogen that attacks plant roots and induces a water stress that decreases growth and yield. At the end of the study, they found that the pathogenic infection had reduced total plant biomass by nearly 30 percent at both atmospheric CO_2 concentrations. However, the elevated CO_2 had increased the total biomass of the healthy and diseased plants by the same amount (+30 percent), with the result that the infected tomato plants grown at 700 ppm CO_2 had biomass values that were essentially identical to those of the healthy tomato plants grown at 350 ppm CO_2. Thus, the extra CO_2 completely counterbalanced the negative effect of the pathogenic infection on overall plant productivity.

Chakraborty and Datta (2003) studied the aggressiveness of the fungal anthracnose pathogen *Colletotrichum gloeosporioides* by inoculating two isolates of the pathogen onto two cultivars of the tropical pasture legume *Stylosanthes scabra* (Fitzroy, which is susceptible to the fungal pathogen, and Seca, which is more resistant) over 25 sequential infection cycles in controlled-environment chambers filled with air of either 350 or 700 ppm CO_2. By these means they determined that the aggressiveness of the pathogen was reduced at the twice-ambient level of atmospheric CO_2, where aggressiveness is defined as "a property of the pathogen reflecting the relative amount of damage caused to the host without regard to resistance genes (Shaner *et al*., 1992)." As they describe it, "at twice-ambient CO_2 the overall level of aggressiveness of the two [pathogen] isolates was significantly reduced on both cultivars."

Simultaneously, however, pathogen fecundity was found to increase at twice-ambient CO_2. Of this finding, Chakraborty and Datta report that their results "concur with the handful of studies that have demonstrated increased pathogen fecundity at elevated CO_2 (Hibberd *et al*., 1996a; Klironomos *et al*., 1997; Chakraborty *et al*., 2000)." How this happened in the situation they investigated, according to Chakraborty and Datta, is that the overall increase in fecundity at high CO_2 "is a reflection of the altered canopy environment," wherein "the 30% larger *S. scabra* plants at high CO_2 (Chakraborty *et al*., 2000) makes the canopy microclimate more conducive to anthracnose development."

In view of these opposing changes in pathogen behavior at elevated levels of atmospheric CO_2, it is difficult to know the outcome of atmospheric CO_2 enrichment for this specific pathogen-host relationship. More research, especially under realistic field conditions, will be needed to clarify the situation; and, of course, different results are likely to be observed for different pathogen-host associations. What is more, results could also differ under different climatic conditions. Nevertheless, the large number of ways in which elevated CO_2 has been demonstrated to increase plant resistance to pathogen attack gives us reason to believe that plants will gain the advantage as the air's CO_2 content continues to climb in the years ahead.

Another study that fuels this optimism was conducted by Parsons *et al*. (2003), who grew two-year-old saplings of paper birch and three-year-old saplings of sugar maple in well-watered and fertilized pots from early May until late August in glasshouse rooms maintained at either 400 or 700 ppm CO_2. In these circumstances, the whole-plant biomass of paper birch was increased by 55 percent in the CO_2-enriched portions of the glasshouse, while that of sugar maple was increased by 30 percent. Also, concentrations of condensed tannins were increased by 27 percent in the paper birch (but not the sugar maple) saplings grown in the CO_2-enriched air; in light of this finding, Parsons *et al*. conclude that "the higher condensed tannin concentrations that were present in the birch fine roots may offer these tissues greater protection against soil-borne pathogens and herbivores."

Within this context, it is interesting to note that Parsons *et al*. report that CO_2-induced increases in fine root concentrations of total phenolics and condensed tannins have also been observed in warm temperate conifers by King *et al.* (1997), Entry *et al.* (1998), Gebauer *et al.* (1998), and Runion *et al.* (1999), as well as in cotton by Booker (2000).

In another intriguing study, Gamper *et al.* (2004) begin by noting that arbuscular mycorrhizal fungi (AMF) are expected to modulate plant responses to elevated CO_2 by "increasing resistance/tolerance of plants against an array of environmental stressors (Smith and Read, 1997)." In investigating this subject in a set of experiments conducted over a seven-year period of free-air CO_2-enrichment on two of the world's most extensively grown cool-season forage crops (*Lolium perenne* and *Trifolium repens*) at the Swiss free-air CO_2 enrichment (FACE) facility near Zurich, they determined that "at elevated CO_2 and under [two] N treatments, AMF root colonization of both host plant species was increased," and that "colonization levels of all three measured intraradical AMF structures (hyphae, arbuscules and vesicles) tended to be higher." Hence, they concluded that these CO_2-induced benefits may lead to "increased protection against pathogens and/or herbivores."

Pangga *et al.* (2004) grew well-watered and fertilized seedlings of a cultivar (Fitzroy) of the pencilflower (*Stylosanthes scabra*)—an important legume crop that is susceptible to anthracnose disease caused by *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc.—within a controlled-environment facility maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm, where they inoculated six-, nine- and 12-week-old plants with conidia of *C. gloeosporioides.* Then, 10 days after inoculation, they counted the anthracnose lesions on the plants and classified them as either resistant or susceptible.

Adherence to this protocol revealed, in their words, that "the mean number of susceptible, resistant, and total lesions per leaf averaged over the three plant ages was significantly ($P<0.05$) greater at 350 ppm than at 700 ppm CO_2, reflecting the development of a level of resistance in susceptible cv. Fitzroy at high CO_2." In fact, with respect to the plants inoculated at 12 weeks of age, they say that those grown "at 350 ppm had 60 and 75% more susceptible and resistant lesions per leaf, respectively, than those [grown] at 700 ppm CO_2."

In terms of infection efficiency (IE), the Australian scientists say their work "clearly shows that at 350 ppm overall susceptibility of the canopy increases with increasing age because more young leaves are produced on secondary and tertiary branches of the more advanced plants." However, they report that "at 700 ppm CO_2, IE did not increase with increasing plant age despite the presence of many more young leaves in the enlarged canopy," which finding, in their words, "points to reduced pathogen efficiency or an induced partial resistance to anthracnose in Fitzroy at 700 ppm CO_2." Consequently, as the air's CO_2 content continues to rise, it would appear that the Fitzroy cultivar of the pasture legume *Stylosanthes scabra* will acquire a greater intrinsic resistance to the devastating anthracnose disease.

McElrone *et al.* (2005) "assessed how elevated CO_2 affects a foliar fungal pathogen, *Phyllosticta minima*, of *Acer rubrum* [red maple] growing in the understory at the Duke Forest free-air CO_2 enrichment experiment in Durham, North Carolina, USA ... in the 6th, 7th, and 8th years of the CO_2 exposure." Surveys conducted in those years, in their words, "revealed that elevated CO_2 [to 200 ppm above ambient] significantly reduced disease incidence, with 22%, 27% and 8% fewer saplings and 14%, 4%, and 5% fewer leaves infected per plant in the three consecutive years, respectively." In addition, they report that the elevated CO_2 "also significantly reduced disease severity in infected plants in all years (e.g. mean lesion area reduced 35%, 50%, and 10% in 2002, 2003, and 2004, respectively)."

What underlying mechanism or mechanisms produced these beneficent consequences? Thinking it could have been a direct deleterious effect of elevated CO_2 on the fungal pathogen, McElrone *et al.* performed some side experiments in controlled-environment chambers. However, they found that the elevated CO_2 benefited the fungal pathogen as well as the red maple saplings, observing that "exponential growth rates of *P. minima* were 17% greater under elevated CO_2." And they obtained similar results when they repeated the *in vitro* growth analysis two additional times in different growth chambers.

Taking another tack when "scanning electron micrographs verified that conidia germ tubes of *P. minima* infect *A. rubrum* leaves by entering through the stomata," the researchers turned their attention to the pathogen's mode of entry into the saplings' foliage. In this investigation they found that both stomatal size and density were unaffected by atmospheric CO_2 enrichment, but that "stomatal conductance was reduced by 21-36% under elevated CO_2, providing smaller openings for infecting germ tubes." In addition, they concluded that reduced disease severity under elevated CO_2 was also likely due to altered leaf chemistry, as elevated CO_2

increased total leaf phenolic concentrations by 15 percent and tannin concentrations by 14 percent.

Because the phenomena they found to be important in reducing the amount and severity of fungal pathogen infection (leaf spot disease) of red maple have been demonstrated to be operative in most other plants as well, McElrone *et al.* say these CO_2-enhanced leaf defensive mechanisms "may be prevalent in many plant pathosystems where the pathogen targets the stomata." Indeed, they state that their results "provide concrete evidence for a potentially generalizable mechanism to predict disease outcomes in other pathosystems under future climatic conditions."

Matros *et al.* (2006) grew tobacco plants (*Nicotiana tabacum* L.) in 16-cm-diameter pots filled with quartz sand in controlled-climate chambers maintained at either 350 or 1,000 ppm CO_2 for a period of eight weeks, where they were irrigated daily with a complete nutrient solution containing either 5 or 8 mM NH_4NO_3. In addition, some of the plants in each treatment were mechanically infected with the *potato virus Y* (PVY) when they were six weeks old. Then, at the end of the study, the plants were harvested and a number of their chemical constitutes identified and quantified.

This work revealed, in the researchers words, that "plants grown at elevated CO_2 and 5 mM NH_4NO_3 showed a marked and significant decrease in content of nicotine in leaves as well as in roots," while at 8 mM NH_4NO_3 the same was found to be true of upper leaves but not of lower leaves and roots. With respect to the PVY part of the study, they further report that the "plants grown at high CO_2 showed a markedly decreased spread of virus." Both of these findings would likely be considered beneficial by most people, as *potato virus Y* is an economically important virus that infects many crops and ornamental plants throughout the world, while nicotine is nearly universally acknowledged to have significant negative impacts on human health (Topliss *et al*., 2002).

Braga *et al.* (2006) conducted three independent experiments where they grew well-watered soybean (*Glycine max* (L.) Merr) plants of two cultivars (IAC-14, susceptible to stem canker disease, and IAC-18, resistant to stem canker disease) from seed through the cotyledon stage in five-liter pots placed within open-top chambers maintained at atmospheric CO_2 concentrations of either 360 or 720 ppm in a glasshouse, while they measured various plant properties and processes, concentrating on the production of *glyceollins* (the major *phytoalexins*, or anti-microbial compounds, produced in soybeans) in response to the application of ß-glucan elicitor (derived from mycelial walls of *Phythophthora sojae*) to carefully created and replicated wounds in the surfaces of several soybean cotyledons. In doing so, they found that the IAC-14 cultivar did *not* exhibit a CO_2-induced change in glyceollin production in response to elicitation—as Braga *et al.* had hypothesized would be the case, since this cultivar is susceptible to stem canker disease—but they found that the IAC-18 cultivar (which has the potential to resist the disease to varying degrees) experienced a 100 percent CO_2-induced increase in the amount of glyceollins produced after elicitation, a response the researchers described as *remarkable*. As for its significance, Braga *et al.* say the CO_2-induced response they observed "may increase the potential of the soybean defense since infection at early stages of plant development, followed by a long incubation period before symptoms appear, is characteristic of the stem canker disease cycle caused by Dpm [*Diaporthe phaseolorum* (Cooke & Ellis) Sacc. f. sp. *meridionalis* Morgan-Jones]." They say the response they observed "indicates that raised CO_2 levels forecasted for next decades may have a real impact on the defensive chemistry of the cultivars."

Last, in a study conducted within the BioCON (Biodiversity, Carbon dioxide, and Nitrogen effects on ecosystem functioning) FACE facility located at the Cedar Creek Natural History Area in east-central Minnesota, USA, Strengbom and Reich (2006) evaluated the effects of an approximate 190-ppm increase in the air's daytime CO_2 concentration on leaf photosynthetic rates of stiff goldenrod (*Solidago rigida*) growing in monoculture for two full seasons, together with its concomitant effects on the incidence and severity of leaf spot disease. Although they found that elevated CO_2 had no significant effect on plant photosynthetic rate in their study, they report that "both disease incidence and severity were lower on plants grown under elevated CO_2." More specifically, they found that "disease incidence was on average *more than twice as high* [our italics] under ambient as under elevated CO_2," and that "disease severity (proportion of leaf area with lesions) was on average 67% lower under elevated CO_2 compared to ambient conditions."

In discussing their results, Strengbom and Reich say the "indirect effects from elevated CO_2, i.e., lower disease incidence, had a stronger effect on realized photosynthetic rate than the direct effect of higher CO_2," which as noted above was negligible in their study. They conclude "it may be necessary to consider potential changes in susceptibility to foliar diseases to correctly estimate the effects on plant photosynthetic rates of elevated CO_2." In addition, they note that the plants grown in CO_2-enriched air had lower leaf nitrogen concentrations than the plants grown in ambient air, as is often observed in studies of this type; and they say that their results "are, thus, also in accordance with other studies that have found reduced pathogen performance following reduced nitrogen concentration in plants grown under elevated CO_2 (Thompson and Drake, 1994)." What is more, they conclude that their results are "also in accordance with studies that have found increased [disease] susceptibility following increased nitrogen concentration of host plants (Huber and Watson, 1974; Nordin *et al*., 1998; Strengbom *et al*., 2002)." It is possible, therefore, that the ongoing rise in the air's CO_2 content may help many plants of the future reduce the deleterious impacts of various pathogenic fungal diseases that currently beset them, thereby enabling them to increase their productivities above and beyond what is typically provided by the more direct growth stimulation resulting from the aerial fertilization effect of elevated atmospheric CO_2 concentrations.

In summation, the bulk of the available data shows atmospheric CO_2 enrichment asserts its greatest positive influence on infected as opposed to healthy plants. Moreover, it would appear that elevated CO_2 has the ability to significantly ameliorate the deleterious effects of various stresses imposed upon plants by numerous pathogenic invaders. Consequently, as the atmosphere's CO_2 concentration continues its upward climb, earth's vegetation should be increasingly better equipped to successfully deal with pathogenic organisms and the damage they have traditionally done to mankind's crops, as well as to the plants that sustain the rest of the planet's animal life.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/disease.php

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7.3.2. Herbivory

Insect pests have greatly vexed earth's plants in the past and will likely continue to do so in the future. It is possible, however, that the ongoing rise in the atmosphere's CO_2 content may affect this phenomenon, for better or for worse. In this section we review the results of several studies that have addressed this subject as it applies to herbaceous and woody plants.

Additional information on this topic, including reviews on herbivory not discussed here, can be found at http://www.co2science.org/subject/h/subject_h.php under the heading Herbivory.

7.3.2.1. Herbaceous Plants

Kerslake *et al.* (1998) grew five-year-old heather (*Calluna vulgaris*) plants collected from a Scottish moor in open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 600 ppm. At two different times during the study, larvae of the destructive winter moth *Operophtera brumata*—whose outbreaks periodically cause extensive damage to heather moorland—were allowed to feed upon current-year shoots. Feeding upon the high-CO_2-grown foliage did not affect larval growth rates, development, or final pupal weights; neither was moth survivorship significantly altered. The authors concluded that their study "provides no evidence that increasing atmospheric CO_2 concentrations will affect the potential for outbreak of *Operophtera brumata* on this host." What it did show, however, was a significant CO_2-induced increase in heather water use efficiency.

Newman *et al*. (1999) inoculated tall fescue (*Festuca arundinacea*) plants growing in open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm with bird cherry-oat aphids (*Rhopalosiphum padi*). After nine weeks, the plants growing in the CO_2-enriched air had experienced a 37 percent increase in productivity and were covered with many fewer aphids than the plants growing in ambient air.

Goverde *et al*. (1999) collected four genotypes of *Lotus corniculatus* near Paris and grew them in controlled environment chambers kept at atmospheric CO_2 concentrations of 350 and 700 ppm. Larvae of the Common Blue Butterfly (*Polyommatus icarus*) that were allowed to feed upon the foliage produced in the CO_2-enriched air ate more, grew larger, and experienced shorter development times than larvae feeding on the foliage produced in the ambient-air treatment, suggesting that this butterfly species will likely become more robust and plentiful as the air's CO_2 content continues to rise.

Brooks and Whittaker (1999) removed grassland monoliths containing eggs of the xylem-feeding spittlebug *Neophilaenus lineatus* from the UK's Great Dun Fell in Cumbria and placed them in glasshouses maintained at atmospheric CO_2 concentrations of 350 and 600 ppm for two years. Survival of the spittlebug's nymphal states was reduced by 24 percent in both of the generations produced in their experiment, suggesting that this particular insect will likely cause less tissue damage to the plants of this species-poor grassland in a CO_2-enriched world of the future.

Joutei *et al*. (2000) grew bean (*Phaseolus vulgaris*) plants in controlled environments kept at atmospheric CO_2 concentrations of 350 and 700 ppm, to which they introduced the destructive agricultural mite *Tetranychus urticae*, observing that female mites produced 34 percent and 49 percent less offspring in the CO_2-enriched chambers in their first and second generations, respectively. This CO_2-induced reduction in the reproductive success of this invasive insect, which negatively affects more than 150 crop species worldwide, bodes well for mankind's ability to grow the food we will need to feed our growing numbers in the years ahead.

Peters *et al*. (2000) fed foliage derived from FACE plots of calcareous grasslands of Switzerland (maintained at 350 and 650 ppm CO_2) to terrestrial slugs, finding they exhibited no preference with respect to the CO_2 treatment from which the foliage was derived. Also, in a study that targeted no specific insect pest, Castells *et al*. (2002) found that a doubling of the air's CO_2 content enhanced the total phenolic concentrations of two Mediterranean perennial grasses (*Dactylis glomerata* and *Bromus erectus*) by 15 percent and 87 percent, respectively, which compounds tend to enhance plant defensive and resistance mechanisms to attacks by both herbivores and pathogens.

Coviella and Trumbel (2000) determined that toxins produced by *Bacillus thuringiensis* (Bt), which are applied to crop plants by spraying as a means of combating various crop pests, were "more efficacious" in cotton grown in an elevated CO_2 environment than in ambient air, which is a big plus for modern agriculture. In addition, Coviella *et al*. (2000) determined that "elevated CO_2 appears to eliminate differences between transgenic [Bt-containing] and nontransgenic plants for some key insect developmental/fitness variables including length of the larval stage and pupal weight."

In summary, the majority of evidence that has been accumulated to date suggests that rising atmospheric CO_2 concentrations may reduce the frequency and severity of pest outbreaks that are detrimental to agriculture, while not seriously impacting herbivorous organisms found in natural ecosystems that are normally viewed in a more favorable light.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/h/herbivoresherbplants.php.

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7.3.2.2. Woody Plants

7.3.2.2.1. Maple

Working with *Acer rubrum* saplings beginning their fourth year of growth in open-top chambers maintained at four different atmospheric CO_2/temperature conditions—(1) ambient temperature, ambient CO_2, (2) ambient temperature, elevated CO_2 (ambient + 300 ppm), (3) elevated temperature (ambient + 3.5°C), ambient CO_2, and (4) elevated temperature, elevated CO_2—Williams *et al.* (2003) bagged first instar gypsy moth larvae on various branches of the trees and observed their behavior. The data they obtained demonstrated, in their words, "that larvae feeding on CO_2-enriched foliage ate a comparably poorer food source than those feeding on ambient CO_2-grown plants, irrespective of temperature," and that there was a minor reduction in leaf water content due to CO_2 enrichment. Nevertheless, they found the "CO_2-induced reductions in foliage quality (e.g. nitrogen and water) were unrelated [our italics] to insect mortality, development rate and pupal weight," and that these and any other phytochemical changes that may have occurred "resulted in no negative effects on gypsy moth performance." They also found that "irrespective of CO_2 concentration, on average, male larvae pupated 7.5 days earlier and female larvae 8 days earlier at elevated temperature," and noting that anything that prolongs the various development stages of insects potentially exposes them to greater predation and parasitism risk, they concluded that the observed temperature-induced hastening of the insects' development would likely expose them to *less* predation and parasitism risk.

One year later, Hamilton *et al.* (2004) began the report of their study of this important subject by noting that many single-species investigations have suggested that increases in atmospheric CO_2 will increase herbivory (Bezemer and Jones, 1998; Cannon, 1998; Coviella and Trumble, 1999; Hunter, 2001; Lincoln *et al.*, 1993; Whittaker, 1999). However, because there are so many feedbacks and complex interactions among the numerous components of real-world ecosystems, they warned that one ought not put too much faith in these predictions until relevant real-world ecosystem-level experiments have been completed.

In one such study they conducted at the Duke Forest FACE facility near Chapel Hill, North Carolina, USA, Hamilton *et al.* "measured the amount of leaf tissue damaged by insects and other herbivorous arthropods during two growing seasons in a deciduous forest understory continuously exposed to ambient (360 ppm) and elevated (560 ppm) CO_2 conditions." This forest is dominated by loblolly pine trees that account for fully 92 percent of the ecosystem's total woody biomass. In addition, it contains 48 species of other woody plants (trees, shrubs, and vines) that have naturally established themselves in the forest's understory. In their study of this ecosystem, Hamilton *et al.* quantified the loss of foliage due to herbivory that was experienced by three deciduous tree species, one of which was *Acer rubrum*.

As Hamilton *et al*. describe it, "we found that elevated CO_2 led to a trend toward *reduced herbivory* [our italics] in [the] deciduous understory in a situation that included the full complement of naturally occurring plant and insect species." In 1999, for example, they determined that "elevated CO_2 reduced overall herbivory by more than 40 percent," while in 2000 they say they observed "the same pattern and magnitude of reduction."

With respect to changes in foliage properties that might have been expected to lead to increases in herbivory, Hamilton *et al*. report they "found no evidence for significant changes in leaf nitrogen, C/N ratio, sugar, starch or total leaf phenolics in either year of [the] study," noting that these findings agree with those of "another study performed at the Duke Forest FACE site that also found no effect of elevated CO_2 on the chemical composition of leaves of understory trees (Finzi and Schlesinger, 2002)."

Hamilton *et al*. thus concluded their landmark paper by emphasizing that "despite the large number of studies that predict increased herbivory, particularly from leaf chewers, under elevated CO_2, our study found a trend toward reduced herbivory two years in a row." In addition, they note that their real-world results "agree with the only other large-scale field experiment that quantified herbivory for a community exposed to elevated CO_2 (Stiling *et al*., 2003)."

Consequently, and in spite of the predictions of increased destruction of natural ecosystems by insects and other herbivorous arthropods in a CO_2-enriched world of the future, just the opposite would appear to be the more likely outcome; i.e., greater plant productivity plus less foliage consumption by herbivores, "whether expressed on an absolute or a percent basis," as Hamilton *et al*. found to be the case in their study.

In another study conducted at the same site, Knepp *et al*. (2005) quantified leaf damage by chewing insects on saplings of seven species (including *Acer rubrum*) in 2001, 2002, and 2003, while five additional species (including *Acer barbatum*) were included in 2001 and 2003. This work revealed, in their words, that "across the seven species that were measured in each of the three years, elevated CO_2 caused a reduction in the percentage of leaf area removed by chewing insects," which was such that "the percentage of leaf tissue damaged by insect herbivores was 3.8 percent per leaf under ambient CO_2 and 3.3 percent per leaf under elevated CO_2." Greatest effects were observed in 2001, when they report that "across 12 species the average damage per leaf under ambient CO_2 was 3.1 percent compared with 1.7 percent for plants under elevated CO_2," which was "indicative of a 46 percent decrease in the total area and total mass of leaf tissue damaged by chewing insects in the elevated CO_2 plots."

What was responsible for these welcome results? Knepp *et al*. say that "given the consistent reduction in herbivory under high CO_2 across species in 2001, it appears that some universal feature of chemistry or structure that affected leaf suitability was altered by the treatment." Another possibility they discuss is that "forest herbivory may decrease under elevated CO_2 because of a decline in the abundance of chewing insects," citing the observations of Stiling *et al*. (2002) to this effect and noting that "slower rates of development under elevated CO_2 prolongs the time that insect herbivores are susceptible to natural enemies, which may be abundant in open-top chambers and FACE experiments but absent from greenhouse experiments." In addition, they suggest that "decreased foliar quality and increased per capita consumption under elevated CO_2 may increase exposure to toxins and insect mortality," also noting that "CO_2-induced changes in host plant quality directly decrease insect fecundity," citing the work of Coviella and Trumble (1999) and Awmack and Leather (2002).

So what's the bottom line with respect to the outlook for earth's forests, and especially its maple trees, in a high-CO_2 world of the future? In their concluding paragraph, Knepp *et al*. say that "By contrast to the view that herbivore damage will increase under elevated CO_2 as a result of compensatory feeding on lower quality foliage, our results and those of Stiling *et al*. (2002) and Hamilton *et al*. (2004) in open experimental systems suggest that damage to trees may decrease."

But what if herbivore-induced damage in fact increases in a future CO_2-enriched world? The likely answer is provided by the work of Kruger *et al*. (1998), who grew well-watered and fertilized one-year-old *Acer saccharum* saplings in glasshouses maintained at atmospheric CO_2 concentrations of either 356 or 645 ppm for 70 days to determine the effects of elevated CO_2 on photosynthesis and growth. In addition, on the 49th day of differential CO_2 exposure, 50 percent of the saplings' leaf area was removed from half of the trees in order to study the impact of simulated herbivory. This protocol revealed that the 70-day CO_2 enrichment treatment increased the total dry weight of the non-defoliated seedlings by about 10 percent. When the trees were stressed by simulated herbivory, however, the CO_2-enriched maples produced 28 percent more dry weight over the final phase of the study than the maples in the ambient-air treatment did. This result thus led Kruger *et al*. to conclude that in a high-CO_2 world of the future "sugar maple might be more capable of tolerating severe defoliation events which in the past have been implicated in widespread maple declines."

It appears that earth's maple trees—and probably many, if not most, other trees—will fare much better in the future with respect to the periodic assaults of leaf-damaging herbivores, as the air's CO_2 content continues its upward climb.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/h/herbivoresmaple.php.

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7.3.2.2.2. Oak

Dury *et al*. (1998) grew four-year-old *Quercus robur* seedlings in pots in greenhouses maintained at ambient and twice-ambient atmospheric CO_2 concentrations in combination with ambient and elevated (ambient plus 3°C) air temperatures for approximately one year to study the interactive effects of elevated CO_2 and temperature on leaf nutritional quality. In doing so, they found that the elevated air temperature treatment significantly reduced leaf palatability, and that leaf toughness increased as a consequence of temperature-induced increases in condensed tannin concentrations. In addition, the higher temperatures significantly reduced leaf nitrogen content, while elevated CO_2 caused a temporary increase in leaf phenolic concentrations and a decrease in leaf nitrogen content.

In one of the first attempts to move outside the laboratory/greenhouse and study the effects of atmospheric CO_2 enrichment on trophic food webs in a natural ecosystem, Stiling *et al*. (1999) enclosed portions of a native scrub-oak community in Florida (USA) within 3.6-m-diameter open-top chambers and fumigated them with air having CO_2 concentrations of either 350 or 700 ppm for approximately one year, in order to see if elevated CO_2 would impact leaf miner densities, feeding rates, and mortality in this nutrient-poor ecosystem.

Adherence to this protocol led to the finding that total leaf miner densities were 38 percent less on the foliage of trees growing in CO_2-enriched air than on the foliage of trees growing in ambient air. In addition, atmospheric CO_2 enrichment consistently reduced the absolute numbers of the study's six leaf miner species. At the same time, however, the elevated CO_2 treatment increased the leaf area consumed by the less abundant herbivore miners by approximately 40 percent relative to the areas mined by the more abundant herbivores present on the foliage exposed to ambient air; but in spite of this increase in feeding, the leaf miners in the CO_2-enriched chambers experienced significantly greater mortality than those in the ambient-air chambers. Although CO_2-induced reductions in leaf nitrogen content played a role in this phenomenon, the greatest factor contributing to increased herbivore mortality was a four-fold increase in parasitization by various wasps, which could more readily detect the more-exposed leaf miners on the CO_2-enriched foliage.

If extended to agricultural ecosystems, these findings suggest that crops may experience less damage from such herbivores in a high-CO_2 world of the future, thus increasing potential harvest and economic gains. In addition, with reduced numbers of leaf miners in CO_2-enriched air, farmers could reduce their dependency upon chemical pesticides to control them.

In another study conducted on five scrub-oak forest species at the same experimental facility, Stiling *et al*. (2003) investigated the effects of an approximate doubling of the air's CO_2 concentration on a number of characteristics of several insect herbivores. As before, they found that the "relative levels of damage by the two most common herbivore guilds, leaf-mining moths and leaf-chewers (primarily larval lepidopterans and grasshoppers), were significantly lower in elevated CO_2 than in ambient CO_2, for all five plant species," *and* they found that "the response to elevated CO_2 was the same across all plant species." In addition, they report that "more host-plant induced mortality was found for all miners on all plants in elevated CO_2 than in ambient CO_2." These effects were so powerful that in addition to the relative densities of insect herbivores being reduced in the CO_2-enriched chambers, and "even though there were more leaves of most plant species in the elevated CO_2 chambers," the total densities of leaf miners in the high-CO_2 chambers were also lower for all plant species. Consequently, it would appear that in a high-CO_2 world of the future, many of earth's plants may be able to better withstand the onslaughts of various insect pests that have plagued them in the past. Another intriguing implication of this finding, as Stiling *et al*. note, is that "reductions in herbivore loads in elevated CO_2 could boost plant growth beyond what might be expected based on pure plant responses to elevated CO_2."

Continuing to investigate the same ecosystem, which is dominated by two species of scrub oak (*Quercus geminata* and *Q. myrtifolia*) that account for more than 90 percent of the ecosystem's biomass, and focusing on the abundance of a guild of lepidopteran leafminers that attack the leaves of *Q. myrtifolia*, as well as various leaf chewers that also like to munch on this species, Rossi *et al*. (2004) followed 100 marked leaves in each of 16 open-top chambers (half exposed to ambient air and half exposed to air containing an extra 350 ppm of CO_2) for a total of nine months, after which, in their words, "differences in mean percent of leaves with leafminers and chewed leaves on trees from ambient and elevated chambers were assessed using paired *t*-tests."

In reporting their findings the researchers wrote that "both the abundance of the guild of leafmining lepidopterans and damage caused by leaf chewing insects attacking myrtle oak were depressed in elevated CO_2." Specifically, they found that leafminer abundance was 44 percent lower ($P = 0.096$) in the CO_2-enriched chambers compared to the ambient-air chambers, and that the abundance of leaves suffering chewing damage was 37 percent lower ($P = 0.072$) in the CO_2-enriched air. The implications of these findings are obvious: Myrtle oak trees growing in their natural habitat will likely suffer less damage from both leaf miners and leaf chewers as the air's CO_2 concentration continues to rise in the years and decades ahead.

Still concentrating on the same ecosystem, where atmospheric enrichment with an extra 350 ppm of CO_2 was begun in May 1996, Hall *et al*. (2005b) studied the four species that dominate the community and are present in every experimental chamber: the three oaks (*Quercus myrtifolia*, *Q. chapmanii* and *Q. geminata*) plus the nitrogen-fixing legume *Galactia elliottii*. At three-month intervals from May 2001 to May 2003, undamaged leaves were removed from each of these species in all chambers and analyzed for various chemical constituents, while 200 randomly selected leaves of each species in each chamber were scored for the presence of six types of herbivore damage.

Throughout the study there were no significant differences between the CO_2-enriched and ambient-treatment leaves of any single species in terms of either condensed tannins, hydrolyzable tannins, total phenolics, or lignin. However, in all four species together there were always greater concentrations of all four leaf constituents in the CO_2-enriched leaves, with accross-species mean increases of 6.8 percent for condensed tannins, 6.1 percent for hydrolyzable tannins, 5.1 percent for total phenolics, and 4.3 percent for lignin. In addition, there were large and often significant CO_2-induced decreases in all leaf damage categories among all species: chewing (-48 percent, $P < 0.001$), mines (-37 percent, $P = 0.001$), eye spot gall (-45 percent, $P < 0.001$), leaf tier (-52 percent, $P = 0.012$), leaf mite (-23 percent, $P = 0.477$), and leaf gall (-16 percent, $P = 0.480$). Hall *et al*. thus concluded that the changes they observed in leaf chemical constituents and herbivore damage "suggest that damage to plants may decline as atmospheric CO_2 levels continue to rise."

In one additional study to come out of the Florida scrub-oak ecosystem, Hall *et al*. (2005a) studied the effects of an extra 350 ppm of CO_2 on litter quality, herbivore activity and their interactions. Over the three years of this experiment (2000, 2001, 2002), they determined that "changes in litter chemistry from year to year were far larger than effects of CO_2 or insect damage, suggesting that these may have only minor effects on litter decomposition." The one exception to this finding, in their words, was that "condensed tannin concentrations increased under elevated CO_2 regardless of species, herbivore damage, or growing season," rising by 11 percent in 2000, 18 percent in 2001, and 41 percent in 2002 as a result of atmospheric CO_2 enrichment, as best we can determine from their bar graphs. Also, the five researchers report that "lepidopteran larvae can exhibit slower growth rates when feeding on elevated CO_2 plants (Fajer *et al*., 1991) and become more susceptible to pathogens, parasitoids, and predators (Lindroth, 1996; Stiling *et al*., 1999)," noting further that at their field site, "which hosts the longest continuous study of the effects of elevated CO_2 on insects, herbivore populations decline[d] markedly under elevated CO_2 (Stiling *et al*., 1999, 2002, 2003; Hall *et al*., 2005b)."

In conclusion, from the evidence accumulated to date with respect to herbivory in oak trees, it would appear that ever less damage will be done to such trees by various insect pests as the air's CO_2 concentration continues to climb ever higher.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/h/herbivoreswoodoak.php.

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7.3.2.2.3. Other

Stiling *et al*. (1999) enclosed portions of a Florida scrub-oak community in open-top chambers and maintained them at atmospheric CO_2 concentrations of 350 and 700 ppm for approximately one year, while they studied the effects of this treatment on destructive leaf miners. Among their many findings, the researchers noted that the individual areas consumed by leaf miners munching on leaves in the CO_2-enriched chambers were larger than those created by leaf miners dining on leaves in the ambient-air chambers. As a result, there was a *four-fold increase* in parasitization by various wasps that could more readily detect the more-exposed leaf miners on the CO_2-enriched foliage. Consequently, leaf miners in the elevated CO_2 chambers suffered significantly greater mortality than those in the control chambers.

In a subsequent and much expanded study of the same ecosystem, Stiling *et al*. (2002) investigated several characteristics of a number of insect herbivores found on the five species of plants that accounted for more than 98 percent of the total plant biomass within the chambers. As they describe their results, the "relative levels of damage by the two most common herbivore guilds, leaf-mining moths and leaf-chewers (primarily larval lepidopterans and grasshoppers), were significantly lower in elevated CO_2 than in ambient CO_2, for all five plant species."

In another study that did not involve herbivores, Gleadow *et al*. (1998) grew eucalyptus seedlings in glasshouses maintained at 400 and 800 ppm CO_2 for a period of six months, observing biomass increases of 98 percent and 134 percent in high and low nitrogen treatments, respectively. They also studied a sugar-based compound called *prunasin*, which produces cyanide in response to tissue damage caused by foraging herbivores. Although elevated CO_2 caused no significant change in leaf prunasin content, it was determined that the proportion of nitrogen allocated to prunasin increased by approximately 20 percent in the CO_2-enriched saplings, suggestive of a *potential* for increased prunasin production had the saplings been under attack by herbivores.

Lovelock *et al*. (1999) grew seedlings of the tropical tree *Copaifera aromatica* for 50 days in pots placed within open-top chambers maintained at atmospheric CO_2 concentrations of 390 and 860 ppm. At the 14-day point of the experiment, half of the seedlings in each treatment had about 40 percent of their total leaf area removed. In this case, none of the defoliated trees of either CO_2 treatment fully recovered from this manipulation, but at the end of the experiment, the total plant biomass of the defoliated trees in the CO_2-enriched treatment was 15 percent greater than that of the defoliated trees in the ambient-CO_2 treatment, again attesting to the benefits of atmospheric CO_2 enrichment in helping trees to deal with herbivory.

Docherty *et al*. (1997) grew beech and sycamore saplings in glasshouses maintained at atmospheric CO_2 concentrations of 350 and 600 ppm, while groups of three sap-feeding aphid species and two sap-feeding leafhopper species were allowed to feed on them. Overall, elevated CO_2 had few significant effects on the performance of the insects, although there was a non-significant tendency for elevated CO_2 to reduce the individual weights and population sizes of the aphids.

Finally, Hattenschwiler and Schafellner (1999) grew seven-year-old spruce (*Picea abies*) trees at atmospheric CO_2 concentrations of 280, 420, and 560 ppm and various nitrogen deposition treatments for three years, allowing nun moth larvae to feed on current-year needles for a period of 12 days. Larvae placed upon the CO_2-enriched foliage consumed less needle biomass than larvae placed upon the ambiently grown foliage, regardless of nitrogen treatment. This effect was so pronounced that the larvae feeding on needles produced by the CO_2-enriched trees attained an average final biomass that was only two-thirds of that attained by the larvae that fed on needles produced at 280 ppm CO_2. Since the nun moth is a deadly defoliator that resides in most parts of Europe and East Asia between 40° and 60°N latitude and is commonly regarded as the coniferous counterpart of its close relative the gypsy moth, which feeds primarily on deciduous trees, the results of this study suggest that the ongoing rise in the air's CO_2 content will likely lead to significant reductions in damage to spruce and other coniferous trees by this voracious insect pest in the years and decades ahead.

In light of these several observations, the balance of evidence seems to suggest that earth's woody plants will be better able to deal with the challenges provided by herbivorus insects as the air's CO_2 content continues to rise.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/h/herbivoreswoodyplants.php.

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7.3.3. Insects

As the atmosphere's CO_2 concentration climbs ever higher, it is important to determine how this phenomenon will affect the delicate balance that exists between earth's plants and the insects that feed on them. In this section we thus review what has been learned about this subject with respect to aphids, moths, and other insects.

Additional information on this topic, including reviews on insects not discussed here, can be found at http://www.co2science.org/subject/i/subject_i.php under the heading Insects.

7.3.3.1. Aphids

Docherty *et al*. (1997) grew beech and sycamore saplings in glasshouses maintained at atmospheric CO_2 concentrations of 350 and 600 ppm, while groups of three sap-feeding aphid species were allowed to feed on the saplings. Overall, the elevated CO_2 had few significant effects on aphid feeding and performance. There was, however, a non-significant tendency for elevated CO_2 to reduce the individual weights and population sizes of the aphids, suggesting that future increases in the air's CO_2 content *might* reduce aphid feeding pressures on beech and sycamore saplings, and possibly other plants as well.

Whittaker (1999) reviewed the scientific literature dealing with population responses of herbivorous insects to atmospheric CO_2 enrichment, concentrating on papers resulting from relatively long-term studies. Based on all pertinent research reports available at that time, the only herbivorous insects that exhibited population increases in response to elevated CO_2 exposure were those classified as phloem feeders, specifically, aphids. Although this finding appeared to favor aphids over plants, additional studies would complicate the issue and swing the pendulum back the other way.

Newman *et al*. (1999) grew tall fescue plants for two weeks in open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm before inoculating them with aphids (*Rhopalosiphum padi*). After nine additional weeks of differential CO_2 exposure, the plants were harvested and their associated aphids counted. Although elevated CO_2 increased plant dry matter production by 37 percent, the plants grown in air of elevated CO_2 concentration contained fewer aphids than the plants grown in ambient air.

Percy *et al*. (2002) grew the most widely distributed tree species in all of North America—trembling aspen—in twelve 30-m-diameter FACE rings in air maintained at (1) ambient CO_2 and O_3 concentrations, (2) ambient O_3 and elevated CO_2 (560 ppm during daylight hours), (3) ambient CO_2 and elevated O_3 (46.4-55.5 ppb during daylight hours), and (4) elevated CO_2 and O_3 over each growing season from 1998 through 2001. Throughout their experiment they assessed a number of the young trees' growth characteristics, as well as the responses of the sap-feeding aphid *Chaitophorus stevensis*, which they say "infests aspen throughout its range." This experiment revealed that, by itself, elevated CO_2 did not affect aphid abundance, but it increased the densities of natural enemies of the aphids, which over the long term would tend to reduce aphid numbers. Also, by itself, elevated O_3 did not affect aphid abundance, but it had a strong negative effect on natural enemies of aphids, which over the long term would tend to increase aphid numbers. When both trace gases were applied together, elevated CO_2 *completely counteracted* the reduction in the abundance of natural enemies of aphids caused by elevated O_3. Hence, elevated CO_2 tended to reduce the negative impact of aphids on trembling aspen in this comprehensive study.

At about the same time, Holopainen (2002) reviewed the scientific literature dealing with the joint effects of elevated concentrations of atmospheric O_3 and CO_2 on aphid-plant interactions. After compiling the results of 26 pertinent studies, it was found that atmospheric CO_2 enrichment increased aphid performance in six studies, decreased it in six studies, and had no significant impact on it in the remaining 14 studies. Similar results were found for aphid-plant interactions in the presence of elevated O_3 concentrations.

Newman (2003) reviewed what was known and not known about aphid responses to concurrent increases in atmospheric CO_2 and air temperature, while also investigating the subject via the aphid population model of Newman *et al.* (2003). This literature review and model analysis led him to conclude that when the air's CO_2 concentration and temperature are both elevated, "aphid population dynamics will be more similar to current ambient conditions than expected from the results of experiments studying either factor alone." We can draw only the general conclusion, according to Newman, that "insect responses to CO_2 are *unlikely* to all be in the same direction." Nevertheless, he says that "the lack of a simple common phenomenon does not deny that there is some overriding generality in the responses by the system." It's just that we did not at that time know what that overriding generality was, which is why experimental work on the subject has continued apace.

Concentrating on thermal effects alone, Ma *et al.* (2004) conducted detailed experiments on the effects of high temperature, period of exposure, and developmental stage on the survival of the aphid *Metopolophium dirhodum*, which they say "is the most abundant of the three cereal aphid species in Germany and central European countries." This protocol revealed, in their words, that "temperatures over 29°C for 8 hours significantly reduced survival, which decreased generally as the temperature increased." They also determined that "exposing aphids to 32.5°C for 4 hours or longer significantly reduced survival," and that "mature aphids had a lower tolerance of high temperatures than nymphs." In light of what they observed, therefore, as well as what a number of other scientists had observed, Ma *et al.* concluded that "global warming may play a role in the long-term changes in the population abundance of *M. dirhodum*." Specifically, they say that "an increase in TX [daily average temperature] of 1°C and MaxT [maximum daily temperature] of 1.3°C during the main period of the aphid population increase would result in a 33 percent reduction in peak population size," while "an increase in TX of 2°C and MaxT of 2.6°C would result in an early population collapse (74 percent reduction of population size)." It would appear that a little global warming could greatly decrease aphid infestations of cereal crops grown throughout Germany and Central Europe.

Returning to the subject of joint CO_2 and O_3 effects on aphids, Awmack *et al.* (2004) conducted a two-year study at the Aspen FACE site near Rhinelander, Wisconsin, USA, of the individual and combined effects of elevated CO_2 (+200 ppm) and O_3 (1.5 x ambient) on the performance of *Cepegillettea betulaefoliae* aphids feeding on paper birch trees in what they call "the first investigation of the long-term effects of elevated CO_2 and O_3 atmospheres on natural insect herbivore populations." At the individual scale, they report that "elevated CO_2 and O_3 did not significantly affect [aphid] growth rates, potential fecundity (embryo number) or offspring quality." At the population scale, on the other hand, they found that "elevated O_3 had a strong positive effect," but that "elevated CO_2 did not significantly affect aphid populations."

In comparing their results with those of prior related studies, the three scientists report that "the responses of other aphid species to elevated CO_2 or O_3 are also complex." In particular, they note that "tree-feeding aphids show few significant responses to elevated CO_2 (Docherty *et al.*, 1997), while crop-feeding species may respond positively (Awmack *et al.*, 1997; Bezemer *et al.*, 1998; Hughes and Bazzaz, 2001; Zhang *et al.*, 2001; Stacey and Fellowes, 2002), negatively (Newman *et al.*, 1999), or not at all (Hughes and Bazzaz, 2001), and the same species may show different responses on different host plant species (Awmack *et al.*, 1997; Bezemer *et al.*, 1999)." In summarizing their observations, they stated that "aphid individual performance did not predict population responses to CO_2 and O_3," and they concluded that "elevated CO_2 and O_3 atmospheres are unlikely to affect *C. betulaefoliae* populations in the presence of natural enemy communities."

In a study of a different aphid (*Chaitophorus stevensis*) conducted at the same FACE site, Mondor *et al*. (2004) focused on the subject of pheromones, which they say "are utilized by insects for several purposes, including alarm signaling," and which in the case of phloem-feeding aphids induces high-density groups of them on exposed leaves of trembling aspen trees to disperse and move to areas of lower predation risk. In this experiment the four treatments were: control (367 ppm CO_2, 38 ppb O_3), elevated CO_2 (537 ppm), elevated O_3 (51 ppb), and elevated CO_2 and O_3 (537 ppm CO_2, 51 ppb O_3). Within each treatment, several aspen leaves containing a single aphid colony of 25 ± 2 individuals were treated in one of two different ways: (1) an aphid was prodded lightly on the thorax so as to *not* produce a visible pheromone droplet, or (2) an aphid was prodded more heavily on the thorax and induced to emit a visible pheromone droplet, after which, in the words of the scientists, "aphids exhibiting any dispersal reactions in response to pheromone emission as well as those exhibiting the most extreme dispersal response, walking down the petiole and off the leaf, were recorded over 5 min."

Mondor *et al*.'s observations were striking. They found that the aphids they studied "have diminished escape responses in enriched carbon dioxide environments, while those in enriched ozone have augmented escape responses, to alarm pheromone." In fact, they report that "0 percent of adults dispersed from the leaf under elevated CO_2, while 100 percent dispersed under elevated O_3," indicating that the effects of elevated CO_2 and elevated O_3 on aphid response to pheromone alarm signaling are diametrically opposed to each other, with elevated O3 (which is detrimental to vegetation) helping aphids to escape predation and therefore live to do further harm to the leaves they infest, but with elevated CO_2 (which is beneficial to vegetation) making it more difficult for aphids to escape predation and thereby providing yet an additional benefit to plant foliage. Within this context, therefore, ozone may be seen to be doubly bad for plants, while carbon dioxide may be seen to be doubly good. In addition, Mondor *et al*. state that this phenomenon may be of broader scope than what is revealed by their specific study, noting that other reports suggest that "parasitoids and predators are more abundant and/or efficacious under elevated CO_2 levels (Stiling *et al*., 1999; Percy *et al*., 2002), but are negatively affected by elevated O_3 (Gate *et al*., 1995; Percy *et al*., 2002)."

In another intriguing study, Chen *et al*. (2004) grew spring wheat from seed to maturity in high-fertility well-watered pots out-of-doors in open-top chambers (OTCs) maintained at atmospheric CO_2 concentrations of 370, 550, and 750 ppm. Approximately two months after seeding, 20 apterous adult aphids (*Sitobion avenae*) from an adjacent field were placed upon the wheat plants of each of 25 pots in each OTC, while 15 pots were left as controls; and at subsequent 5-day intervals, both apterous and alate aphids were counted. Then, about one month later, 10 alate morph fourth instar nymphs were introduced onto the plants of each of nine control pots; for the next two weeks the number of offspring laid on those plants were recorded and removed daily to measure reproductive activity. At the end of the study, the wheat plants were harvested and their various growth responses determined.

Adherence to these protocols revealed that the introduced aphid populations increased after infestation, peaked during the grain-filling stage, and declined a bit as the wheat matured. On the final day of measurement, aphids in the 550-ppm CO_2 treatment were 32 percent more numerous than those in ambient air, while aphids in the 750-ppm treatment were 50 percent more numerous. Alate aphids also produced more offspring on host plants grown in elevated CO_2: 13 percent more in the 550-ppm treatment and 19 percent more in the 750-ppm treatment. As for the wheat plants, Chen *et al*. report that "elevated CO_2 generally enhanced plant height, aboveground biomass, ear length, and number of and dry weight of grains per ear, consistent with most other studies." With respect to above-ground biomass, for example, the 550-ppm treatment displayed an increase of 36 percent, while the 750-ppm treatment displayed an increase of 50 percent, in the case of both aphid-infested and non-infested plants.

In commenting on their findings, Chen *et al*. report that "aphid infestation caused negative effects on all the plant traits measured ... but the negative effects were smaller than the positive effects of elevated CO_2 on the plant traits." Hence, they concluded that "the increased productivity occurring in plants exposed to higher levels of CO_2 more than compensate for the increased capacity of the aphids to cause damage." In this experiment, therefore, we have a situation where both the plant and the insect that feeds on it were simultaneously benefited by the applied increases in atmospheric CO_2 concentration.

Last, in a study that investigated a number of plant-aphid-predator relationships, Chen *et al*. (2005) grew transgenic cotton plants for 30 days in well watered and fertilized sand/vermiculite mixtures in pots set in controlled-environment chambers maintained at atmospheric CO_2 concentrations of 370, 700, and 1050 ppm. A subset of aphid-infected plants was additionally supplied with predatory ladybugs, while three generations of cotton aphids (*Aphis gossypii*) were subsequently allowed to feed on some of the plants. Based on measurements made throughout this complex set of operations, Chen *et al*. found that (1) "plant height, biomass, leaf area, and carbon:nitrogen ratios were significantly higher in plants exposed to elevated CO_2 levels," (2) "more dry matter and fat content and less soluble protein were found in *A. gossypii* in elevated CO_2," (3) "cotton aphid fecundity significantly increased ... through successive generations reared on plants grown under elevated CO_2," (4) "significantly higher mean relative growth rates were observed in lady beetle larvae under elevated CO_2," and (5) "the larval and pupal durations of the lady beetle were significantly shorter and [their] consumption rates increased when fed *A. gossypii* from elevated CO_2 treatments." In commenting on the significance of their findings, Chen *et al*. say their study "provides the first empirical evidence that changes in prey quality mediated by elevated CO_2 can alter the prey preference of their natural enemies," and in this particular case, they found that this phenomenon could "enhance the biological control of aphids by lady beetle."

In considering the totality of these many experimental findings, it would appear that the ongoing rise in the air's CO_2 content will likely not have a major impact, one way or the other, on aphid-plant interactions, although the scales do appear to be slightly tipped in favor of plants over aphids. Yet a third possibility is that both plants and aphids will be benefited by atmospheric CO_2 enrichment, but with plants benefiting more.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/i/insectsaphids.php.

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7.3.3.2. Butterflies

How will earth's butterflies respond to atmospheric CO_2 enrichment and global warming? We here explore what has been learned about the question over the past few years, beginning with a review of studies that focus on carbon dioxide and concluding with studies that focus on temperature.

In a study of *Lotus corniculatus* (a cyanogenic plant that produces foliar cyanoglycosides to deter against herbivory by insects) and the Common Blue Butterfly (*Polyommatus icarus*, which regularly feeds upon *L. corniculatus* because it possesses an enzyme that detoxifies cyanide-containing defensive compounds), Goverde *et al.* (1999) collected four genotypes of *L. corniculatus* differing in their concentrations of cyanoglycosides and tannins (another group of defensive compounds) near Paris, France. They then grew them in controlled-environment chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm, after which they determined the effects of the doubled CO_2 concentration on leaf quality and allowed the larvae of the Common Blue Butterfly to feed upon the plants' leaves. This work revealed that elevated CO_2 significantly increased leaf tannin and starch contents in a genotypically dependent and -independent manner, respectively, while decreasing leaf cyanoglycoside contents independent of genotype. These CO_2-induced changes in leaf chemistry increased leaf palatability, as indicated by greater dry weight consumption of CO_2-enriched leaves by butterfly larvae. In addition, the increased consumption of CO_2-enriched leaves led to greater larval biomass and shorter larval development times, positively influencing the larvae of the Common Blue Butterfly. Hence, it is not surprising that larval mortality was lower when feeding upon CO_2-enriched as opposed to ambiently grown leaves.

Goverde *et al.* (2004) grew *L. corniculatus* plants once again, this time from seed in tubes recessed into the ground under natural conditions in a nutrient-poor calcareous grassland, where an extra 232 ppm of CO_2 was supplied to them via a Screen-Aided CO_2 Control (SACC) system (Leadley *et al.*, 1997, 1999), and where insect larvae were allowed to feed on the plants (half of which received extra phosphorus fertilizer) for the final month of the experiment. The atmospheric CO_2 enrichment employed in this experiment increased the total dry weight of plants growing on the unfertilized soil by 21.5 percent and that of plants growing on the phosphorus-enriched soil by 36.3 percent. However, the elevated CO_2 treatment had no effect on pupal and adult insect mass, although Goverde *et al.* report there were "genotype-specific responses in the development time of *P. icarus* to elevated CO_2 conditions," with larvae originating from different mothers developing better under either elevated CO_2 or ambient CO_2, while for still others the air's CO_2 concentration had no effect on development.

In another study by some of the same researchers, Goverde *et al.* (2002) raised larvae of the satyrid butterfly (*Coenonympha pamphilus*) in semi-natural undisturbed calcareous grassland plots exposed to atmospheric CO_2 concentrations of 370 and 600 ppm for five growing seasons. In doing so, they found that the elevated CO_2 concentration increased foliar concentrations of total nonstructural carbohydrates and condensed tannins in the grassland plants; but in what is often considered a negative impact, they found that it also decreased foliar nitrogen concentrations. Nevertheless, this phenomenon had no discernible effect on butterfly growth and performance. Larval development time, for example, was not affected by elevated CO_2, nor was adult dry mass. In fact, the elevated CO_2 increased lipid concentrations in adult male butterflies by nearly 14 percent, while it marginally increased the number of eggs in female butterflies. The former of these responses is especially important, because lipids are used as energy resources in these and other butterflies, while increased egg numbers in females also suggests an increase in fitness.

Turning to the study of temperature effects on butterflies, Parmesan *et al*. (1999) analyzed distributional changes over the past century of non-migratory species whose northern boundaries were in northern Europe (52 species) and whose southern boundaries were in southern Europe or northern Africa (40 species). This work revealed that the northern boundaries of the first group shifted northward for 65 percent of them, remained stable for 34 percent, and shifted southward for 2 percent, while the southern boundaries of the second group shifted northward for 22 percent of them, remained stable for 72 percent, and shifted southward for 5 percent, such that "nearly all northward shifts involved extensions at the northern boundary with the southern boundary remaining stable."

This behavior is precisely what we would expect to see if the butterflies were responding to shifts in the ranges of the plants upon which they depend for their sustenance, because increases in atmospheric CO_2 concentration tend to ameliorate the effects of heat stress in plants and induce an upward shift in the temperature at which they function optimally. These phenomena tend to cancel the impetus for poleward migration at the warm edge of a plant's territorial range, yet they continue to provide the opportunity for poleward expansion at the cold edge of its range. Hence, it is possible that the observed changes in butterfly ranges over the past century of concomitant warming and rising atmospheric CO_2 concentration are related to matching changes in the ranges of the plants upon which they feed. Or, this similarity could be due to some more complex phenomenon, possibly even some direct physiological effect of temperature and atmospheric CO_2 concentration on the butterflies themselves.

In any event, and in the face of the 0.8°C of global warming that occurred in Europe over the twentieth century, the consequences for European butterflies were primarily beneficial because, as Parmesan *et al*. describe the situation, "most species effectively expanded the size of their range when shifting northwards," since "nearly all northward shifts involved extensions at the northern boundary with the southern boundary remaining stable."

Across the Atlantic in America, Fleishman *et al*. (2001) used comprehensive data on butterfly distributions from six mountain ranges in the U.S. Great Basin to study how butterfly assemblages of that region may respond to IPCC-projected climate change. Whereas prior, more-simplistic analyses have routinely predicted the extirpation of great percentages of the butterfly species in this region in response to model-predicted increases in air temperature, Fleishman *et al*.'s study revealed that "few if any species of montane butterflies are likely to be extirpated from the entire Great Basin (i.e., lost from the region as a whole)."

In further discussing their results, the three researchers note that "during the Middle Holocene, approximately 8000-5000 years ago, temperatures in the Great Basin were several degrees warmer than today." Thus, they go on say that "we might expect that most of the montane species—including butterflies—that currently inhabit the Great Basin would be able to tolerate the magnitude of climatic warming forecast over the next several centuries." Consequently, it would appear that even if the global warming projections of the IPCC were true, the predictions of butterfly extinctions associated with those projections are almost certainly false.

Returning to the British Isles, Thomas *et al*. (2001) documented an unusually rapid expansion of the ranges of two butterfly species (the silver-spotted skipper butterfly and the brown argus butterfly) along with two cricket species (the long-winged cone-head and Roesel's bush cricket). They write that the warming-induced "increased habitat breadth and dispersal tendencies have resulted in about 3- to 15-fold increases in expansion rates."

In commenting on these findings, Pimm (2001) truly states the obvious when he says the geographical ranges of these insects are "expanding faster than expected," and that the synergies involved in the many intricacies of the range expansion processes are also "unexpected."

Crozier (2004) writes that "*Atalopedes campestris*, the sachem skipper butterfly, expanded its range from northern California into western Oregon in 1967, and into southwestern Washington in 1990," where she reports that temperatures rose by 2-4°C over the prior half-century. Thus intrigued, and in an attempt to assess the importance of this regional warming for the persistence of *A. campestris* in the recently colonized areas, Crozier "compared population dynamics at two locations (the butterfly's current range edge and just inside the range) that differ by 2-3°C." Then, to determine the role of over-winter larval survivorship, she "transplanted larvae over winter to both sites."

This work revealed, in her words, that "combined results from population and larval transplant analyses indicate that winter temperatures directly affect the persistence of *A. campestris* at its northern range edge, and that winter warming was a prerequisite for this butterfly's range expansion." Noting that "populations are more likely to go extinct in colder climates," Crozier says "the good news about rapid climate change [of the warming type] is that new areas may be available for the introduction of endangered species." Her work also demonstrates that the species she studied has responded to regional warming by extending its northern range boundary and thereby expanding its range.

Two years later, Davies *et al*. (2006) introduced their study of the silver-spotted skipper butterfly (*Hesperia comma* L.) by noting that during the twentieth century it "became increasingly rare in Britain [as] a result of the widespread reduction of sparse, short-turfed calcareous grassland containing the species' sole larval host plant, sheep's fescue grass [*Festuca ovina* L]." As a result, they describe the "refuge" colonies of 1982 as but a "remnant" of what once had been. The four researchers analyzed population density data together with estimates of the percentage bare ground and the percentage of sheep's fescue available to the butterflies, based on surveys conducted in Surrey in the chalk hills of the North Downs, south of London, in *1982* (Thomas *et al*., 1986), *1991* (Thomas and Jones, 1993), *2000* (Thomas *et al*., 2001; Davies *et al*., 2005), and *2001* (R.J. Wilson, unpublished data). In addition, they assessed egg-laying rates in different microhabitats, as well as the effects of ambient and oviposition site temperatures on egg laying, and the effects of sward composition on egg location. This work revealed, in their words, that "in 1982, 45 habitat patches were occupied by *H. comma* [but] in the subsequent 18-year period, the species expanded and, by 2000, a further 29 patches were colonized within the habitat network." In addition, they found that "the mean egg-laying rate of *H. comma* females increased with rising ambient temperatures," and that "a wider range of conditions have become available for egg-laying."

In discussing their findings, Davies *et al*. state that "climate warming has been an important driving force in the recovery of *H. comma* in Britain [as] the rise in ambient temperature experienced by the butterfly will have aided the metapopulation re-expansion in a number of ways." First, they suggest that "greater temperatures should increase the potential fecundity of *H. comma* females," and that "if this results in larger populations, for which there is some evidence (e.g. 32 of the 45 habitat patches occupied in the Surrey network experienced site-level increases in population density between 1982 and 2000), they will be less prone to extinction," with "larger numbers of dispersing migrant individuals being available to colonize unoccupied habitat patches and establish new populations." Second, they state that "the wider range of thermal and physical microhabitats used for egg-laying increased the potential resource density within each grassland habitat fragment," and that "this may increase local population sizes." Third, they argue that "colonization rates are likely to be greater as a result of the broadening of the species realized niche, [because] as a larger proportion of the calcareous grassland within the species' distribution becomes thermally suitable, the relative size and connectivity of habitat patches within the landscape increases." Fourth, they note that "higher temperatures may directly increase flight (dispersal) capacity, and the greater fecundity of immigrants may improve the likelihood of successful population establishment." Consequently, Davies *et al*. conclude that "the warmer summers predicted as a consequence of climate warming are likely to be beneficial to *H. comma* within Britain," and they suggest that "warmer winter temperatures could also allow survival in a wider range of microhabitats."

In a concurrent study, Menendez *et al*. (2006) provided what they call "the first assessment, at a geographical scale, of how species richness has changed in response to climate change," concentrating on British butterflies. This they did by testing "whether average species richness of resident British butterfly species has increased in recent decades, whether these changes are as great as would be expected given the amount of warming that has taken place, and whether the composition of butterfly communities is changing towards a dominance by generalist species." By these means they determined that "average species richness of the British butterfly fauna at 20 x 20 km grid resolution has increased since 1970-82, during a period when climate warming would lead us to expect increases." They also found, as expected, that "southerly habitat generalists increased more than specialists," which require a specific type of habitat that is sometimes difficult for them to find, especially in the modern world where habitat destruction is commonplace. In addition, they were able to determine that observed species richness increases lagged behind those expected on the basis of climate change.

These results "confirm," according to the nine UK researchers, "that the average species richness of British butterflies has increased since 1970-82." However, some of the range shifts responsible for the increase in species richness take more time to occur than those of other species; they say their results imply "it may be decades or centuries before the species richness and composition of biological communities adjusts to the current climate."

Also working in Britain, Hughes *et al*. (2007) examined evolutionary changes in adult flight morphology in six populations of the speckled wood butterfly—*Pararge aegeria* L. (Satyrinae)—along a transect from its distribution core to its warming-induced northward expanding range margin. The results of this exercise were then compared with the output of an individual-based spatially explicit model that was developed "to investigate impacts of habitat availability on the evolution of dispersal in expanding populations." This work indicated that the empirical data the researchers gathered "were in agreement with model output," and that they "showed increased dispersal ability with increasing distance from the distribution core," which included favorable changes in thorax shape, abdomen mass, and wing aspect ratio for both males and females, as well as thorax mass and wing loading for females. In addition, they say that "increased dispersal ability was evident in populations from areas colonized >30 years previously."

In discussing their findings, Hughes *et al*. suggest that "evolutionary increases in dispersal ability in expanding populations may help species track future climate changes and counteract impacts of habitat fragmentation by promoting colonization." However, they report that in the specific situation they investigated, "at the highest levels of habitat loss, increased dispersal was less evident during expansion and reduced dispersal was observed at equilibrium, indicating that for many species, continued habitat fragmentation is likely to outweigh any benefits from dispersal." Put another way, it would appear that global warming is proving not to be an insurmountable problem for the speckled wood butterfly, which is evolving physical characteristics that allow it to better keep up with the poleward migration of its current environmental niche, but that the direct destructive assaults of humanity upon its natural habitat could still end up driving it to extinction.

Analyzing data pertaining to the general abundance of Lepidoptera in Britain over the period 1864-1952, based on information assembled by Beirne (1955) via his examination of "several thousand papers in entomological journals describing annual abundances of moths and butterflies," were Dennis and Sparks (2007), who report that "abundances of British Lepidoptera were significantly positively correlated with Central England temperatures in the current year for each month from May to September and November," and that "increased overall abundance in Lepidoptera coincided significantly with increased numbers of migrants," which latter data were derived from the work of Williams (1965). In addition, they report that Pollard (1988) subsequently found much the same thing for 31 butterfly species over the period 1976-1986, and that Roy *et al*. (2001) extended the latter investigation to 1997, finding "strong associations between weather and population fluctuations and trends in 28 of 31 species which confirmed Pollard's (1988) findings," all of which observations indicate that the warming-driven increase in Lepidopteran species and numbers in Britain has been an ongoing phenomenon ever since the end of the Little Ice Age.

Returning to North America for one final study, White and Kerr (2006), as they describe it, "report butterfly species' range shifts across Canada between 1900 and 1990 and develop spatially explicit tests of the degree to which observed shifts result from climate or human population density," the latter of which factors they describe as "a reasonable proxy for land use change," within which broad category they include such things as "habitat loss, pesticide use, and habitat fragmentation," all of which anthropogenic-driven factors have been tied to declines of various butterfly species. In addition, they say that to their knowledge, "this is the broadest scale, longest term dataset yet assembled to quantify global change impacts on patterns of species richness."

This exercise led White and Kerr to discover that butterfly species richness "generally increased over the study period, a result of range expansion among the study species," and they further found that this increase "from the early to late part of the twentieth century was positively correlated with temperature change," which had to have been the *cause* of the change, for they also found that species richness was "negatively correlated with human population density change."

Contrary to the doom-and-gloom prognostications of some experts, the supposedly unprecedented global warming of the twentieth century has been beneficial for the butterfly species that inhabit Canada, Britain, and the United States, as their ranges have expanded and greater numbers of species are now being encountered in each country.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/i/summaries/butterflies.php.

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7.3.3.3. Moths

Kerslake *et al*. (1998) collected five-year-old heather plants from a Scottish moor and grew them in open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 600 ppm for 20 months, with and without soil nitrogen fertilization. At two different times during the study, larvae of *Operophtera brumata*, a voracious winter moth whose outbreaks have caused extensive damage to heather moorland in recent years, were allowed to feed upon current-year shoots for up to one month. The results obtained from this experiment revealed that the survivorship of larvae placed on CO_2-enriched foliage was not significantly different from that of larvae placed on foliage produced in ambient air, regardless of nitrogen treatment. In addition, feeding upon CO_2-enriched foliage did not affect larval growth rate, development, or final pupal weight. Consequently, Kerslake *et al*. concluded that their study "provides no evidence that increasing atmospheric CO_2 concentrations will affect the potential for outbreak of *Operophtera brumata* on this host."

Hattenschwiler and Schafellner (1999) grew seven-year-old spruce trees at atmospheric CO_2 concentrations of 280, 420, and 560 ppm in various nitrogen deposition treatments for three years, after which they performed needle quality assessments and allowed nun moth (*Lymantria monacha*) larvae to feed upon current-year needles for 12 days. This moth is an especially voracious defoliator that resides in most parts of Europe and East Asia between 40 and 60° N latitude, and it is commonly regarded as the "coniferous counterpart" of its close relative the gypsy moth, which feeds primarily upon deciduous trees.

The two scientists determined from their observations that elevated CO_2 significantly enhanced needle starch, tannin, and phenolic concentrations, while significantly decreasing needle water and nitrogen contents. Thus, atmospheric CO_2 enrichment reduced overall needle quality from the perspective of this foliage-consuming moth, as nitrogen content is the primary factor associated with leaf quality. Increasing nitrogen deposition, on the other hand, tended to enhance needle quality, for it lowered starch, tannin, and phenolic concentrations while boosting needle nitrogen content. Nevertheless, the positive influence of nitrogen deposition on needle quality was not large enough to completely offset the quality reduction caused by elevated CO_2.

In light of these observations, it was no surprise that larvae placed on CO_2-enriched foliage consumed less needle biomass than larvae placed on low-CO_2-grown foliage, regardless of nitrogen treatment, and that the larvae feeding on CO_2-enriched foliage exhibited reduced relative growth rates and attained an average biomass that was only two-thirds of that attained by larvae consuming foliage produced at 280 ppm CO_2. As a result, Hattenschwiler and Schafellner concluded that "altered needle quality in response to elevated CO_2 will impair the growth and development of *Lymantria monacha* larvae," which should lead to reductions in the degree of spruce tree destruction caused by this voracious defoliator.

Stiling *et al*. (2002) studied the effects of an approximate doubling of the air's CO_2 concentration on a number of characteristics of several insect herbivores feeding on plants native to a scrub-oak forest ecosystem at the Kennedy Space Center, Florida, USA, in eight ambient and eight CO_2-enriched open-top chambers. They say that the "relative levels of damage by the two most common herbivore guilds, leaf-mining moths and leaf-chewers (primarily larval lepidopterans and grasshoppers), were significantly lower in elevated CO_2 than in ambient CO_2," and that "the response to elevated CO_2 was the same across all plant species."

In a follow-up study to that of Stiling *et al*., which was conducted at the same facilities, Rossi *et al*. (2004), focused on the abundance of a guild of lepidopteran leafminers that attack the leaves of myrtle oak, as well as various leaf chewers that also like to munch on this species. Specifically, they periodically examined 100 marked leaves in each of the 16 open-top chambers for a total of nine months, after which, in their words, "differences in mean percent of leaves with leafminers and chewed leaves on trees from ambient and elevated chambers were assessed using paired *t*-tests." This protocol revealed, in their words, that "both the abundance of the guild of leafmining lepidopterans and damage caused by leaf chewing insects attacking myrtle oak were depressed in elevated CO_2." Leafminer abundance was 44 percent lower ($P = 0.096$) in the CO_2-enriched chambers compared to the ambient-air chambers, while the abundance of leaves suffering chewing damage was 37 percent lower ($P = 0.072$) in the CO_2-enriched air.

Working with red maple saplings, Williams *et al*. (2003) bagged first instar gypsy moth larvae on branches of trees that were entering their fourth year of growth within open-top chambers maintained at four sets of CO_2/temperature conditions: (1) ambient temperature, ambient CO_2, (2) ambient temperature, elevated CO_2 (ambient + 300 ppm), (3) elevated temperature (ambient + 3.5°C), ambient CO_2, and (4) elevated temperature, elevated CO_2. For these conditions they measured several parameters that were required to test their hypothesis that a CO_2-enriched atmosphere would lead to reductions in foliar nitrogen concentrations and increases in defensive phenolics that would in turn lead to increases in insect mortality. The results they obtained indicated, in their words, "that larvae feeding on CO_2-enriched foliage ate a comparably poorer food source than those feeding on ambient CO_2-grown plants, irrespective of temperature." Nevertheless, they determined that "CO_2-induced reductions in foliage quality were unrelated to insect mortality, development rate and pupal weight." As a result, they were forced to conclude that "phytochemical changes resulted in no negative effects on gypsy moth performance," but neither did they help them.

Noting that increases in the atmosphere's CO_2 concentration typically lead to greater decreases in the concentrations of nitrogen in the foliage of C_3 as opposed to C_4 grasses, Barbehenn *et al.* (2004) say "it has been predicted that insect herbivores will increase their feeding damage on C_3 plants to a greater extent than on C_4 plants (Lincoln *et al.*, 1984, 1986; Lambers, 1993). To test this hypothesis, they grew *Lolium multiflorum* (Italian ryegrass, a common C_3 pasture grass) and *Bouteloua curtipendula* (sideoats gramma, a native C_4 rangeland grass) in chambers maintained at either the ambient atmospheric CO_2 concentration of 370 ppm or the doubled CO_2 concentration of 740 ppm for two months, after which newly molted sixth-instar larvae of *Pseudaletia unipuncta* (a grass-specialist noctuid) and *Spodoptera frugiperda* (a generalist noctuid) were allowed to feed upon the two grasses.

As expected, Barbehenn *et al.* found that foliage protein concentration decreased by 20 percent in the C_3 grass, but by only 1 percent in the C_4 grass, when they were grown in CO_2-enriched air; and they say that "to the extent that protein is the most limiting of the macronutrients examined, these changes represent a decline in the nutritional quality of the C_3 grass." However, and "contrary to our expectations," in the words of Barbehenn *et al.*, "neither caterpillar species significantly increased its consumption rate to compensate for the lower concentration of protein in [the] C_3 grass," and they note that "this result does not support the hypothesis that C_3 plants will be subject to greater rates of herbivory relative to C_4 plants in future [high-CO_2] atmospheric conditions (Lincoln *et al.*, 1984)." In addition, and "despite significant changes in the nutritional quality of *L. multiflorum* under elevated CO_2," they note that "no effect on the relative growth rate of either caterpillar species on either grass species resulted," and that there were "no significant differences in insect performance between CO_2 levels." By way of explanation of these results, they suggest that "post-ingestive mechanisms could provide a sufficient means of compensation for the lower nutritional quality of C_3 plants grown under elevated CO_2."

In light of these observations, Barbehenn *et al.* suggest "there will not be a single pattern that characterizes all grass feeders" with respect to their feeding preferences and developmental responses in a world where certain C_3 plants may experience foliar protein concentrations that are lower than those they exhibit today, nor will the various changes that may occur necessarily be detrimental to herbivore development or to the health and vigor of their host plants. Nevertheless, subsequent studies continue to suggest that various moth species will likely be negatively affected by the ongoing rise in the air's CO_2 content.

A case in point is the study of Chen *et al.* (2005), who grew well watered and fertilized cotton plants of two varieties (one expressing *Bacillus thurigiensis* toxin genes and one a non-transgenic cultivar from the same recurrent parent) in pots placed within open-top chambers maintained at either 376 or 754 ppm CO_2 in Sanhe County, Hebei Province, China, from planting in mid-May to harvest in October, while immature bolls were periodically collected and analyzed for various chemical characteristics and others were stored under refrigerated conditions for later feeding to larvae of the cotton bollworm. By these means they found that the elevated CO_2 treatment increased immature boll concentrations of condensed tannins by approximately 22 percent and 26 percent in transgenic and non-transgenetic cotton, respectively, and that it slightly decreased the body biomass of the cotton bollworm and reduced moth fecundity. The Bt treatment was even more effective in this regard; and in the combined Bt-high-CO_2 treatment, the negative cotton bollworm responses were expressed most strongly of all.

Bidart-Bouzat *et al.* (2005) grew three genotypes of mouse-ear cress (*Arabidopsis thaliana*) from seed in pots within controlled-environment chambers maintained at either ambient CO_2 (360 ppm) or elevated CO_2 (720 ppm). On each of half of the plants (the herbivory treatment) in each of these CO_2 treatments, they placed two second-instar larvae of the diamondback moth (*Plutella xylostella*) at bolting time and removed them at pupation, which resulted in an average of 20 percent of each plant's total leaf area in the herbivory treatment being removed. Then, each pupa was placed in a gelatin capsule until adult emergence and ultimate death, after which insect gender was determined and the pupa's weight recorded. At the end of this herbivory trial, the leaves of the control and larvae-infested plants were analyzed for concentrations of individual glucosinolates—a group of plant-derived chemicals that can act as herbivore deterrents (Maruicio and Rausher, 1997)—while total glucosinolate production was determined by summation of the individual glucosinolate assays. Last, influences of elevated CO_2 on moth performance and its association with plant defense-related traits were evaluated.

Overall, it was determined by these means that herbivory by larvae of the diamondback moth did not induce any increase in the production of glucosinolates in the mouse-ear cress in the ambient CO_2 treatment. However, the three scientists report that "herbivory-induced increases in glucosinolate contents, ranging from 28% to 62% above basal levels, were found under elevated CO_2 in two out of the three genotypes studied." In addition, they determined that "elevated CO_2 decreased the overall performance of diamondback moths." And because "induced defenses can increase plant fitness by reducing subsequent herbivore attacks (Agrawal, 1999; Kessler and Baldwin, 2004)," according to Bidart-Bouzat *et al*., they suggest that "the pronounced increase in glucosinolate levels under CO_2 enrichment may pose a threat not only for insect generalists that are likely to be more influenced by rapid changes in the concentration of these chemicals, but also for other insect specialists more susceptible than diamondback moths to high glucosinolate levels (Stowe, 1998; Kliebenstein *et al*., 2002)."

In a study of a major crop species, Wu *et al.* (2006) grew spring wheat (*Triticum aestivum* L.) from seed to maturity in pots placed within open-top chambers maintained at either 370 or 750 ppm CO_2 in Sanhe County, Hebei Province, China, after which they reared three generations of cotton bollworms (*Helicoverpa armigera* Hubner) on the milky grains of the wheat, while monitoring a number of different bollworm developmental characteristics. In doing so, as they describe it, "significantly lower pupal weights were observed in the first, second and third generations," and "the fecundity of *H. armigera* decreased by 10% in the first generation, 13% in the second generation and 21% in the third generation," resulting in a "potential population decrease in cotton bollworm by 9% in the second generation and 24% in the third generation." In addition, they say that "population consumption was significantly reduced by 14% in the second generation and 24% in the third generation," and that the efficiency of conversion of ingested food was reduced "by 18% in the first generation, 23% in the second generation and 30% in the third generation." As a result, they concluded that the "net damage of cotton bollworm on wheat will be less under elevated atmospheric CO_2," while noting that "at the same time, gross wheat production is expected to increase by 63% under elevated CO_2."

In another report of their work, Wu *et al.* (2007) write that "significant decreases in the protein, total amino acid, water and nitrogen content by 15.8%, 17.7%, 9.1% and 20.6% and increases in free fatty acid by 16.1% were observed in cotton bolls grown under elevated CO_2." And when fed with these cotton bolls, they say that the larval survival rate of *H. armigera* "decreased by 7.35% in the first generation, 9.52% in the second generation and 11.48% in the third generation under elevated CO_2 compared with ambient CO_2." In addition, they observed that "the fecundity of *H. armigera* decreased by 7.74% in the first generation, 14.23% in the second generation and 16.85% in the third generation," while noting that "fecundity capacity is likely to be reduced even further in the next generation."

The synergistic effects of these several phenomena, in the words of Wu *et al*., "resulted in a potential population decrease in cotton bollworm by 18.1% in the second generation and 52.2% in the third generation under elevated CO_2," with the result that "the potential population consumption of cotton bollworm decreased by 18.0% in the second generation and 55.6% in the third generation ... under elevated CO_2 compared with ambient CO_2." And in light of these several findings, they concluded that "the potential population dynamics and potential population consumption of cotton bollworm will alleviate the harm to [cotton] plants in the future rising-CO_2 atmosphere."

In a different type of study, Esper *et al.* (2007) reconstructed an annually resolved history of population cycles of a foliage-feeding Lepidopteran commonly known as the larch budmoth (*Zeiraphera* *diniana* Gn.)—or LBM for short—within the European Alps in the southern part of Switzerland. As is typical of many such insect pests, they note that "during peak activity, populations may reach very high densities over large areas," resulting in "episodes of massive defoliation and/or tree mortality" that could be of great ecological and economic significance.

The first thing the team of Swiss and US researchers thus did in this regard was develop a history of LBM outbreaks over the 1,173-year period AD 832-2004, which they describe as "the longest continuous time period over which any population cycle has ever been documented."

They accomplished this feat using radiodensitometric techniques to characterize the tree-ring density profiles of 180 larch (*Larix deciduas* Mill.) samples, where "LBM outbreaks were identified based upon characteristic maximum latewood density (MXD) patterns in wood samples, and verified using more traditional techniques of comparison with tree-ring chronologies from non-host species," i.e., fir and spruce. Then, they developed a matching temperature history for the same area, which was accomplished by combining "a tree-ring width-based reconstruction from AD 951 to 2002 integrating 1527 pine and larch samples (Buntgen *et al*., 2005) and a MXD-based reconstruction from AD 755 to 2004 based upon the same 180 larch samples used in the current study for LBM signal detection (Buntgen *et al*., 2006)."

Over almost the entire period studied, from its start in AD 832 to 1981, there were a total of 123 LBM outbreaks with a mean reoccurrence time of 9.3 years. In addition, the researchers say "there was never a gap that lasted longer than two decades." From 1981 to the end of their study in 2004, however, there were *no* LBM outbreaks; since there had never before (within their record) been such a long outbreak hiatus, they concluded that "the absence of mass outbreaks since the 1980s is truly exceptional."

To what do Esper *et al.* attribute this unprecedented recent development? Noting that "conditions during the late twentieth century represent the warmest period of the past millennium"—as per their temperature reconstruction for the region of the Swiss Alps within which they worked—they point to "the role of extraordinary climatic conditions as the cause of outbreak failure," and they discuss what they refer to as the "probable hypothesis" of Baltensweiler (1993), who described a scenario by which local warmth may lead to reduced LBM populations.

Such may well be the case, but we hasten to add that atmospheric CO_2 concentrations since 1980 have also been unprecedented over the 1,173-year period of Esper *et al.*'s study. Hence, the suppression of LBM outbreaks over the past quarter-century may have been the result of some *synergistic* consequence of the two factors (temperature and CO_2) acting in unison, while a third possibility may involve only the increase in the air's CO_2 content.

Esper *et al.* say their findings highlight the "vulnerability of an otherwise stable ecological system in a warming environment," in what would appear to be an attempt to attach an undesirable connotation to the observed outcome. This wording seems strange indeed, for it is clear that the "recent disruption of a major disturbance regime," as Esper *et al.* refer to the suppression of LBM outbreaks elsewhere in their paper, would be considered by most people to be a positive outcome, and something to actually be welcomed.

Working with *Antheraea polyphemus*—a leaf-chewing generalist lepidopteran herbivore that represents the most abundant feeding guild in the hardwood trees that grow beneath the canopy of the unmanaged loblolly pine plantation that hosts the Forest Atmosphere Carbon Transfer and Storage (FACTS-1) research site in the Piedmont region of North Carolina, USA, where the leaf-chewer can consume 2-15 percent of the forest's net primary production in any given year—Knepp *et al.* (2007) focused their attention on two species of oak tree—*Quercus alba* L. (white oak) and *Quercus velutina* Lam. (black oak)—examining host plant preference and larval performance of *A. polyphemus* when fed foliage of the two tree species that had been grown in either ambient or CO_2-enriched air (to 200 ppm above ambient) in this long-running FACE experiment. In doing so, they determined that "growth under elevated CO_2 reduced the food quality of oak leaves for caterpillars," while "consuming leaves of either oak species grown under elevated CO_2 slowed the rate of development of *A. polyphemus* larvae." In addition, they found that feeding on foliage of *Q. velutina* that had been grown under elevated CO_2 led to reduced consumption by the larvae and greater mortality. As a result, they concluded that "reduced consumption, slower growth rates, and increased mortality of insect larvae may explain [the] lower total leaf damage observed previously in plots of this forest exposed to elevated CO_2," as documented by Hamilton *et al.*

(2004) and Knepp *et al*. (2005), which finding bodes well indeed for the growth and vitality of such forests in the years and decades ahead, as the air's CO_2 content continues to rise.

Kampichler *et al*. (2008) also worked with oak trees. Noting, however, that "systems studied so far have not included mature trees," they attempted to remedy this situation by determining "the abundance of dominant leaf-galls (spangle-galls induced by the cynipid wasps *Neuroterus quercusbaccarum* and *N. numismalis*) and leaf-mines (caused by the larvae of the moth *Tischeria ekebladella*) on freely colonized large oaks in a mixed forest in Switzerland, which received CO_2 enrichment [540 ppm vs. 375 ppm during daylight hours] from 2001 to 2004" via "the Swiss Canopy Crane (SCC) and a new CO_2 enrichment technique (web-FACE)" in a forest that they say "is 80-120 years old with a canopy height of 32-38 m, consisting of seven deciduous and four coniferous species." This work allowed the German, Mexican, and Swiss researchers to discover that although elevated CO_2 reduced various leaf parameters (water content, proteins, non-structural carbohydrates, tannins, etc.) at the SCC site, "on the long term, their load with cynipid spangle-galls and leaf-mines of *T. ekebladella* was not distinguishable from that in oaks exposed to ambient CO_2 after 4 years of treatment." Kampichler *et al*. concluded that in the situation they investigated, "CO_2 enrichment had no lasting effect in all three [animal] taxa, despite the substantial and consistent change in leaf chemistry of oak due to growth in elevated CO_2."

In conclusion, therefore, and considering the results of all of the studies reviewed in this section, it would appear that the ongoing rise in the air's CO_2 content will *not* result in greater damage to earth's vegetation by the larvae of the many moths that inhabit the planet, and could reduce the damage they cause.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/i/summaries/moths.php.

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7.3.3.4. Other Insects

Docherty *et al*. (1997), in addition to studying aphids, studied two sap-feeding leafhopper species that were allowed to feed on saplings of beech and sycamore that were grown in glasshouses maintained at atmospheric CO_2 concentrations of 350 and 600 ppm. As far as they could determine, there were no significant effects of the extra CO_2 on either the feeding or performance characteristics of either leafhopper species.

In a literature review of more than 30 studies published two years later, Whittaker (1999) found that chewing insects (leaf chewers and leaf miners) showed either no change or reductions in abundance in response to atmospheric CO_2 enrichment, noting, however, that population reductions in this feeding guild were often accompanied by increased herbivory in response to CO_2-induced reductions in leaf nitrogen content.

In an experiment conducted on a natural ecosystem in Wisconsin, USA—comprised predominantly of trembling aspen (*Populus tremuloides* Michx.)—Percy *et al*. (2002) studied the effects of increases in CO_2 alone (to 560 ppm during daylight hours), O_3 alone (to 46.4-55.5 ppb during daylight hours), and CO_2 and O_3 together on the forest tent caterpillar (*Malacosoma disstria*), a common leaf-chewing lepidopteran found in North American hardwood forests. By itself, elevated CO_2 reduced caterpillar performance by reducing female pupal mass; while elevated O_3 alone improved caterpillar performance by increasing female pupal mass. When both gases were applied together, however, the elevated CO_2 completely counteracted the enhancement of female pupal mass caused by elevated O_3. Hence, either alone or in combination with undesirable increases in the air's O_3 concentration, elevated CO_2 tended to reduce the performance of the forest tent caterpillar. This finding is particularly satisfying because, in the words of Percy *et al*., "historically, the forest tent catepillar has defoliated more deciduous forest than any other insect in North America," and because "outbreaks can reduce timber yield up to 90% in one year, and increase tree vulnerability to disease and environmental stress."

In a study of yet another type of insect herbivore, Brooks and Whittaker (1999) removed grassland monoliths from the Great Dun Fell of Cumbria, UK—which contained eggs of a destructive xylem-feeding spittlebug (*Neophilaenus lineatus*)—and grew them in glasshouses maintained for two years at atmospheric CO_2 concentrations of 350 and 600 ppm. During the course of their experiment, two generations of the xylem-feeding insect were produced; in each case, elevated CO_2 reduced the survival of nymphal stages by an average of 24 percent. Brooks and Whittaker suggest that this reduction in survival rate may have been caused by CO_2-induced reductions in stomatal conductance and transpirational water loss, which may have reduced xylem nutrient-water availability. Whatever the mechanism, the results of this study bode well for the future survival of these species-poor grasslands as the air's CO_2 content continues to rise.

In summing up the implications of the various phenomena described in this section, it would appear that both CO_2-induced and warming-induced changes in the physical characteristics and behavioral patterns of a diverse assemblage of insect types portend good things for the biosphere in the years and decades to come.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/i/insectsother.php.

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7.3.4. Shade

Is the growth-enhancing effect of atmospheric CO_2 enrichment reduced when light intensities are less than optimal? The question may be important if a warmer world is also a cloudier world, as some climate models predict.

In a review of the scientific literature designed to answer this question, Kerstiens (1998) analyzed the results of 15 previously published studies of trees having differing degrees of shade tolerance, finding that elevated CO_2 caused greater relative biomass increases in shade-tolerant species than in shade-intolerant or sun-loving species. In more than half of the studies analyzed, shade-tolerant species experienced CO_2-induced relative growth increases that were two to three times greater than those of less shade-tolerant species.

In an extended follow-up review analyzing 74 observations from 24 studies, Kerstiens (2001) reported that twice-ambient CO_2 concentrations increased the relative growth response of shade-tolerant and shade-intolerant woody species by an average of 51 and 18 percent, respectively. Similar results were reported by Poorter and Perez-Soba (2001), who performed a detailed meta-analysis of research results pertaining to this topic, and more recently by Kubiske *et al.* (2002), who measured photosynthetic acclimation in aspen and sugar maple trees. On the other hand, a 200-ppm increase in the air's CO_2 concentration was found to enhance the photosynthetic rates of sunlit and shaded leaves of sweetgum trees by 92 and 54 percent, respectively, at one time of year, and by 166 and 68 percent at another time (Herrick and Thomas, 1999). Likewise, Naumburg and Ellsworth (2000) reported that a 200-ppm increase in the air's CO_2 content boosted steady-state photosynthetic rates in leaves of four hardwood understory species by an average of 60 and 40 percent under high and low light intensities, respectively. Even though these photosynthetic responses were significantly less in shaded leaves, they were still substantial, with mean increases ranging from 40 to 68 percent for a 60 percent increase in atmospheric CO_2 concentration.

Under extremely low light intensities, the benefits arising from atmospheric CO_2 enrichment may be small, but oftentimes they are very important in terms of plant carbon budgeting. In the study of Hattenschwiler (2001), for example, seedlings of five temperate forest species subjected to an additional 200-ppm CO_2 under light intensities that were only 3.4 and 1.3 percent of full sunlight exhibited CO_2-induced biomass increases that ranged from 17 to 74 percent. Similarly, in the study of Naumburg *et al.* (2001), a 200-ppm increase in the air's CO_2 content enhanced photosynthetic carbon uptake in three of four hardwood understory species by more than two-fold in three of the four species under light irradiances that were as low as 3 percent of full sunlight.

In a final study, in which potato plantlets inoculated with an arbuscular mycorrhizal fungus were grown at various light intensities and *super* CO_2 enrichment of approximately 10,000 ppm, Louche-Tessandier *et al.* (1999) found that the unusually high CO_2 concentration produced an unusually high degree of root colonization by the beneficial mycorrhizal fungus, which typically helps supply water and nutrients to plants. And it did so irrespective of the degree of light intensity to which the potato plantlets were exposed.

So, whether light intensity is high or low, or leaves are shaded or sunlit, when the CO_2 content of the air is increased, so too are the various biological processes that lead to plant robustness. Less than optimal light intensities do not negate the beneficial effects of atmospheric CO_2 enrichment.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/lightinteraction.php.

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7.3.5. Ozone

Plants grown in CO_2-enriched air nearly always exhibit increased photosynthetic rates and biomass production relative to plants grown at the current ambient CO_2 concentration. By contrast, plants exposed to elevated ozone concentrations typically display reductions in photosynthesis and growth in comparison with plants grown at the current ambient ozone concentration.

In discussing the problem of elevated tropospheric ozone (O_3) concentrations, Liu *et al.*

(2004) wrote that "ozone is considered to be one of the air pollutants most detrimental to plant growth and development in both urban and rural environments (Lefohn, 1992; Skarby *et al*., 1998; Matyssek and Innes, 1999)," because it "reduces the growth and yield of numerous agronomic crops as well as fruit and forest trees (Retzlaff *et al*., 1997; Fumagalli *et al*., 2001; Matyssek and Sandermann, 2003)." In addition, they say that ozone concentrations are "currently two to three times higher than in the early 1900s (Galloway, 1998; Fowler *et al*., 1999)," and that they likely "will remain high in the future (Elvingson, 2001)."

It is important to determine how major plants respond to concomitant increases in the abundances of these two trace gases of the atmosphere, as their concentrations will likely continue to increase for many years to come. We begin with a review of the literature with respect to various agriculture species, followed by a discussion on trees.

Additional information on this topic, including reviews on the interaction of CO_2 and O_3 not discussed here, can be found at http://www.co2science.org/subject/o/subject_o.php under the heading Ozone.

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7.3.5.1. Agricultural Species

Several studies have used soybean as a model plant to study the effects of elevated CO_2 and ozone on photosynthesis and growth. Reid *et al*. (1998), for example, grew soybeans for an entire season at different combinations of atmospheric CO_2 and ozone, reporting that elevated CO_2 enhanced rates of photosynthesis in the presence or absence of ozone and that it typically ameliorated the negative effects of elevated ozone on carbon assimilation. At the cellular level, Heagle *et al*. (1998a) reported that at twice the current ambient ozone concentration, soybeans simultaneously exposed to twice the current ambient atmospheric CO_2 concentration exhibited less foliar injury while maintaining significantly greater leaf chlorophyll contents than control plants exposed to elevated ozone and ambient CO_2 concentrations. By harvest time, the plants grown in the elevated ozone/elevated CO_2 treatment combination had produced 53 percent more total biomass than their counterparts did at elevated ozone and ambient CO_2 concentrations (Miller *et al*., 1998). Finally, in analyzing seed yield, it was determined that atmospheric CO_2 enrichment enhanced this parameter by 20 percent at ambient ozone, while it increased it by 74 percent at twice the ambient ozone concentration (Heagle *et al*., 1998b). Thus, elevated CO_2 completely ameliorated the negative effects of elevated ozone concentration on photosynthetic rate and yield production in soybean.

The ameliorating responses of elevated CO_2 to ozone pollution also have been reported for various cultivars of spring and winter wheat. In the study of Tiedemann and Firsching (2000), for example, atmospheric CO_2 enrichment not only overcame the detrimental effects of elevated ozone on photosynthesis and growth, it overcame the deleterious consequences resulting from inoculation with a biotic pathogen as well. Although infected plants displayed less absolute yield than non-infected plants at elevated ozone concentrations, atmospheric CO_2 enrichment caused the greatest relative yield increase in infected plants (57 percent vs. 38 percent).

McKee *et al*. (2000) reported that O_3-induced reductions in leaf rubisco contents in spring wheat were reversed when plants were simultaneously exposed to twice-ambient concentrations of atmospheric CO_2. In the study of Vilhena-Cardoso and Barnes (2001), elevated ozone concentrations reduced photosynthetic rates in spring wheat grown at three different soil nitrogen levels. However, when concomitantly exposed to twice-ambient atmospheric CO_2 concentrations, elevated ozone had no effect on rates of photosynthesis, regardless of soil nitrogen. Going a step further, Pleijel *et al*. (2000) observed that ozone-induced reductions in spring wheat yield were partially offset by concomitant exposure to elevated CO_2 concentrations. Similar results have been reported in spring wheat by Hudak *et al*. (1999) and in winter wheat by Heagle *et al*. (2000).

Cotton plants grown at elevated ozone concentrations exhibited 25 and 48 percent reductions in leaf mass per unit area and foliar starch concentration, respectively, relative to control plants grown in ambient air. When simultaneously exposed to twice-ambient CO_2 concentrations, however, the reductions in these parameters were only 5 and 7 percent, respectively (Booker, 2000). With respect to potato, Wolf and van Oijen (2002) used a validated potato model to predict increases in European tuber production ranging from 1,000 to 3,000 kg of dry matter per hectare in spite of concomitant increases in ozone concentrations and air temperatures.

It is clear from these studies that elevated CO_2 reduces, and nearly always completely overrides, the negative effects of ozone pollution on plant photosynthesis, growth, and yield. When explaining the mechanisms behind such responses, most authors suggest that atmospheric CO_2 enrichment tends to reduce stomatal conductance, which causes less indiscriminate uptake of ozone into internal plant air spaces and reduces subsequent conveyance to tissues where damage often results to photosynthetic pigments and proteins, reducing plant growth and biomass production.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/o/ozoneplantsag.php.

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7.3.5.2. Woody Species

7.3.5.2.1. Aspen

Karnosky *et al*. (1999) grew O_3-sensitive and O_3-tolerant aspen clones in 30-m diameter plots at the Aspen FACE site near Rhinelander, Wisconsin, USA, which were maintained at atmospheric CO_2 concentrations of 360 and 560 ppm with and without exposure to elevated O_3 (1.5 times ambient ozone concentration). After one year of growth at ambient CO_2, elevated O_3 had caused visible injury to leaves of both types of aspen, with the average percent damage in O_3-sensitive clones being more than three times as great as that observed in O_3-tolerant clones (55 percent vs. 17 percent, respectively). In combination with elevated CO_2, however, O_3-induced damage to leaves of these same clones was only 38 percent and 3 percent, respectively. Thus, elevated CO_2 ameliorated much of the foliar damage induced by high O_3 concentrations.

King *et al*. (2001) studied the same plants for a period of two years, concentrating on below-ground growth, where elevated O_3 alone had no effect on fine-root biomass. When the two aspen clones were simultaneously exposed to elevated CO_2 and O_3, however, there was an approximate 66 percent increase in the fine-root biomass of both of them.

Also in the same experiment, Noormets *et al*. (2001) studied the interactive effects of O_3 and CO_2 on photosynthesis, finding that elevated CO_2 increased rates of photosynthesis in both clones at all leaf positions. Maximum rates of photosynthesis were increased in the O_3-tolerant clone by averages of 33 and 49 percent due to elevated CO_2 alone and in combination with elevated O_3, respectively, while in the O_3-sensitive clone they were increased by 38 percent in both situations. Hence, CO_2-induced increases in maximal rates of net photosynthesis were typically maintained, and sometimes increased, during simultaneous exposure to elevated O_3.

Yet again in the same experiment, Oksanen *et al*. (2001) reported that after three years of treatment, ozone exposure caused significant structural injuries to thylakoid membranes and the stromal compartment within chloroplasts, but that these injuries were largely ameliorated by atmospheric CO_2 enrichment. Likewise, leaf thickness, mesophyll tissue thickness, the amount of chloroplasts per unit cell area, and the amount of starch in leaf chloroplasts were all decreased in the high ozone treatment, but simultaneous exposure of the ozone-stressed trees to elevated CO_2 more than compensated for the ozone-induced reductions.

After four years of growing five aspen clones with varying degrees of tolerance to ozone under the same experimental conditions, McDonald *et al*. (2002) developed what they termed a “competitive stress index,” based on the heights of the four nearest neighbors of each tree, to study the influence of competition on the CO_2 growth response of the various clones as modified by ozone. In general, elevated O_3 reduced aspen growth independent of competitive status, while the authors noted an “apparent convergence of competitive performance responses in $+CO_2$ $+O_3$ conditions,” which they say suggests that “stand diversity may be maintained at a higher level” in such circumstances.

Percy *et al*. (2002) utilized the same experimental setting to assess a number of the trees’ growth characteristics, as well as the responses of one plant pathogen and two insects with different feeding strategies that typically attack the trees. Of the plant pathogen studied, they say that “the poplar leaf rust, *Melampsora medusae*, is common on aspen and belongs to the most widely occurring group of foliage diseases.” As for the two insects, they report that “the forest tent caterpillar, *Malacosoma disstria*, is a common leaf-chewing lepidopteran in North American hardwood forests” and that “the sap-feeding aphid, *Chaitophorus stevensis*, infests aspen throughout its range.” Hence, the rust and the two insect pests the scientists studied are widespread and have significant deleterious impacts on trembling aspen and other tree species. As but one example of this fact, the authors note that, “historically, the forest tent caterpillar has defoliated more deciduous forest than any other insect in North America" and that "outbreaks can reduce timber yield up to 90% in one year, and increase tree vulnerability to disease and environmental stress."

Percy *et al*. found that by itself, elevated O_3 decreased tree height and trunk diameter, increased rust occurrence by nearly fourfold, improved tent caterpillar performance by increasing female pupal mass by 31 percent, and had a strong negative effect on the natural enemies of aphids. The addition of the extra CO_2, however, completely ameliorated the negative effects of elevated O_3 on tree height and trunk diameter, reduced the O_3-induced enhancement of rust development from nearly fourfold to just over twofold, completely ameliorated the enhancement of female tent caterpillar pupal mass caused by elevated O_3, and completely ameliorated the reduction in the abundance of natural enemies of aphids caused by elevated O_3.

In a final study from the Aspen FACE site, Holton *et al*. (2003) raised parasitized and non-parasitized forest tent caterpillars on two quaking aspen genotypes (O_3-sensitive and O_3-tolerant) alone and in combination for one full growing season; they, too, found that elevated O_3 improved tent caterpillar performance under ambient CO_2 conditions, but not in CO_2-enriched air.

In summary, it is clear that elevated ozone concentrations have a number of significant negative impacts on the well-being of North America's most widely distributed tree species, while elevated carbon dioxide concentrations have a number of significant positive impacts. In addition, elevated CO_2 often completely eliminates the negative impacts of elevated O_3. If the tropospheric O_3 concentration continues to rise as expected (Percy *et al.* note that "damaging O_3 concentrations currently occur over 29% of the world's temperate and subpolar forests but are predicted to affect fully 60% by 2100"), we might hope the air's CO_2 content continues to rise as well.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/o/ozoneaspen.php.

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7.3.5.2.2. Beech

Liu *et al*. (2005) grew three- and four-year-old seedlings of European beech (*Fagus sylvatica* L.) for five months in well watered and fertilized soil in containers located within walk-in phytotrons maintained at either ambient or ambient + 300 ppm CO_2 (each subdivided into ambient and double-ambient O_3 concentration treatments, with maximum ozone levels restricted to <150 ppb), in both monoculture and in competition with Norway spruce, after which they examined the effects of each treatment on leaf non-structural carbohydrate levels (soluble sugars and starch). They found that the effects of elevated O_3 alone on non-structural carbohydrate levels were small when the beech seedlings were grown in monoculture. When they were grown in mixed culture, however, the elevated O_3 slightly enhanced leaf sugar levels, but reduced starch levels by 50 percent.

With respect to elevated CO_2 alone, for the beech seedlings grown in both monoculture and mixed culture, levels of sugar and starch were significantly enhanced. Hence, when elevated O_3 and CO_2 significantly affected non-structural carbohydrate levels, elevated CO_2 tended to enhance them, whereas elevated O_3 tended to reduce them. In addition, the combined effects of elevated CO_2 and O_3 acting together were such as to produce a significant increase in leaf non-structural carbohydrates in both mixed and monoculture conditions. As a result, the researchers concluded that "since the responses to the combined exposure were more similar to elevated pCO_2 than to elevated pO_3, apparently elevated pCO_2 overruled the effects of elevated pO_3 on non-structural carbohydrates."

In a slightly longer study, Grams *et al*. (1999) grew European beech seedlings in glasshouses maintained at average atmospheric CO_2 concentrations of either 367 or 667 ppm for a period of one year. Then, throughout the following year, in addition to being exposed to the same set of CO_2 concentrations the seedlings were exposed to either ambient or twice-ambient levels of O_3. This protocol revealed that elevated O_3 significantly reduced photosynthesis in beech seedlings grown at ambient CO_2 concentrations by a factor of approximately three. By contrast, in the CO_2-enriched air the seedlings did not exhibit any photosynthetic reduction due to the doubled O_3 concentrations. In fact, the photosynthetic rates of the CO_2-enriched seedlings actually rose by 8 percent when simultaneously fumigated with elevated O_3, leading the researchers to conclude that "long-term acclimation to elevated CO_2 supply does counteract the O_3-induced decline of photosynthetic light and dark reactions."

In a still longer study, Liu *et al*. (2004) grew three- and four-year-old beech seedlings for two growing seasons under the same experimental conditions as Liu *et al*. (2005) after the seedlings had been pre-acclimated for one year to either the ambient or elevated CO_2 treatment. At the end of the study, the plants were harvested and fresh weights and dry biomass values were determined for leaves, shoot axes, coarse roots, and fine roots, as were carbohydrate (starch and soluble sugar) contents and concentrations for the same plant parts. This work falsified the hypothesis that "prolonged exposure to elevated CO_2 does not compensate for the adverse ozone effects on European beech," as it revealed that all "adverse effects of ozone on carbohydrate concentrations and contents were counteracted when trees were grown in elevated CO_2."

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/o/ozonebeech.php.

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7.3.5.2.3. Birch

At the FACE facility near Rhinelander, Wisconsin, USA, King *et al*. (2001) grew a mix of paper birch and quaking aspen trees in 30-m diameter plots that were maintained at atmospheric CO_2 concentrations of 360 and 560 ppm with and without exposure to elevated O_3 (1.5 times the ambient O_3 concentration) for a period of two years. In their study of the below-ground environment of the trees, they found that the extra O_3 had no effect on the growth of fine roots over that time period, but that elevated O_3 and CO_2 together increased the fine-root biomass of the mixed stand by 83 percent.

One year later at the same FACE facility, Oksanen *et al*. (2001) observed O_3-induced injuries in the thylokoid membranes of the chloroplasts of the birch trees' leaves; the injuries were partially ameliorated in the elevated CO_2 treatment. And in a study conducted two years later, Oksanen *et al*.

(2003) say they "were able to visualize and locate ozone-induced H_2O_2 accumulation within leaf mesophyll cells, and relate oxidative stress with structural injuries." However, they report that "H_2O_2 accumulation was found only in ozone-exposed leaves and not in the presence of elevated CO_2," adding that "CO_2 enrichment appears to alleviate chloroplastic oxidative stress."

Across the Atlantic in Finland, Kull *et al*. (2003) constructed open-top chambers around two clones (V5952 and K1659) of silver birch saplings that were rooted in the ground and had been growing there for the past seven years. These chambers were fumigated with air containing 360 and 720 ppm CO_2 in combination with 30 and 50 ppb O_3 for two growing seasons, after which it was noted that the extra O_3 had significantly decreased branching in the trees' crowns. This malady, however, was almost completely ameliorated by a doubling of the air's CO_2 concentration. In addition, after one more year of study, Eichelmann *et al*. (2004) reported that, by itself, the increase in the air's CO_2 content increased the average net photosynthetic rates of both clones by approximately 16 percent, while the increased O_3 by itself caused a 10 percent decline in the average photosynthetic rate of clone V5952, but not of clone K1659. When both trace gases were simultaneously increased, however, the photosynthetic rate of clone V5952 once again experienced a 16 percent increase in net photosynthesis, as if the extra O_3 had had no effect when applied in the presence of the extra CO_2.

After working with the same trees for one additional year, Riikonen *et al*. (2004) harvested them and reported finding that "the negative effects of elevated O_3 were found mainly in ambient CO_2, not in elevated CO_2." In fact, whereas doubling the air's O_3 concentration decreased total biomass production by 13 percent across both clones, simultaneously doubling the air's CO_2 concentration increased total biomass production by 30 percent, thereby more than compensating for the deleterious consequences of doubling the atmospheric ozone concentration.

In commenting on this ameliorating effect of elevated CO_2, the team of Finnish scientists said it "may be associated with either increased detoxification capacity as a consequence of higher carbohydrate concentrations in leaves grown in elevated CO_2, or decreased stomatal conductance and thus decreasing O_3 uptake in elevated CO_2 conditions (e.g., Rao *et al*., 1995)." They also noted that "the ameliorating effect of elevated CO_2 is in accordance with the results of single-season open-top chamber and growth chamber studies on small saplings of various deciduous tree species (Mortensen 1995; Dickson *et al*., 1998; Loats and Rebbeck, 1999) and long-term open-field and OTC studies with aspen and yellow-poplar (Percy *et al*., 2002; Rebbeck and Scherzer, 2002)."

In another paper to come out of the Finnish silver birch study, Peltonen *et al*. (2005) evaluated the impacts of doubled atmospheric CO_2 and O_3 concentrations on the accumulation of 27 phenolic compounds in the leaves of the trees, finding that elevated CO_2 increased the concentration of phenolic acids (+25 percent), myricetin glycosides (+18 percent), catechin derivatives (+13 percent), and soluble condensed tannins (+19 percent). Elevated O_3, on the other hand, increased the concentration of one glucoside by 22 percent, chlorogenic acid by 19 percent, and flavone aglycons by 4 percent. However, Peltonen *et al*. say this latter O_3-induced production of antioxidant phenolic compounds "did not seem to protect the birch leaves from detrimental O_3 effects on leaf weight and area, but may have even exacerbated them." Last, in the combined elevated CO_2 and O_3 treatment, they found that "elevated CO_2 did seem to protect the leaves from elevated O_3 because all the O_3-derived effects on the leaf phenolics and traits were prevented by elevated CO_2."

Meanwhile, back at the FACE facility near Rhinelander, Wisconsin, USA, Agrell *et al*. (2005) examined the effects of ambient and elevated concentrations of atmospheric CO_2 and O_3 on the foliar chemistry of birch and aspen trees, plus the consequences of these effects for host plant preferences of forest tent caterpillar larvae. In doing so, they found that "the only chemical component showing a somewhat consistent co-variation with larval preferences was condensed tannins," and they discovered that "the tree becoming relatively less preferred as a result of CO_2 or O_3 treatment was in general also the one for which average levels of condensed tannins were most positively (or least negatively) affected by that treatment." The mean condensed tannin concentration of birch leaves was 18 percent higher in the elevated CO_2 and O_3 treatment. Consequently, as atmospheric concentrations of CO_2 and O_3 continue to rise, the increases in condensed tannin concentrations likely to occur in the foliage of birch trees should lead to their leaves becoming less preferred for consumption by the forest tent caterpillar.

Concurrent with the work of Agrell *et al*., King *et al*. (2005) evaluated the effect of CO_2 enrichment alone, O_3 enrichment alone, and the net effect of both CO_2 and O_3 enrichment together on the growth of the Rhinelander birch trees, finding that relative to the ambient-air control treatment, elevated CO_2 increased total biomass by 45 percent in the aspen-birch community, while elevated O_3 caused a 13 percent reduction in total biomass relative to the control. Of most interest, the combination of elevated CO_2 and O_3 resulted in a total biomass increase of 8.4 percent relative to the control aspen-birch community. King *et al*. thus concluded that "exposure to even moderate levels of O_3 significantly reduces the capacity of net primary productivity to respond to elevated CO_2 in some forests." Consequently, they suggested it makes sense to move forward with technologies that reduce anthropogenic precursors to photochemical O_3 formation, because the implementation of such a policy would decrease an important constraint on the degree to which forest ecosystems can positively respond to the ongoing rise in the air's CO_2 concentration.

Another paper to come out of the Finnish silver birch study was that of Kostiainen *et al*. (2006), who studied the effects of elevated CO_2 and O_3 on various wood properties. Their work revealed that the elevated CO_2 treatment had no effect on wood structure, but that it increased annual ring width by 21 percent, woody biomass by 23 percent, and trunk starch concentration by 7 percent. Elevated O_3, on the other hand, decreased stem vessel percentage in one of the clones by 10 percent; it had no effect on vessel percentage in the presence of elevated CO_2.

In discussing their results, Kostiainen *et al*. note that "in the xylem of angiosperms, water movement occurs principally in vessels (Kozlowski and Pallardy, 1997)," and that "the observed decrease in vessel percentage by elevated O_3 may affect water transport," lowering it. However, as they continue, "elevated CO_2 ameliorated the O_3-induced decrease in vessel percentage." In addition, they note that "the concentration of nonstructural carbohydrates (starch and soluble sugars) in tree tissues is considered a measure of carbon shortage or surplus for growth (Korner, 2003)." They conclude that "starch accumulation observed under elevated CO_2 in this study indicates a surplus of carbohydrates produced by enhanced photosynthesis of the same trees (Riikonen *et al*., 2004)." In addition, they report that "during winter, starch reserves in the stem are gradually transformed to soluble carbohydrates involved in freezing tolerance (Bertrand *et al*., 1999; Piispanen and Saranpaa, 2001), so the increase in starch concentration may improve acclimation in winter."

Rounding out the suite of Rhinelander FACE studies of paper birch is the report of Darbah *et al*. (2007), who found that the total number of trees that flowered increased by 139 percent under elevated CO_2 but only 40 percent under elevated O_3. Likewise, with respect to the quantity of flowers produced, they found that elevated CO_2 led to a 262 percent increase, while elevated O_3 led to only a 75 percent increase. They also determined that elevated CO_2 had significant positive effects on birch catkin size, weight, and germination success rate, with elevated CO_2 increasing the germination rate of birch by 110 percent, decreasing seedling mortality by 73 percent, increasing seed weight by 17 percent, and increasing new seedling root length by 59 percent. They found just the *opposite* was true of elevated O_3, as it decreased the germination rate of birch by 62 percent, decreased seed weight by 25 percent, and increased new seedling root length by only 15 percent.

In discussing their findings, Darbah *et al*. additionally report that "the seeds produced under elevated O_3 had much less stored carbohydrate, lipids, and proteins for the newly developing seedlings to depend on and, hence, the slow growth rate." As a result, they conclude that "seedling recruitment will be enhanced under elevated CO_2 but reduced under elevated O_3."

In summary, from their crowns to their roots, birch trees are generally negatively affected by rising ozone concentrations. When the air's CO_2 content is also rising, however, these negative consequences may often be totally eliminated and replaced by positive responses.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/o/ozonebirch.php.

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7.3.5.2.4. Yellow-Poplar

Scherzel *et al.* (1998) grew yellow-poplar seedlings in open-top chambers for four years at three different combinations of atmospheric O_3 and CO_2—(1) ambient O_3 and ambient CO_2, (2) doubled O_3 and ambient CO_2, and (3) doubled O_3 and doubled CO_2—to study the interactive effects of these gases on leaf-litter decomposition. This experiment revealed that the decomposition rates of yellow-poplar leaves were similar for all three treatments for nearly five months, after which time litter produced in the elevated O_3 and elevated CO_2 air decomposed at a significantly slower rate, such that even after two years of decomposition, litter from the elevated O_3 and elevated CO_2 treatment still contained about 12 percent more biomass than litter produced in the other two treatments. This reduced rate of decomposition under elevated O_3 and CO_2 conditions will likely result in greater carbon sequestration in soils supporting yellow-poplar trees over the next century or more.

Loats and Rebbeck (1999) grew yellow-poplar seedlings for ten weeks in pots they placed within growth chambers filled with ambient air, air with twice the ambient CO_2 concentration, air with twice the ambient O_3 concentration, and air with twice the ambient CO_2 and O_3 concentrations to determine the effects of elevated CO_2 and O_3 on photosynthesis and growth in this deciduous tree species. In doing so, they found that doubling the air's CO_2 concentration increased the rate of net photosynthesis by 55 percent in ambient O_3 air, and that at twice the ambient level of O_3 it stimulated net photosynthesis by an average of 50 percent. Similarly, the doubled CO_2 concentration significantly increased total biomass by 29 percent, while the doubled O_3 concentration had little impact on growth.

Last, Rebbeck *et al*. (2004) grew yellow poplar seedlings for five years within open-top chambers in a field plantation at Delaware, Ohio, USA, exposing them continuously from mid-May through mid-October of each year to either (1) charcoal-filtered air to remove ambient O_3, (2) ambient O_3, (3) 1.5 times ambient O_3, and (4) 1.5 times ambient O_3 plus 350 ppm CO_2 above ambient CO_2, while they periodically measured a number of plant parameters and processes. Throughout the study, the trees were never fertilized, and they received no supplemental water beyond some given in the first season.

Averaged over the experiment's five growing seasons, the midseason net photosynthetic rate of upper canopy foliage at saturating light intensities declined by 10 percent when the trees were grown in ambient O_3-air and by 14 percent when they were grown in elevated O_3-air, when compared to the trees that were grown in the charcoal-filtered air, while seasonal net photosynthesis of foliage grown in the combination of elevated O_3 and elevated CO_2 was 57-80 percent higher than it was in the trees exposed to elevated O_3 alone. There was also no evidence of any photosynthetic down regulation in the trees exposed to the elevated O_3 and CO_2 air, with some of the highest rates being observed during the final growing season. Consequently, Rebbeck *et al*. concluded that "elevated CO_2 may ameliorate the negative effects of increased tropospheric O_3 on yellow-poplar." In fact, their results suggest that a nominally doubled atmospheric CO_2 concentration more than compensates for the deleterious effects of a 50 percent increase in ambient O_3 levels.

As the air's CO_2 content continues to rise, earth's yellow-poplar trees will likely display substantial increases in photosynthetic rate and biomass production, even under conditions of elevated O_3 concentrations; and the soils in which the trees grow should sequester ever greater quantities of carbon.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/o/ozoneyellowpoplar.php.

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7.3.6. Low Temperatures

Only a handful of studies have attempted to determine what relationship, if any, exists between atmospheric CO_2 enrichment and the ability of plants to withstand the rigors of low temperatures.

Loik *et al*. (2000) grew three *Yucca* species (*brevifolia*, *schidigera*, and *whipplei*) in pots placed within glasshouses maintained at atmospheric CO_2 concentrations of 360 and 700 ppm and day/night air temperatures of 40/24°C for seven months, after which some of the plants were subjected to a two-week day/night air temperature treatment of 20/5°C. In addition, leaves from each *Yucca* species were removed and placed in a freezer that was cooled at a rate of 3°C per hour until a minimum temperature of -15°C was reached. These manipulations indicated that elevated CO_2 lowered the air temperature at which 50 percent low-temperature-induced cell mortality occurred by 1.6, 1.4 and 0.8°C in *brevifolia*, *schidigera* and *whipplei*, respectively. On the basis of the result obtained for *Y. brevifolia*, Dole *et al*. (2003) estimated that "the increase in freezing tolerance caused by doubled CO_2 would increase the potential habitat of this species by 14%."

By contrast, Obrist *et al*. (2001) observed the opposite response. In an open-top chamber study of a temperate grass ecosystem growing on a nutrient-poor calcareous soil in northwest Switzerland, portions of which had been exposed to atmospheric CO_2 concentrations of 360 and 600 ppm for a period of six years, they determined that the average temperature at which 50 percent low-temperature-induced leaf mortality occurred in five prominent species actually *rose* by an average of 0.7°C in response to the extra 240 ppm of CO_2 employed in their experiment.

Most relevant investigations, however, have produced evidence of positive CO_2 effects on plant low temperature tolerance. Sigurdsson (2001), for example, grew black cottonwood seedlings near Gunnarsholt, Iceland within closed-top chambers maintained at ambient and twice-ambient atmospheric CO_2 concentrations for a period of three years, finding that elevated CO_2 tended to hasten the end of the growing season. This effect was interpreted as enabling the seedlings to better avoid the severe cold-induced dieback of newly produced tissues that often occurs with the approach of winter in this region. Likewise, Wayne *et al*. (1998) found that yellow birch seedlings grown at an atmospheric CO_2 concentration of 800 ppm exhibited greater dormant bud survivorship at low air temperatures than did seedlings grown at 400 ppm CO_2.

Schwanz and Polle (2001) investigated the effects of elevated CO_2 on chilling stress in micropropagated hybrid poplar clones that were subsequently potted and transferred to growth chambers maintained at either ambient (360 ppm) or elevated (700 ppm) CO_2 for a period of three months. They determined that "photosynthesis was less diminished and electrolyte leakage was lower in stressed leaves from poplar trees grown under elevated CO_2 as compared with those from ambient CO_2." Although severe chilling did cause pigment and protein degradation in all stressed leaves, the damage was expressed to a lower extent in leaves from the elevated CO_2 treatment. This CO_2-induced chilling protection was determined to be accompanied by a rapid induction of superoxide dismutase activity, as well as by slightly higher stabilities of other antioxidative enzymes.

Another means by which chilling-induced injury may be reduced in CO_2-enriched air is suggested by the study of Sgherri *et al*. (1998), who reported that raising the air's CO_2 concentration from 340 to 600 ppm increased lipid concentrations in alfalfa thylakoid membranes while simultaneously inducing a higher degree of unsaturation in the most prominent of those lipids. Under well-watered conditions, for example, the 76 percent increase in atmospheric CO_2 enhanced overall thylakoid lipid concentration by about 25 percent, while it increased the degree of unsaturation of the two main lipids by approximately 17 percent and 24 percent. Under conditions of water stress, these responses were found to be even greater, as thylakoid lipid concentration rose by approximately 92 percent, while the degree of unsaturation of the two main lipids rose by about 22 percent and 53 percent.

Several studies conducted over the past decade explain what these observations have to do with a plant's susceptibility to chilling injury. Working with wild-type *Arabidopsis thaliana* and two mutants deficient in thylakoid lipid unsaturation, Hugly and Somerville (1992) found that "chloroplast membrane lipid polyunsaturation contributes to the low-temperature fitness of the organism," and that it "is required for some aspect of chloroplast biogenesis." When lipid polyunsaturation was low, they observed "dramatic reductions in chloroplast size, membrane content, and organization in developing leaves." There was a positive correlation "between the severity of chlorosis in the two mutants at low temperatures and the degree of reduction in polyunsaturated chloroplast lipid composition."

Working with tobacco, Kodama *et al*. (1994) demonstrated that the low-temperature-induced suppression of leaf growth and concomitant induction of chlorosis observed in wild-type plants was much less evident in transgenic plants containing a gene that allowed for greater expression of unsaturation in the fatty acids of leaf lipids. This observation and others led them to conclude that substantially unsaturated fatty acids "are undoubtedly an important factor contributing to cold tolerance."

In a closely related study, Moon *et al*. (1995) found that heightened unsaturation of the membrane lipids of chloroplasts stabilized the photosynthetic machinery of transgenic tobacco plaints against low-temperature photoinibition "by accelerating the recovery of the photosystem II protein complex." Likewise, Kodama *et al*. (1995), also working with transgenic tobacco plants, showed that increased fatty acid desaturation is one of the prerequisites for normal leaf development at low, nonfreezing temperatures; and Ishizaki-Nishizawa *et al*. (1996) demonstrated that transgenic tobacco plants with a reduced level of saturated fatty acids in most membrane lipids "exhibited a significant increase in chilling resistance."

Many economically important crops, such as rice, maize and soybeans, are classified as chilling-sensitive and experience injury or death at temperatures between 0 and 15°C (Lyons, 1973). If atmospheric CO_2 enrichment enhances their production and degree-of-unsaturation of thylakoid lipids, as it does in alfalfa, a continuation of the ongoing rise in the air's CO_2 content could increase the abilities of these important agricultural species to withstand periodic exposure to debilitating low temperatures. This phenomenon could provide the extra boost in food production that will be needed to sustain an increasing population in the years and decades ahead.

Earth's natural ecosystems would also benefit from a CO_2-induced increase in thylakoid lipids containing more-highly unsaturated fatty acids. Many plants of tropical origin, for example, suffer cold damage when temperatures fall below 20°C (Graham and Patterson, 1982). With improved lipid characteristics provided by the ongoing rise in the air's CO_2 content, such plants would be able to expand their ranges both poleward and upward in a higher-CO_2 world.

More research remains to be done before we can accurately assess the extent of these potential biological benefits. In particular, we must conduct more studies of the effects of atmospheric CO_2 enrichment on the properties of thylakoid lipids in a greater variety of plants. In the same experiments, we must assess the efficacy of these lipid property changes in enhancing plant tolerance of low temperatures. Such studies should rank high on the to-do list of relevant funding agencies.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/f/frosthardiness.php.

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7.3.7. Nitrogen Deficiency

Numerous studies have investigated the effects of different soil nitrogen (N) concentrations on plant responses to increases in the air's CO_2 content, as it has been claimed that a deficiency of soil nitrogen lessens the relative growth stimulation in plants that is typically provided by elevated concentrations of atmospheric CO_2. In this section, we evaluate the credibility of that claim for various crops, fungi, grasses and trees.

The results of these experiments indicate that some plants sometimes will not respond at all to atmospheric CO_2 enrichment at low levels of soil N, while some will. Some plants respond equally well to increases in the air's CO_2 content when growing in soils exhibiting a whole range of N concentrations. Most common, however, is the observation that plants respond ever better to rising atmospheric CO_2 concentrations as soil N concentrations rise. Interestingly, the current state of earth's atmosphere and land surface is one of jointly increasing CO_2 and N concentrations. Hence, the outlook is good for continually increasing terrestrial vegetative productivity in the years and decades ahead, as these trends continue.

Additional information on this topic, including reviews on nitrogen not discussed here, can be found at http://www.co2science.org/subject/g/subject_g.php under the heading Growth Response to CO_2 With Other Variables: Nutrients: Nitrogen, as well as at http://www.co2science.org/subject/n/subject_n.php under the headings Nitrogen, Nitrogen Fixation and Nitrogen Use Efficiency.

7.3.7.1. Crops

7.3.7.1.1. Rice

Does a deficiency of soil nitrogen lessen the relative growth and yield stimulation of rice that is typically provided by elevated levels of atmospheric CO_2? In exploring this question, Weerakoon *et al*. (1999) grew seedlings of two rice cultivars for 28 days in glasshouses maintained at atmospheric CO_2 concentrations of 373, 545, 723 and 895 ppm under conditions of low, medium and high soil nitrogen content. After four weeks of treatment, photosynthesis was found to significantly increase with increasing nitrogen availability and atmospheric CO_2 concentration. Averaged across all nitrogen regimes, plants grown at 895 ppm CO_2 exhibited photosynthetic rates that were 50 percent greater than those observed in plants grown at ambient CO_2. Total plant dry weight also increased with increasing atmospheric CO_2. In addition, the percentage growth enhancement resulting from CO_2 enrichment increased with increasing soil nitrogen; from 21 percent at the lowest soil nitrogen concentration to 60 percent at the highest concentration.

Using a different CO_2 enrichment technique, Weerakoon *et al.* (2000) grew rice in open-top chambers maintained at atmospheric CO_2 concentrations of approximately 350 and 650 ppm during a wet and dry growing season and under a range of soil nitrogen contents. Early in both growing seasons, plants exposed to elevated atmospheric CO_2 concentrations intercepted significantly more sunlight than plants fumigated with ambient air, due to CO_2-induced increases in leaf area index. This phenomenon occurred regardless of soil nitrogen content, but disappeared shortly after canopy closure in all treatments. Later, mature canopies achieved similar leaf area indexes at identical levels of soil nitrogen supply; but mean season-long radiation use efficiency, which is the amount of biomass produced per unit of solar radiation intercepted, was 35 percent greater in CO_2-enriched vs. ambiently grown plants and tended to increase with increasing soil nitrogen content.

Utilizing a third approach to enriching the air about a crop with elevated levels of atmospheric CO_2, Kim *et al.* (2003) grew rice crops from the seedling stage to maturity at atmospheric CO_2 concentrations of ambient and ambient plus 200 ppm using FACE technology and three levels of applied nitrogen—low (LN, 4 g N m^{-2}), medium (MN, 8 and 9 g N m^{-2}) and high (HN, 15 g N m^{-2})—for three cropping seasons (1998-2000). They report that "the yield response to elevated CO_2 in crops supplied with MN (+14.6%) or HN (+15.2%) was about twice that of crops supplied with LN (+7.4%)," confirming the importance of nitrogen availability to the response of rice to atmospheric CO_2 enrichment previously determined by Kim *et al*. (2001) and Kobaysahi *et al*. (2001).

In light of these observations, it would appear that the maximum benefits of elevated levels of atmospheric CO_2 for the growth and grain production of rice cannot be realized in soils that are highly deficient in nitrogen. Increasing nitrogen concentrations above what is considered adequate may not result in proportional gains in CO_2-induced growth and yield enhancement.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/n/nitrogenrice.php.

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7.3.7.1.2. Wheat

Smart *et al*. (1998) grew wheat from seed for 23 days in controlled environment chambers maintained at atmospheric CO_2 concentrations of 360 and 1000 ppm and two concentrations of soil nitrate, finding that the extra CO_2 increased average plant biomass by approximately 15 percent, irrespective of soil nitrogen content. In a more realistic FACE experiment, however, Brooks *et al*. (2000) grew spring wheat for two seasons at atmospheric CO_2 concentrations of 370 and 570 ppm at both high and low levels of nitrogen fertility; and they obtained *twice* the yield enhancement (16 percent vs. 8 percent) in the high nitrogen treatment.

In an experiment with one additional variable, Vilhena-Cardoso and Barnes (2001) grew spring wheat for two months in environmental chambers fumigated with air containing atmospheric CO_2 concentrations of either 350 or 700 ppm at ambient and elevated (75 ppb) ozone concentrations, while the plants were simultaneously subjected to either low, medium or high levels of soil nitrogen. With respect to biomass production, the elevated CO_2 treatment increased total plant dry weight by 44, 29 and 12 percent at the high, medium and low soil nitrogen levels, respectively. In addition, although elevated ozone alone reduced plant biomass, the simultaneous application of elevated CO_2 completely ameliorated its detrimental effects on biomass production, irrespective of soil nitrogen supply.

Why do the plants of some studies experience a major reduction in the relative growth stimulation provided by atmospheric CO_2 enrichment under low soil nitrogen conditions, while other studies find the aerial fertilization effect of elevated CO_2 to be independent of root-zone nitrogen concentration? Based on studies of both potted and hydroponically grown plants, Farage *et al*. (1998) determined that low root-zone nitrogen concentrations need not lead to photosynthetic acclimation (less than maximum potential rates of photosynthesis) in elevated CO_2, as long as root-zone nitrogen *supply* is adequate to meet plant nitrogen *needs* to maintain the enhanced relative growth rate that is made possible by atmospheric CO_2 enrichment. When supply cannot meet this need, as is often the case in soils with limited nitrogen reserves, the aerial fertilization effect of atmospheric CO_2 enrichment begins to be reduced and less-than-potential CO_2-induced growth stimulation is observed. Nevertheless, the acclimation process is the plant's "first line of defense" to keep its productivity from falling even further than it otherwise would, as it typically mobilizes nitrogen from "excess" rubisco and sends it to more needy plant sink tissues to allow for their continued growth and development (Theobald *et al*., 1998).

In conclusion, although atmospheric CO_2 enrichment tends to increase the growth and yield of wheat under a wide range of soil nitrogen concentrations, including some that are very low, considerably greater CO_2-induced enhancements are possible when more soil nitrogen is available, although the response can saturate at high soil nitrogen levels, with excess nitrogen providing little to no extra yield.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/n/nitrogenwheat.php.

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7.3.7.1.3. Other

Zerihun *et al*. (2000) grew sunflowers for one month in pots of three different soil nitrogen concentrations that were placed within open-top chambers maintained at atmospheric CO_2 concentrations of 360 and 700 ppm. The extra CO_2 of the CO_2-enriched chambers reduced average rates of root nitrogen uptake by about 25 percent, which reduction, by itself, would normally tend to reduce tissue nitrogen contents and the relative growth rates of the seedlings. However, the elevated CO_2 also increased photosynthetic nitrogen-use efficiency by an average of 50 percent, which increase normally tends to increase the relative growth rates of seedlings. Of these two competing effects, the latter was the more powerful, leading to an increase in whole plant biomass. After the one month of the study, for example, the CO_2-enriched plants exhibited whole plant biomass values that were 44, 13 and 115 percent greater than those of the plants growing in ambient air at low, medium and high levels of soil nitrogen, respectively, thus demonstrating that low tissue nitrogen contents do not necessarily preclude a growth response to atmospheric CO_2 enrichment, particularly if photosynthetic nitrogen-use efficiency is enhanced, which is typically the case, as it was in this study. Nevertheless, the greatest CO_2-induced growth increase of Zerihun *et al.*'s study was exhibited by the plants growing in the high soil nitrogen treatment.

Deng and Woodward (1998) grew strawberries in environment-controlled glasshouses maintained at atmospheric CO_2 concentrations of 390 and 560 ppm for nearly three months. In addition, the strawberries were supplied with fertilizers containing three levels of nitrogen. The extra CO_2 increased rates of net photosynthesis and total plant dry weight at all three nitrogen levels, but the increases were not significant. Nevertheless, they provided the CO_2-enriched plants with enough additional sugar and physical mass to support significantly greater numbers of flowers and fruits than the plants grown at 390 ppm CO_2. This effect consequently led to total fresh fruit weights that were 42 and 17 percent greater in the CO_2-enriched plants that received the highest and lowest levels of nitrogen fertilization, respectively, once again indicating a greater growth response at higher nitrogen levels.

Newman *et al*. (2003) investigated the effects of two levels of nitrogen fertilization and an approximate doubling of the air's CO_2 concentration on the growth of tall fescue, which is an important forage crop. The plants with which they worked were initially grown from seed in greenhouse flats, but after sixteen weeks they were transplanted into 19-liter pots filled with potting media that received periodic applications of a slow-release fertilizer. Then, over the next two years of outdoor growth, they were periodically clipped, divided and repotted to ensure they did not become root-bound; and at the end of that time, they were placed within twenty 1.3-m-diameter open-top chambers, half of which were maintained at the ambient atmospheric CO_2 concentration and half of which were maintained at an approximately doubled CO_2 concentration of 700 ppm. In addition, half of the pots in each CO_2

treatment received 0.0673 kg N m^{-2} applied over a period of three consecutive days, while half of them received only one-tenth that amount, with the entire procedure being repeated three times during the course of the 12-week experiment. Newman *et al.* report that the plants grown in the high-CO_2 air photosynthesized 15 percent more and produced 53 percent more dry matter (DM) under low N conditions and 61 percent more DM under high N conditions. In addition, they report that the percent organic matter (OM) was little changed, except under elevated CO_2 and high N, when %OM (as %DM) increased by 3 percent. In this study too, therefore, the greatest relative increase in productivity occurred under high, as opposed to low, soil N availability.

Demmers-Derks *et al.* (1998) grew sugar beets as an annual crop in controlled-environment chambers at atmospheric CO_2 concentrations of 360 and 700 ppm and air temperatures of ambient and ambient plus 3°C for three consecutive years. In addition to being exposed to these CO_2 and temperature combinations, the sugar beets were supplied with solutions of low and high nitrogen content. Averaged across all three years and both temperature regimes, the extra CO_2 of this study enhanced total plant biomass by 13 and 25 percent in the low and high nitrogen treatments, respectively. In addition, it increased root biomass by 12 and 26 percent for the same situations. As was the case with sunflowers, strawberries and tall fescue, elevated CO_2 elicited the largest growth responses in the sugar beets that received a high, as opposed to a low, supply of nitrogen.

Also working with sugar beets were Romanova *et al.* (2002), who grew them from seed for one month in controlled environment chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm, while fertilizing them with three different levels of nitrate-nitrogen. In this study, the plants grown in CO_2-enriched air exhibited rates of net photosynthesis that were approximately 50 percent greater than those displayed by the plants grown in ambient air, regardless of soil nitrate availability. These CO_2-induced increases in photosynthetic carbon uptake contributed to 60, 40 and 30 percent above-ground organ dry weight increases in plants receiving one-half, standard, and three-fold levels of soil nitrate, respectively. Root weights, however, were less responsive to atmospheric CO_2 enrichment, displaying 10 and 30 percent increases in dry weight at one-half and standard nitrate levels, but no increase at the high soil nitrate concentration. In this study, therefore, the role of soil nitrogen fertility was clearly opposite to that observed in the four prior studies in the case of above-ground biomass production, but was mixed in the case of belowground biomass production.

Switching to barley, Fangmeier *et al.* (2000) grew plants in containers placed within open-top chambers maintained at atmospheric CO_2 concentrations of either 360 or 650 ppm and either a high or low nitrogen fertilization regime. As in the case of the above-ground biomass response of the sugar beets of Romanova *et al.*, the elevated CO_2 had the greatest relative impact on yield when the plants were grown under the *less*-than-optimum *low*-nitrogen regime, i.e., a 48 percent increase vs. 31 percent under high-nitrogen conditions.

Last, we report the pertinent results of the review and analysis of Kimball *et al.* (2002), who summarized the findings of most FACE studies conducted on agricultural crops since the introduction of that technology back in the late 1980s. In response to a 300-ppm increase in the air's CO_2 concentration, rates of net photosynthesis in several C_3 grasses were enhanced by an average of 46 percent under conditions of ample soil nitrogen supply and by 44 percent when nitrogen was limiting to growth. With respect to above-ground biomass production, the differential was much larger, with the C_3 grasses wheat, rice and ryegrass experiencing an average increase of 18 percent at ample nitrogen but only 4 percent at low nitrogen; while with respect to belowground biomass production, they experienced an average increase of 70 percent at ample nitrogen and 58 percent at low nitrogen. Similarly, clover experienced a 38 percent increase in belowground biomass production at ample soil nitrogen, and a 32 percent increase at low soil nitrogen. Finally, with respect to agricultural yield, which is the bottom line in terms of food and fiber production, wheat and ryegrass experienced an average increase of 18 percent at ample nitrogen, while wheat experienced only a 10 percent increase at low nitrogen.

In light of these several results, it can be safely concluded that although there are some significant exceptions to the rule, most agricultural crops generally experience somewhat greater CO_2-induced relative (percentage) increases in net photosynthesis and biomass production even when soil nitrogen concentrations are a limiting factor.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/n/nitrogenagriculture.php.

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7.3.7.2. Fungi

Nearly all of earth's plants become involved in intimate relationships with different fungal species at one point or another in their life cycles. Among other things, the fungi commonly aid plants in the acquisition of water and important soil nutrients. In addition, fungal-plant interactions are often impacted by variations in both atmospheric CO_2 and soil nitrogen concentrations. In this subsection, we review how various aspects of fungal-plant interactions are influenced by elevated CO_2 under varying soil nitrogen regimes.

In a one-year study conducted by Walker *et al.* (1998), ponderosa pine seedlings exposed to atmospheric CO_2 concentrations of 525 and 700 ppm displayed total numbers of ectomycorrhizal fungi on their roots that were 170 and 85 percent greater, respectively, than those observed on roots of ambiently grown seedlings.

In the study of Rillig *et al.* (1998), three grasses and two herbs fumigated with ambient air and air containing an extra 350 ppm CO_2 for four months displayed various root infection responses by arbuscular mycorrhizal fungi, which varied with soil nitrogen supply. At low soil nitrogen contents, elevated CO_2 increased the percent root infection by this type of fungi in all five annual grassland species. However, at high soil nitrogen contents, this trend was reversed in four of the five species.

Finally, in the study of Rillig and Allen (1998), several important observations were made with respect to the effects of elevated CO_2 and soil nitrogen status on fungal-plant interactions. First, after growing three-year-old shrubs at an atmospheric CO_2 concentration of 750 ppm for four months, they reported insignificant 19 and 9 percent increases in percent root infected by arbuscular mycorrhizal fungi at low and high soil nitrogen concentrations, respectively. However, elevated CO_2 significantly increased the percent root infection by arbuscules, which are the main structures involved in the symbiotic exchange of carbon and nutrients between a host plant and its associated fungi, by more than 14-fold at low soil nitrogen concentrations. In addition, the length of fungal hyphae more than doubled with atmospheric CO_2 enrichment in the low soil nitrogen regime. In the high soil nitrogen treatment, elevated CO_2 increased the percent root infection by vesicles, which are organs used by arbuscular mycorrhizal fungi for carbon storage, by approximately 2.5-fold.

In conclusion, these observations suggest that elevated CO_2 will indeed affect fungal-plant interactions in positive ways that often depend upon soil nitrogen status. Typically, it appears that CO_2-induced stimulations of percent root infection by various fungal components is greater under lower, rather than higher, soil nitrogen concentrations. This tendency implies that elevated CO_2 will enhance fungal-plant interactions to a greater extent when soil nutrition is less-than-optimal for plant growth, which is the common case for most of earth's ecosystems that are not subjected to cultural fertilization practices typical of intensive agricultural production.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/n/nitrogenfungi.php.

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7.3.7.3. Grasses

Perennial ryegrass (*Lolium perenne* L.) has been used as a model species in many experiments to help elucidate grassland responses to atmospheric CO_2 enrichment and soil nitrogen availability. In the FACE study of Rogers *et al*. (1998), for example, plants exposed to 600 ppm CO_2 exhibited a 35 percent increase in their photosynthetic rates without regard to soil nitrogen availability. However, when ryegrass was grown in plastic ventilated tunnels at twice-ambient concentrations of atmospheric CO_2, the CO_2-induced photosynthetic response was about 3-fold greater in a higher, as opposed to a lower, soil nitrogen regime (Casella and Soussana, 1997). Similarly, in an open-top chamber study conducted by Davey *et al*. (1999), it was reported that an atmospheric CO_2 concentration of 700 ppm stimulated photosynthesis by 30 percent in this species when it was grown with moderate, but not low, soil nitrogen availability. Thus, CO_2-induced photosynthetic stimulations in perennial ryegrass can be influenced by soil nitrogen content, with greater positive responses typically occurring under higher, as opposed to lower, soil nitrogen availability.

With respect to biomass production, van Ginkel and Gorissen (1998) reported that a doubling of the atmospheric CO_2 concentration increased shoot biomass of perennial ryegrass by 28 percent, regardless of soil nitrogen concentration. In the more revealing six-year FACE study of Daepp *et al*. (2000), plants grown at 600 ppm CO_2 and high soil nitrogen availability continually increased their dry matter production over that observed in ambient-treatment plots, from 8 percent more in the first year to 25 percent more at the close of year six. When grown at a low soil nitrogen availability, however, CO_2-enriched plants exhibited an initial 5 percent increase in dry matter production, which dropped to a negative 11 percent in year two; but this negative trend was thereafter turned around, and it continually rose to reach a 9 percent stimulation at the end of the study. Thus, these data demonstrate that elevated CO_2 increases perennial ryegrass biomass, even under conditions of low soil nitrogen availability, especially under conditions of long-term atmospheric CO_2 enrichment.

Lutze *et al*. (1998) reported that microcosms of the C_3 grass *Danthonia richardsonii* grown for four years in glasshouses fumigated with air containing 720 ppm CO_2 displayed total photosynthetic carbon gains that were 15-34 percent higher than those of ambiently grown microcosms, depending on the soil nitrogen concentration. In a clearer depiction of photosynthetic responses to soil nitrogen, Davey *et al*. (1999) noted that photosynthetic rates of *Agrostis capillaries* subjected to twice-ambient levels of atmospheric CO_2 for two years were 12 and 38 percent greater than rates measured in control plants grown at 350 ppm CO_2 under high and low soil nitrogen regimes, respectively. They also reported CO_2-induced photosynthetic stimulations of 25 and 74 percent for *Trifolium repens* subjected to high and low soil nitrogen regimes, respectively. Thus, we see that the greatest CO_2-induced percentage increase in photosynthesis can sometimes occur under the *least* favorable soil nitrogen conditions.

With respect to biomass production, Navas *et al*. (1999) reported that 60 days' exposure to 712 ppm CO_2 increased biomass production of *Danthonia richardsonii*, *Phalaris aquatica*, *Lotus pedunculatus*, and *Trifolium repens* across a large soil nitrogen gradient. With slightly more detail, Cotrufo and Gorissen (1997) reported average CO_2-induced increases in whole-plant dry weights of *Agrostis capillaries* and *Festuca ovina* that were 20 percent greater than those of their respective controls, regardless of soil nitrogen availability. In the study of Ghannoum and Conroy (1998), three *Panicum* grasses grown for two months at twice-ambient levels of atmospheric CO_2 and high soil nitrogen availability displayed similar increases in total plant dry mass that were about 28 percent greater than those of their respective ambiently grown controls. At low nitrogen, however, elevated CO_2 had no significant effect on the dry mass of two of the species, while it actually decreased that of the third species.

In summary, it is clear that atmospheric CO_2 enrichment stimulates photosynthesis and biomass production in grasses and grassland species when soil nitrogen availability is high and/or moderate. Under lower soil nitrogen conditions, it is also clear that atmospheric CO_2 enrichment can have the same positive effect on these parameters, but that it can also have a reduced positive effect, no effect, or (in one case) a negative effect. In light of the one long-term study that lasted six years, however, it is likely that—given enough time—grasslands have the ability to overcome soil nitrogen limitations and produce positive CO_2-induced growth responses. Thus, because the rising CO_2 content of the air is likely to continue for a long time to come, occasional nitrogen limitations on the aerial fertilization effect of atmospheric CO_2 enrichment of grasslands will likely become less and less restrictive as time progresses.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/n/nitrogengrass.php.

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7.3.7.4. Trees

7.3.7.4.1. Aspen

Does a deficiency of soil nitrogen lessen the relative growth stimulation of quaking aspen (*Populus tremuloides* Michx) that is typically provided by elevated concentrations of atmospheric CO_2?

In exploring this question, Kubiske *et al*. (1998) grew cuttings of four quaking aspen genotypes for five months at CO_2 concentrations of 380 or 720 ppm and low or high soil nitrogen in open-top chambers in the field in Michigan, USA. They found that the elevated CO_2 treatment significantly increased net photosynthesis, regardless of soil nitrogen content, although there were no discernible increases in above-ground growth within the five-month study period. Belowground, however, elevated CO_2 significantly increased fine root production, but only in the high soil nitrogen treatment.

Working at the same site, Zak *et al*. (2000) and Curtis *et al*. (2000) grew six aspen genotypes from cuttings in open-top chambers for 2.5 growing seasons at atmospheric CO_2 concentrations of 350 and 700 ppm on soils containing either adequate or inadequate supplies of nitrogen. Curtis *et al*. report that at the end of this period the trees growing in the doubled-CO_2 treatment exhibited rates of net photosynthesis that were 128 percent and 31 percent greater than those of the trees growing in the ambient-air treatment on the high- and low-nitrogen soils, respectively, while Zak *et al*. determined the CO_2-induced biomass increases of the trees in the high- and low-nitrogen soils to be 38 percent and 16 percent, respectively.

In yet another study from the Michigan site, Mikan *et al*. (2000) grew aspen cuttings for two years in open-top chambers receiving atmospheric CO_2 concentrations of 367 and 715 ppm in soils of low and high soil nitrogen concentrations. They report finding that elevated CO_2 increased the total biomass of the aspen cuttings by 50 percent and 26 percent in the high and low soil nitrogen treatments, respectively, and that it increased coarse root biomass by 78 percent and 24 percent in the same respective treatments.

Last, but again at the same site, Wang and Curtis (2001) grew cuttings of two male and two female aspen trees for about five months in open-top chambers maintained at atmospheric CO_2 concentrations of 380 and 765 ppm on soils of high and low nitrogen content. In the male cuttings, there was a modest difference in the CO_2-induced increase in total biomass (58 percent and 66 percent in the high- and low-nitrogen soils, respectively), while in the female cuttings the difference was much greater (82 percent and 22 percent in the same respective treatments).

Considering the totality of these several observations, it would appear that the degree of soil nitrogen availability does indeed impact the aerial fertilization effect of atmospheric CO_2 enrichment on the growth of aspen trees by promoting a greater CO_2-induced growth enhancement in soils of adequate, as opposed to insufficient, nitrogen content.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/n/nitrogenaspen.php.

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7.3.7.4.2. Pine

In a review of eleven of their previously published papers dealing with both loblolly pine (*Pinus taeda* L.) and ponderosa pine (*Pinus ponderosa* Dougl.), Johnson *et al*. (1998) report that when soil nitrogen levels were so low as to be extremely deficient, or so high as to be toxic, growth responses to atmospheric CO_2 enrichment in both species were negligible. For moderate soil nitrogen deficiencies, however, a doubling of the air's CO_2 content sometimes boosted growth by as much as 1,000 percent. In addition, atmospheric CO_2 enrichment mitigated the negative growth response of ponderosa pine to extremely high soil nitrogen concentrations.

In a second paper published by some of the same scientists in the same year, Walker *et al*. (1998) describe how they raised ponderosa pine tree seedlings for two growing seasons in open-top chambers having CO_2 concentrations of 350, 525 and 700 ppm on soils of low, medium and high nitrogen content. They report that elevated CO_2 had little effect on most growth parameters after the first growing season, the one exception being belowground biomass, which increased with both CO_2 and soil nitrogen. After two growing seasons, however, elevated CO_2 significantly increased all growth parameters, including tree height, stem diameter, shoot weight, stem volume and root volume, with the greatest responses typically occurring at the highest CO_2 concentration in the highest soil nitrogen treatment. Root volume at 700 ppm CO_2 and high soil nitrogen, for example, exceeded that of all other treatments by at least 45 percent, as did shoot volume by 42 percent. Similarly, at high CO_2 and soil nitrogen, coarse root and shoot weights exceeded those at ambient CO_2 and high nitrogen by 80 and 88 percent, respectively.

Walker *et al*. (2000) published another paper on the same trees and treatments after five years of growth. At this time, the trees exposed to the twice-ambient levels of atmospheric CO_2 had heights that were 43, 64 and 25 percent greater than those of the trees exposed to ambient air and conditions of high, medium and low levels of soil nitrogen, respectively. Similarly, the trunk diameters of the 700-ppm-trees were 24, 73 and 20 percent greater than the trunk diameters of the ambiently grown trees exposed to high, medium and low levels of soil nitrogen.

Switching to a different species, Entry *et al*. (1998) grew one-year-old longleaf pine seedlings for 20 months in pots of high and low soil nitrogen content within open-top chambers maintained at atmospheric CO_2 concentrations of 365 or 720 ppm, finding that the elevated CO_2 caused no overall change in whole-plant biomass at low soil nitrogen, but that at high soil nitrogen, it increased it by 42 percent. After two years of these treatments, Runion *et al*. (1999) also reported that rates of net photosynthesis were about 50 percent greater in the high CO_2 treatment, irrespective of soil nitrogen content … and water content too.

Last, Finzi and Schlesinger (2003) measured and analyzed the pool sizes and fluxes of inorganic and organic nitrogen (N) in the floor and top 30 cm of mineral soil of the Duke Forest at the five-year point of a long-term FACE study, where half of the experimental plots are enriched with an extra 200 ppm of CO_2. In commencing this study, they had originally hypothesized that "the increase in carbon fluxes to the microbial community under elevated CO_2 would increase the rate of N immobilization over mineralization," leading to a decline in the significant CO_2-induced stimulation of forest net primary production that developed over the first two years of the experiment (DeLucia *et al*., 1999; Hamilton *et al*., 2002). Quite to the contrary, however, they discovered "there was no statistically significant change in the cycling rate of N derived from soil organic matter under elevated CO_2." Neither was the rate of net N mineralization significantly altered by elevated CO_2, nor was there any statistically significant difference in the concentration or net flux of organic and inorganic N in the forest floor and top 30-cm of mineral soil after 5 years of CO_2 fumigation. Hence, at this stage of the study, they could find no support for their original hypothesis, which suggests that the growth stimulation provided by elevated levels of atmospheric CO_2 would gradually dwindle away to something rather insignificant before the stand reached its equilibrium biomass, although they continue to cling to this unsubstantiated belief.

Considering the totality of these several observations, it would appear that the degree of soil nitrogen availability impacts the effect of atmospheric CO_2 enrichment on the growth of pine trees, with greater CO_2-induced growth enhancement occurring in soils of adequate, as opposed to insufficient, nitrogen content. As in the case of aspen, however, there is evidence to suggest that at some point the response to increasing soil nitrogen saturates, and beyond that point, higher N concentrations may sometimes even reduce the forest growth response to elevated CO_2.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/n/nitrogenpine.php.

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7.3.7.4.3. Spruce

Egli *et al*. (1998) rooted saplings of different genotypes of Norway spruce (*Picea abies* L. Karst.) directly into calcareous or acidic soils in open-top chambers and exposed them to atmospheric CO_2 concentrations of 370 or 570 ppm and low or high soil nitrogen contents. They found that elevated CO_2 generally stimulated light-saturated rates of photosynthesis under all conditions by as much as 35 percent, regardless of genotype, which consistently led to increased above-ground biomass production, also regardless of genotype, as well as without respect to soil type or nitrogen content.

Murray *et al*. (2000) grew Sitka spruce (*Picea sitchensis* (Bong.) Carr.) seedlings for two years in pots within open-top chambers maintained at atmospheric CO_2 concentrations of 355 and 700 ppm. In the last year of the study, half of the seedlings received one-tenth of the optimal soil nitrogen supply recommended for this species, while the other half received twice the optimal amount. Under this protocol, the extra CO_2 increased the seedlings' light-saturated rates of net photosynthesis by 19 percent and 33 percent in the low- and high-nitrogen treatments, respectively, while it increased their total biomass by 0 percent and 37 percent in these same treatments. Nevertheless, Murray *et al*. note there was a reallocation of biomass from above-ground organs (leaves and stems) into roots in the low-nitrogen treatment; and they remark that this phenomenon "may provide a long-term mechanism by which Sitka spruce could utilize limited resources both more efficiently and effectively," which suggests that although low soil nitrogen precluded a short-term CO_2-induced growth response in this tree species, it is possible that the negative impact of nitrogen deficiency could be overcome in the course of much longer-term atmospheric CO_2 enrichment.

In a related experiment, Liu *et al*. (2002) grew Sitka spruce seedlings in well-watered and fertilized pots within open-top chambers that were maintained for three years at atmospheric CO_2 concentrations of either 350 or 700 ppm, after which the seedlings were planted directly into native nutrient-deficient forest soil and maintained at the same atmospheric CO_2 concentrations for two more years in larger open-top chambers either with or without extra nitrogen being supplied to the soil. After the first three years of the study, they determined that the CO_2-enriched trees possessed 11.6 percent more total biomass than the ambient-treatment trees. At the end of the next two years, however, the CO_2-enriched trees supplied with extra nitrogen had 15.6 percent more total biomass than their similarly treated ambient-air counterparts, while the CO_2-enriched trees receiving no extra nitrogen had 20.5 percent more biomass than their ambient-treatment counterparts.

In light of these several observations, it would appear that the degree of soil nitrogen availability affects the growth of spruce trees by promoting a greater CO_2-induced growth enhancement in soils of adequate, as opposed to insufficient, nitrogen content. As in the cases of aspen and pine, however, at some point the response of spruce trees to increasing soil nitrogen saturates, and even higher nitrogen concentrations may reduce the growth response to elevated CO_2 below that observed at optimal or low soil nitrogen concentrations.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/n/nitrogenspruce.php.

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7.3.7.4.4. Other

Maillard *et al*. (2001) grew pedunculate oak seedlings for three to four months in greenhouses maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm under conditions of either low or high soil nitrogen concentration. The elevated CO_2 of their study stimulated belowground growth in the seedlings growing in the nitrogen-poor soil, significantly increasing their root-to-shoot ratios. However, it increased both the below- and above-ground biomass of seedlings growing in nitrogen-rich soil. In fact, the CO_2-enriched seedlings growing in the nitrogen-rich soil produced 217 and 533 percent more stem and coarse-root biomass, respectively, than their ambient-air counterparts growing in the same fertility treatment. Overall, the doubled CO_2 concentration of the air in their study enhanced total seedling biomass by approximately 30 and 140 percent under nitrogen-poor and nitrogen-rich soil conditions, respectively.

Schortemeyer *et al*. (1999) grew seedlings of *Acacia melanoxylon* (a leguminous nitrogen-fixing tree native to south-eastern Australia) in hydroponic culture for six weeks in growth cabinets, where the air was maintained at CO_2 concentrations of either 350 or 700 ppm and the seedlings were supplied with water containing nitrogen in a number of discrete concentrations ranging from 3 to 6,400 mmol m^{-3}. In the two lowest of these nitrogen concentration treatments, final biomass was unaffected by atmospheric CO_2 enrichment; but, as in the study of Maillard *et al*., it was increased by 5- to 10-fold at the highest nitrogen concentration.

Temperton *et al*. (2003) measured total biomass production in another N_2-fixing tree—*Alnus glutinosa* (the common alder)—seedlings of which had been grown for three years in open-top chambers in either ambient or elevated (ambient + 350 ppm) concentrations of atmospheric CO_2 and one of two soil nitrogen regimes (full nutrient solution or no fertilizer). In their study, by contrast, they found that the trees growing under low soil nutrient conditions exhibited essentially the *same* growth enhancement as that of the well-fertilized trees.

Rounding out the full gamut of growth responses, Gleadow *et al*. (1998) grew eucalyptus seedlings for six months in glasshouses maintained at atmospheric CO_2 concentrations of either 400 or 800 ppm, fertilizing them twice daily with low or high nitrogen solutions. They found that their doubling of the air's CO_2 concentration increased total seedling biomass by 134 percent in the low nitrogen treatment but by a smaller 98 percent in the high nitrogen treatment. In addition, the elevated CO_2 led to greater root growth in the low nitrogen treatment, as indicated by a 33 percent higher root:shoot ratio.

In conclusion, different species of trees respond differently to atmospheric CO_2 enrichment under conditions of low vs. high soil nitrogen fertility. The most common response is for the growth-promoting effects of atmospheric CO_2 enrichment to be expressed to a greater degree when soil nitrogen fertility is optimal as opposed to less-than-optimal.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/o/ozonetreemisc.php.

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7.3.8. High Salinity

In managed agricultural ecosystems, the buildup of soil salinity from repeated irrigations can sometimes reduce crop yields. Similarly, in natural ecosystems where exposure to brackish or salty water is commonplace, saline soils can induce growth stress in plants not normally adapted to coping with this problem. Thus, it is important to understand how rising atmospheric CO_2 concentrations may interact with soil salinity to affect plant growth.

In the study of Ball *et al*. (1997), it was found that two Australian mangrove species with differing tolerance to salinity exhibited increased rates of net photosynthesis in response to a doubling of the atmospheric CO_2 concentration, but only when exposed to salinity levels that were 25 percent, but not 75 percent, of full-strength seawater.

Mavrogianopoulos *et al*. (1999) reported that atmospheric CO_2 concentrations of 800 and 1200 ppm stimulated photosynthesis in parnon melons by 75 and 120 percent, respectively, regardless of soil salinity, which ranged from 0 to 50 mM NaCl. Moreover, the authors noted that atmospheric CO_2 enrichment partially alleviated the negative effects of salinity on melon yield, which increased with elevated CO_2 at all salinity levels.

Maggio *et al*. (2002) grew tomatos at 400 and 900 ppm in combination with varying degrees of soil salinity and noted that plants grown in elevated CO_2 tolerated an average root-zone salinity threshold value that was about 60 percent greater than that exhibited by plants grown at 400 ppm CO_2 (51 vs. 32 mmol dm^{-3} Cl).

The review of Poorter and Perez-Soba (2001) found no changes in the effect of elevated CO_2 on the growth responses of most plants over a wide range of soil salinities, in harmony with the earlier findings of Idso and Idso (1994).

These various studies suggest that elevated CO_2 concentrations have either positive or no effects on plan growth where mild to moderate stresses may be present due to high soil salinity levels. Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/s/salinity stress.php.

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7.3.9. Elevated Temperature

Will plants continue to exhibit CO_2-induced growth increases under conditions of elevated air temperature? In this section, we review the photosynthetic and growth responses of agricultural crops, grasslands and woody species to answer this question.

7.3.9.1. Agricultural Crops

The optimum growth temperature for several plants has been shown to rise substantially with increasing levels of atmospheric CO_2 (McMurtrie and Wang, 1993; McMurtrie *et al*., 1992; Stuhlfauth and Fock, 1990; Berry and Bjorkman, 1980). This phenomenon was predicted by Long (1991), who calculated from well-established plant physiological principles that most C_3 plants should increase their optimum growth temperature by approximately 5°C for a 300 ppm increase in the air's CO_2 content. One would thus also expect plant photosynthetic rates to rise with concomitant increases in the air's CO_2 concentration and temperature, as has indeed been previously shown to be true by Idso and Idso (1994). We here proceed to see if these positive CO_2 and temperature interactions are still being supported in the recent scientific literature.

In the study of Zhu *et al*. (1999), pineapples grown at 700 ppm CO_2 assimilated 15, 97 and 84 percent more total carbon than pineapples grown at the current ambient CO_2 concentration in day/night air temperature regimes of 30/20 (which is optimal for pineapple growth at ambient CO_2), 30/25, and 35/25 °C, respectively. Similarly, Taub *et al*. (2000) demonstrated that net photosynthetic rates of cucumbers grown at twice-ambient levels of atmospheric CO_2 and air temperatures of 40°C were 3.2 times greater than those displayed by control plants grown at ambient CO_2 and this same elevated air temperature. Thus, at air temperatures normally considered to be deleterious to plant growth, rates of photosynthesis are typically considerably greater for CO_2 enriched vs. ambiently grown plants.

Reddy *et al.* (1999) grew cotton plants at air temperatures ranging from 2°C below to 7°C above ambient air temperatures and reported that plants simultaneously exposed to 720 ppm CO_2 displayed photosynthetic rates that were 137 to 190 percent greater than those displayed by plants exposed to ambient CO_2 concentrations across this temperature spectrum. Similarly, Cowling and Sage (1998) reported that a 200-ppm increase in the air's CO_2 concentration boosted photosynthetic rates of young bean plants by 58 and 73 percent at growth temperatures of 25 and 36°C, respectively. In addition, Bunce (1998) grew wheat and barley at 350 and 700 ppm CO_2 across a wide range of temperatures and reported that elevated CO_2 stimulated photosynthesis in these species by 63 and 74 percent, respectively, at an air temperature of 10°C and by 115 and 125 percent at 30°C. Thus, the percentage increase in photosynthetic rate resulting from atmospheric CO_2 enrichment often increases substantially with increasing air temperature.

Elevated CO_2 often aids in the recovery of plants from high temperature-induced reductions in photosynthetic capacity, as noted by Ferris *et al.* (1998), who grew soybeans for 52 days under normal air temperature and soil water conditions at atmospheric CO_2 concentrations of 360 and 700 ppm, but then subjected them to an 8-day period of high temperature and water stress. After normal air temperature and soil water conditions were restored, the CO_2-enriched plants attained photosynthetic rates that were 72 percent of their unstressed controls, while stressed plants grown at ambient CO_2 attained photosynthetic rates that were only 52 percent of their respective controls.

CO_2-induced increases in plant growth under high air temperatures have also been observed in a number of other agricultural species. In the previously mentioned study of Cowling and Sage (1998), for example, the 200-ppm increase in the air's CO_2 content boosted total plant biomass for wheat and barley by a combined average of 59 and 200 percent at air temperatures of 25 and 36°C. Similarly, Ziska (1998) reported that a doubling of the atmospheric CO_2 concentration increased the total dry weight of soybeans by 36 and 42 percent at root zone temperatures of 25 and 30°C, respectively. Likewise, Hakala (1998) noted that spring wheat grown at 700 ppm CO_2 attained total biomass values that were 17 and 23 percent greater than those attained by ambiently grown plants exposed to ambient and elevated (ambient plus 3°C) air temperatures. In addition, after inputting various observed CO_2-induced growth responses of winter wheat into plant growth models, Alexandrov and Hoogenboom (2000) predicted 12 to 49 percent increases in wheat yield in Bulgaria even if air temperatures rise by as much as 4°C. Finally, in the study of Reddy *et al.* (1998), it was shown that elevated CO_2 (700 ppm) increased total cotton biomass by 31 to 78 percent across an air temperature range from 20 to 40°C. Thus, the beneficial effects of elevated CO_2 on agricultural crop yield is often enhanced by elevated air temperature.

In some cases, however, elevated CO_2 does not interact with air temperature to further increase the growth-promoting effects of atmospheric CO_2 enrichment, but simply allows the maintenance of the status quo. In the study of Demmers-Derks *et al.* (1998), for example, sugar beets grown at 700 ppm CO_2 attained 25 percent more biomass than ambiently grown plants, regardless of air temperature, which was increased by 3°C. Similarly, in the study of Fritschi *et al.* (1999), elevated CO_2 concentrations did not significantly interact with air temperature (4.5°C above ambient) to impact the growth of rhizoma peanut. Nonetheless, the 300-ppm increase in the air's CO_2 content increased total biomass by 52 percent, regardless of air temperature.

Finally, even if the air's CO_2 content were to cease rising or have no effect on plants, it is possible that temperature increases alone would promote plant growth and development. This was the case in the study of Wurr *et al.* (2000), where elevated CO_2 had essentially no effect on the yield of French bean. However, a 4°C increase in air temperature increased yield by approximately 50 percent.

In conclusion, the recent scientific literature continues to indicate that as the air's CO_2 content rises, agricultural crops will likely exhibit enhanced rates of photosynthesis and biomass production that will not be diminished by any global warming that might occur concurrently. In fact, if the ambient air temperature rises, the growth-promoting effects of atmospheric CO_2 enrichment will likely rise along with it.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/tempco2ag.php.

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7.3.9.2. Grassland Species

In the study of Lilley *et al*. (2001), swards of *Trifolium subterraneum* were grown at 380 and 690 ppm CO_2 in combination with simultaneous exposure to ambient and elevated (ambient plus 3.4°C) air temperature. After one year of treatment, they reported that elevated CO_2 increased foliage growth by 19 percent at ambient air temperature. At elevated air temperature, however, plants grown at ambient CO_2 exhibited a 28 percent reduction in foliage growth, while CO_2-enriched plants still displayed a growth enhancement of 8 percent. Similarly, Morgan *et al*. (2001) reported that twice-ambient levels of atmospheric CO_2 increased above-ground biomass in native shortgrass steppe ecosystems by an average of 38 percent, in spite of an average air temperature increase of 2.6°C. Likewise, when bahiagrass was grown across a temperature gradient of 4.5°C, Fritschi *et al*. (1999) reported that a 275 ppm increase in the air's CO_2 content boosted photosynthesis and above-ground biomass by 22 and 17 percent, respectively, independent of air temperature. Thus, at elevated air temperature, CO_2-induced increases in rates of photosynthesis and biomass production are typically equal to or greater than what they are at ambient air temperature.

Other studies report similar results. Greer *et al.* (2000), for example, grew five pasture species at 18 and 28°C and reported that plants concomitantly exposed to 700 ppm CO_2 displayed average photosynthetic rates that were 36 and 70 percent greater, respectively, than average rates exhibited by control plants subjected to ambient CO_2 concentrations. Moreover, the average CO_2-induced biomass increase for these five species rose dramatically with increasing air temperature: from only 8 percent at 18°C to 95 percent at 28°C. Thus, the beneficial effects of elevated CO_2 on grassland productivity is often significantly enhanced by elevated air temperature.

Finally, temperature increases alone can promote grass growth and development. Norton *et al.* (1999) found elevated CO_2 had essentially no effect on the growth of the perennial grass *Agrostis curtisii* after two years of fumigation; however, a 3°C increase in air temperature increased the growth of this species considerably.

In conclusion, grassland plants will likely exhibit enhanced rates of photosynthesis and biomass production as the air's CO_2 content rises that will not be diminished by any global warming that might occur concurrently. If the ambient air temperature rises, the growth-promoting effects of atmospheric CO_2 enrichment will likely rise along with it.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/tempco2grass.php.

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7.3.9.3. Trees

In the study of Kellomaki and Wang (2001), birch seedlings were grown at atmospheric CO_2 concentrations of 350 and 700 ppm in combination with ambient and elevated (ambient plus 3°C) air temperatures. After five months of treatment, the authors reported that photosynthetic rates of CO_2-enriched seedlings were 21 and 28 percent greater than those displayed by their ambiently grown counterparts at ambient and elevated air temperatures, respectfully. In another study, Carter *et al.* (2000) observed that a 300 ppm increase in the air's CO_2 content allowed leaves of sugar maple seedlings to remain green and non-chlorotic when exposed to air temperatures 3°C above ambient air temperature. On the other hand, seedlings fumigated with ambient air exhibited severe foliar chlorosis when exposed to the same elevated air temperatures. These results thus indicate that at elevated air temperatures, rates of photosynthesis are greater and foliar health is typically better in birch and sugar maples trees in CO_2-enriched as opposed to ambient air.

Other studies report similar results. Sheu *et al.* (1999) grew a sub-tropical tree at day/night temperatures of 25/20°C (ambient) and 30/25°C (elevated) for six months and reported that seedlings exposed to 720 ppm CO_2 displayed photosynthetic rates that were 20 and 40 percent higher, respectively, than that of their ambiently grown controls. In addition, the CO_2-induced increases in total dry weight for this species were 14 and 49 percent, respectively, at ambient and elevated air temperatures. Likewise, Maherali *et al*. (2000) observed that a 5°C increase in ambient air temperature increased the CO_2-induced biomass enhancement resulting from a 750 ppm CO_2 enrichment of ponderosa pine seedlings from 42 to 62 percent. Wayne *et al*. (1998) reported that a 5°C increase in the optimal growth temperature of yellow birch seedlings fumigated with an extra 400 ppm CO_2 increased the CO_2-induced increase in biomass from 60 to 227 percent. The beneficial effects of elevated CO_2 on tree species photosynthesis and growth can also be assessed during natural seasonal temperature changes, as documented by Hymus *et al*. (1999) for loblolly pine and Roden *et al*. (1999) for snow gum seedlings.

In some cases, however, there appear to be little interactive effects between elevated CO_2 and temperature on photosynthesis and growth in tree species. When Tjoelker *et al*. (1998a), for example, grew seedlings of quaking aspen, paper birch, tamarack, black spruce and jack pine at atmospheric CO_2 concentrations of 580 ppm, they reported average increases in photosynthetic rates of 28 percent, regardless of temperature, which varied from 18 to 30°C. After analyzing the CO_2-induced increases in dry mass for these seedlings, Tjoelker *et al*. (1998b) further reported that dry mass values were about 50 and 20 percent greater for the deciduous and coniferous species, respectively, regardless of air temperature.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/tempco2trees.php.

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7.3.9.4. Other

In a mechanistic model study of Mediterranean shrub vegetation, Osborne *et al*. (2000) reported that increased warming and reduced precipitation would likely decrease net primary production. However, when the same model was run at twice the ambient atmospheric CO_2 concentration, it predicted a 25 percent increase in vegetative productivity, in spite of the increased warming and reduced precipitation. Although we tend to not review studies based on mechanistic models, it is also interesting to note that Bunce (2000) demonstrated that field-grown *Taraxacum officinale* plants exposed to 525 ppm CO_2 and low air temperatures (between 15 and 25°C) displayed photosynthetic rates that were 10 to 30 percent greater than what was predicted by state-of-the-art biochemical models of photosynthesis for this range of temperatures. Thus, at both high and low air temperatures, elevated CO_2 appears to be capable of significantly increasing the photosynthetic prowess of some plants.

In the real world, Stirling *et al*. (1998) grew five fast-growing native species at various atmospheric CO_2 concentrations and air temperatures, finding that twice-ambient levels of atmospheric CO_2 increased photosynthetic rates by 18-36 percent for all species regardless of air temperature, which was up to 3°C higher than ambient air temperature. In addition, atmospheric CO_2 enrichment increased average plant biomass by 25 percent, also regardless of air temperature. Likewise, in a study of vascular plants from Antarctica, Xiong *et al*. (2000) reported that a 13°C rise in air temperature increased plant biomass by 2- to 3-fold. We can only imagine what the added benefit of atmospheric CO_2 enrichment would do for these species.

Hamerlynck *et al*. (2000) demonstrated that the desert perennial shrub *Larrea tridentata* maintained more favorable midday leaf water potentials during a nine-day high-temperature treatment when fumigated with 700 ppm CO_2, as compared to 350 ppm.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/tempco2growthres.php.

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7.3.10. UV-B Radiation

Zhao *et al*. (2004) report that "as a result of stratospheric ozone depletion, UV-B radiation (280-320 nm) levels are still high at the Earth's surface and are projected to increase in the near future (Madronich *et al*., 1998; McKenzie *et al*., 2003)." In reference to this potential development, they note that "increased levels of UV-B radiation are known to affect plant growth, development and physiological processes (Dai *et al*., 1992; Nogués *et al*., 1999)," stating that high UV-B levels often result in "inhibition of photosynthesis, degradation of protein and DNA, and increased oxidative stress (Jordan *et al*., 1992; Stapleton, 1992)." In light of the above observations, it is important to clarify how the ongoing rise in the air's CO_2 content might affect the deleterious effects of UV-B radiation on earth's vegetation.

To investigate this question, Zhao *et al*. grew well watered and fertilized cotton plants in sunlit controlled environment chambers maintained at atmospheric CO_2 concentrations of 360 or 720 ppm from emergence until three weeks past first-flower stage under three levels of UV-B radiation (0, 8 and 16 kJ m^{-2} d^{-1}). On five dates between 21 and 62 days after emergence, they measured a number of plant physiological processes and parameters. Over the course of the experiment, the mean net photosynthetic rate of the upper-canopy leaves in the CO_2-enriched chambers was increased—relative to that in the ambient-air chambers—by 38.3 percent in the low UV-B treatment (from 30.3 to 41.9 m m^{-2} s^{-1}), 41.1 percent in the medium UV-B treatment (from 28.7 to 40.5 m m^{-2} s^{-1}), and 51.5 percent in the high UV-B treatment (from 17.1 to 25.9 m m^{-2} s^{-1}). In the medium UV-B treatment, the growth stimulation from the elevated CO_2 was sufficient to raise net photosynthesis rates 33.7 percent above the rates experienced in the ambient air and no UV-B treatment (from 30.3 to 40.5 m m^{-2} s^{-1}); but in the high UV-B treatment the radiation damage was so great that even with the help of the 51.5 percent increase in net photosynthesis provided by the doubled-CO_2 air, the mean net photosynthesis rate of the cotton leaves was 14.5 percent less than that experienced in the ambient air and no UV-B treatment (dropping from 30.3 to 25.9 m m^{-2} s^{-1}).

It should be noted that the medium UV-B treatment of this study was chosen to represent the intensity of UV-B radiation presently received on a clear summer day in the major cotton production region of Mississippi, USA, under current stratospheric ozone conditions, while the high UV-B treatment was chosen to represent what might be expected there following a 30 percent depletion of the ozone layer, which has been predicted to double the region's reception of UV-B radiation from 8 to 16 kJ m^{-2} d^{-1}. Consequently, a doubling of the current CO_2 concentration and the current UV-B radiation level would reduce the net photosynthetic rate of cotton leaves by just under 10 percent (from 28.7 to 25.9 m m^{-2} s^{-1}), whereas in the absence of a doubling of the air's CO_2 content, a doubling of the UV-B radiation level would reduce cotton net photosynthesis by just over 40 percent (from 28.7 to 17.1 m m^{-2} s^{-1}).

Viewed in this light, it can be seen that a doubling the current atmospheric CO_2 concentration would compensate for over three-fourths of the loss of cotton photosynthetic capacity caused by a doubling of the current UV-B radiation intensity. It may do better than that, for in the study of Zhao *et al.* (2003), it was reported that both Adamse and Britz (1992) and Rozema *et al.* (1997) found that doubled CO_2 totally compensated for the negative effects of equally high UV-B radiation.

In another study (Qaderi and Reid, 2005), well watered and fertilized canola (*Brassica napus* L.) plants were grown from seed to maturity in pots within controlled environment chambers maintained at either 370 or 740 ppm CO_2 with and without a daily dose of UV-B radiation in the amount of 4.2 kJ m^{-2}, while a number of plant parameters were measured at various times throughout the growing season. With respect to the bottom-line result of final seed yield, this parameter was determined to be 0.98 g/plant in the control treatment (ambient CO_2, with UV-B). Doubling the CO_2 concentration increased yield by 25.5 percent to 1.23 g/plant. Alternatively, removing the UV-B radiation flux increased yield by 91.8 percent to 1.88 g/plant. Doing both (doubling the CO_2 concentration while simultaneously removing the UV-B flux) increased final seed yield most of all, by 175.5 percent to 2.7 g/plant. Viewed from a different perspective, doubling the air's CO_2 concentration in the *presence* of the UV-B radiation flux enhanced final seed yield by 25.5 percent, while doubling CO_2 in the *absence* of the UV-B radiation flux increased seed yield by 43.6 percent. In concluding their paper, the authors note that "previous studies have shown that elevated CO_2 increases biomass and seed yield, whereas UV-B decreases them (Sullivan, 1997; Teramura *et al*., 1990)." Finding much the same thing in their study, they thus reckoned that "elevated CO_2 may have a positive effect on plants by mitigating the detrimental effects caused by UV-B radiation."

Two years later in a similar study of the same plant, Qaderi *et al.* (2007) grew well watered and fertilized canola plants from the 30-day-old stage until 25 days after anthesis in 1-L pots within controlled environment chambers exposed to either 4.2 kJ m^{-2} d^{-1} of UV-B radiation or no such radiation in air of either 370 or 740 ppm CO_2, in order to determine the effects of these two parameters on the photosynthetic rates and water use efficiency of the maturing husks or *siliquas* that surround the plants' seeds. Results indicated that for the plants exposed to 4.2 kJ m^{-2} d^{-1} of UV-B radiation, the experimental doubling of the air's CO_2 concentration led to a 29 percent increase in siliqua net photosynthesis, an 18 percent decrease in siliqua transpiration, and a 58 percent increase in siliqua water use efficiency; while for the plants exposed to no UV-B radiation, siliqua net photosynthesis was increased by a larger 38 percent, transpiration was decreased by a larger 22 percent and water use efficiency was increased by a larger 87 percent in the CO_2-enriched air.

In another noteworthy study, Deckmyn *et al.* (2001) grew white clover plants for four months in four small greenhouses, two of which allowed 88 percent of the incoming UV-B radiation to pass through their roofs and walls and two of which allowed 82 percent to pass through, while one of the two greenhouses in each of the UV-B treatments was maintained at ambient CO_2 (371 ppm) and the other at elevated CO_2 (521 ppm). At the mid-season point of their study, they found that the 40 percent increase in atmospheric CO_2 concentration stimulated the production of flowers in the low UV-B treatment by 22 percent and in the slightly higher UV-B treatment by 43 percent; while at the end of the season, the extra CO_2 was determined to have provided no stimulation of biomass production in the low UV-B treatment, but it significantly stimulated biomass production by 16 percent in the high UV-B treatment.

The results of this study indicate that the positive effects of atmospheric CO_2 enrichment on flower and biomass production in white clover are greater at more realistic or natural values of UV-B radiation than those found in many greenhouses. As a result, Deckmyn *et al.* say their results "clearly indicate the importance of using UV-B transmittant greenhouses or open-top chambers when conducting CO_2 studies," for if this is not done, their work suggests that the results obtained could significantly underestimate the magnitude of the benefits that are being continuously accrued by earth's vegetation as a result of the ongoing rise in the air's CO_2 content.

In 2007, Koti *et al.* (2007) used Soil-Plant-Atmosphere-Research (SPAR) chambers at Mississippi State University (USA) to investigate the effects of doubled atmospheric CO_2 concentration (720 vs. 360 ppm) on the growth and development of six well watered and fertilized soybean (*Glycine max* L.) genotypes grown from seed in pots filled with fine sand and exposed to the dual stresses of high day/night temperatures (38/30°C vs. 30/22°C) and high UV-B radiation levels (10 vs. 0 $kJ/m^2/day$). Results led this group of authors to report that "elevated CO_2 partially compensated [for] the damaging effects on vegetative growth and physiology caused by negative stressors such as high temperatures and enhanced UV-B radiation levels in soybean," specifically noting, in this regard, CO_2's positive influence on the physiological parameters of plant height, leaf area, total biomass, net photosynthesis, total chlorophyll content, phenolic content and wax content, as well as relative plant injury.

In a study that did not include UV-B radiation as an experimental parameter, Estiarte *et al.* (1999) grew spring wheat in FACE plots in Arizona, USA, at atmospheric CO_2 concentrations of 370 and 550 ppm and two levels of soil moisture (50 and 100 percent of potential evapotranspiration). They found that leaves of plants grown in elevated CO_2 had 14 percent higher total flavonoid concentrations than those of plants grown in ambient air, and that soil water content did not affect the relationship. An important aspect of this finding is that one of the functions of flavonoids in plant leaves is to protect them against UV-B radiation. More studies of this nature should be conducted to see how general this beneficial response may be throughout the plant world.

In a study of UV-B and CO_2 effects on a natural ecosystem, which was conducted at the Abisko Scientific Research Station in Swedish Lapland, Johnson *et al.* (2002) studied plots of subarctic heath composed of open canopies of downy birch and dense dwarf-shrub layers containing scattered herbs and grasses. For a period of five years, they exposed the plots to factorial combinations of UV-B radiation—ambient and that expected to result from a 15 percent stratospheric ozone depletion—and atmospheric CO_2 concentration—ambient (around 365 ppm) and enriched (around 600 ppm)—after which they determined the amounts of microbial carbon (C_{mic}) and nitrogen (N_{mic}) in the soils of the plots.

When the plots were exposed to the enhanced UV-B radiation, the amount of C_{mic} in the soil was reduced to only 37 percent of what it was at the ambient UV-B level when the air's CO_2 content was maintained at the ambient concentration. When the UV-B increase was accompanied by the CO_2 increase, however, not only was there not a decrease in C_{mic}, there was an actual increase of 37 percent. The amount of N_{mic} in the soil experienced a 69 percent increase when the air's CO_2 content was maintained at the ambient concentration; and when the UV-B increase was accompanied by the CO_2 increase, N_{mic} rose even more, by 138 percent.

These findings, in the words of Johnson *et al.*, "may have far-reaching implications ... because the productivity of many semi-natural ecosystems is limited by N (Ellenberg, 1988)." The 138 percent increase in soil microbial N observed in this study to accompany a 15 percent reduction in stratospheric ozone and a 64 percent increase in atmospheric CO_2 concentration (experienced in going from 365 ppm to 600 ppm) should significantly enhance the input of plant litter to the soils of these ecosystems, which phenomenon represents the first half of the carbon sequestration process, i.e., the carbon input stage. With respect to the second stage of *keeping* as much of that carbon as possible in the soil, Johnson *et al.* note that "the capacity for subarctic semi-natural heaths to act as major sinks for fossil fuel-derived carbon dioxide is [also] likely to be critically dependent on the supply of N," as is indeed indicated to be the case in the literature review of Berg and Matzner (1997), who report that with more nitrogen in the soil, the long-term storage of carbon is significantly enhanced, as more litter is chemically transformed into humic substances when nitrogen is more readily available, and these more recalcitrant carbon compounds can be successfully stored in the soil for many millennia.

In light of these several findings, we conclude that the ongoing rise in the air's CO_2 content is a powerful antidote for the deleterious biological impacts that might possibly be caused by an increase in the flux of UV-B radiation at the surface of the earth due to any further depletion of the planet's stratospheric ozone layer.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/u/uvbradiation.php.

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7.3.11. Water Stress

As the CO_2 content of the air continues to rise, nearly all of earth's plants will exhibit increases in photosynthesis and biomass production. However, some experts claim that water stress will negate these benefits. In reviewing the scientific literature of the ten-year period 1983-1994, however, Idso and Idso (1994) found that water stress typically will *not* negate the CO_2-induced stimulation of plant productivity. They found that the CO_2-induced percentage increase in plant biomass production was often greater under water-stressed conditions than it was when plants were well-watered. We here review some more recent scientific literature in this area for agricultural, grassland and woody plant species.

7.3.11.1. Agricultural Species

During times of water stress, atmospheric CO_2 enrichment often stimulates plants to develop larger-than-usual and more robust root systems to probe greater volumes of soil for scarce and much-needed moisture. Wechsung *et al.* (1999), for example, observed a 70 percent increase in lateral root dry weights of water-stressed wheat grown at 550 ppm CO_2, while De Luis *et al.* (1999) reported a 269 percent increase in root-to-shoot ratio of water-stressed alfalfa growing at 700 ppm CO_2. Thus, elevated CO_2 elicits stronger-than-usual positive root responses in agricultural species under conditions of water stress.

Elevated levels of atmospheric CO_2 also tend to reduce the openness of stomatal pores on leaves, thus decreasing plant stomatal conductance. This phenomenon, in turn, reduces the amount of water lost to the atmosphere by transpiration and, consequently, lowers overall plant water use. Serraj *et al.* (1999) report that water-stressed soybeans grown at 700 ppm CO_2 reduced their total seasonal water loss by 10 percent relative to that of water-stressed control plants grown at 360 ppm CO_2. In addition, Conley *et al.* (2001) noted that a 200-ppm increase in the air's CO_2 concentration reduced cumulative evapotranspiration in water-stressed sorghum by approximately 4 percent. Atmospheric CO_2 enrichment thus increases plant water acquisition, by stimulating root growth, while it reduces plant water loss, by constricting stomatal apertures; and these dual effects typically enhance plant water-use efficiency, even under conditions of less-than-optimal soil water content. But these phenomena have other implications as well.

CO_2-induced increases in root development together with CO_2-induced reductions in stomatal conductance often contribute to the maintenance of a more favorable plant water status during times of drought. Sgherri *et al.* (1998) reported that leaf water potential, which is a good indicator of overall plant water status, was 30 percent higher (less negative and therefore more favorable) in water-stressed alfalfa grown at an atmospheric CO_2 concentration of 600 ppm CO_2 versus 340 ppm CO_2. Wall (2001) reports that leaf water potentials were similar in CO_2-enriched water-stressed plants and ambiently grown well-watered control plants, which implies a complete CO_2-induced amelioration of water stress in the CO_2-enriched plants. Similarly, Lin and Wang (2002) demonstrated that elevated CO_2 caused a several-day delay in the onset of the water stress-induced production of the highly reactive oxygenated compound H_2O_2 in spring wheat.

If atmospheric CO_2 enrichment thus allows plants to maintain a better water status during times of water stress, it is only logical to expect that such plants should exhibit greater rates of photosynthesis than ambiently grown plants. And so they do. With the onset of water stress in *Brassica juncea*, for example, photosynthetic rates dropped by 40 percent in plants growing in ambient air, while plants growing in air containing 600 ppm CO_2 only experienced a 30 percent reduction in net photosynthesis (Rabha and Uprety, 1998). Ferris *et al.* (1998) reported that after imposing water-stress conditions on soybeans and allowing them to recover following complete rewetting of the soil, plants grown in air containing 700 ppm CO_2 reached pre-stressed rates of photosynthesis after six days, while plants grown in ambient air never recovered to pre-stressed rates.

Reasoning analogously, it is also to be expected that plant biomass production would be enhanced by elevated CO_2 concentrations under drought conditions. In exploring this idea, Ferris *et al.* (1999) reported that water-stressed soybeans grown at 700 ppm CO_2 attained seed yields that were 24 percent greater than those of similarly water-stressed plants grown at ambient CO_2 concentrations, while Hudak *et al.* (1999) reported that water-stress had no effect on yield in CO_2-enriched spring wheat.

In some cases, the CO_2-induced percentage biomass increase is actually greater for water-stressed plants than it is for well-watered plants. Li *et al.* (2000), for example, reported that a 180-ppm increase in the air's CO_2 content increased lower stem grain weights in water-stressed and well-watered spring wheat by 24 and 14 percent, respectively. Similarly, spring wheat grown in air containing an additional 280 ppm CO_2 exhibited 57 and 40 percent increases in grain yield under water-stressed and well-watered conditions, respectively (Schutz and Fangmeier, 2001). Likewise, Ottman *et al.* (2001) noted that elevated CO_2 increased plant biomass in water-stressed sorghum by 15 percent, while no biomass increase occurred in well-watered sorghum.

In summary, the conclusions of Idso and Idso (1994) are well supported by the recent peer-reviewed scientific literature, which indicates that the ongoing rise in the air's CO_2 content will likely lead to substantial increases in plant photosynthetic rates and biomass production, even in the face of stressful conditions imposed by less-than-optimum soil moisture conditions.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/growthwaterag.php.

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7.3.11.2. Grassland Species

In the study of Leymarie *et al.* (1999), twice-ambient levels of atmospheric CO_2 caused significant reductions in the stomatal conductance of water-stressed *Arabidopsis thaliana*. Similarly, Volk *et al.* (2000) reported that calcareous grassland species exposed to elevated CO_2 concentrations (600 ppm) consistently exhibited reduced stomatal conductance, regardless of soil moisture availability. Thus, atmospheric CO_2 enrichment clearly reduces stomatal conductance and plant transpiration and soil water depletion in grassland ecosystems.

In the case of four grassland species comprising a pasture characteristic of New Zealand, Clark *et al.* (1999) found that leaf water potential, which is a good indicator of plant water status, was consistently higher (less negative and, therefore, less stressful) under elevated atmospheric CO_2 concentrations. Similarly, leaf water potentials of the water-stressed

C_4 grass *Panicum coloratum* grown at 1000 ppm CO_2 were always higher than those of their water-stressed counterparts growing in ambient air (Seneweera *et al*., 2001). Indeed, Seneweera *et al*. (1998) reported that leaf water potentials observed in CO_2-enriched water-stressed plants were an amazing three-and-a-half times greater than those observed in control plants grown at 350 ppm during drought conditions (Seneweera *et al*., 1998).

If atmospheric CO_2 enrichment thus allows plants to maintain improved water status during times of water stress, it is only logical to expect that such plants will exhibit greater photosynthetic rates than similar plants growing in ambient air. In a severe test of this concept, Ward *et al*. (1999) found that extreme water stress caused 93 and 85 percent reductions in the photosynthetic rates of two CO_2-enriched grassland species; yet their rates of carbon fixation were still greater than those observed under ambient CO_2 conditions.

In view of the fact that elevated CO_2 enhances photosynthetic rates during times of water stress, one would expect that plant biomass production would also be enhanced by elevated CO_2 concentrations under drought conditions. And so it is. On the American prairie, for example, Owensby *et al*. (1999) reported that tallgrass ecosystems exposed to twice-ambient concentrations of atmospheric CO_2 for eight years only exhibited significant increases in above- and below-ground biomass during years of less-than-average rainfall. Also, in the study of Derner *et al*. (2001), the authors reported that a 150-ppm increase in the CO_2 content of the air increased shoot biomass in two C_4 grasses by 57 percent, regardless of soil water content. Seneweera *et al*. (2001) reported that a 640-ppm increase in the air's CO_2 content increased shoot dry mass in a C_4 grass by 44 and 70 percent under well-watered and water-stressed conditions, respectively. Likewise, Volk *et al*. (2000) grew calcareous grassland assemblages at 360 and 600 ppm CO_2 and documented 18 and 40 percent CO_2-induced increases in whole-community biomass under well-watered and water-stressed conditions, respectively.

In summary, the peer-reviewed scientific literature indicates that the ongoing rise in the air's CO_2 content will likely lead to substantial increases in plant photosynthetic rates and biomass production for grassland species even in the face of stressful environmental conditions imposed by less-than-optimum soil moisture contents.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/growthwatergrass.php.

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7.3.11.3. Woody Species

During times of water stress, atmospheric CO_2 enrichment often stimulates the development of larger-than-usual and more robust root systems in woody perennial species, which allows them to probe greater volumes of soil for scarce and much-needed moisture. Tomlinson and Anderson (1998), for example, report that greater root development in water-stressed red oak seedlings grown at 700 ppm CO_2 helped them effectively deal with the reduced availability of moisture. These trees eventually produced just as much biomass as well-watered controls exposed to ambient air containing 400 ppm CO_2. In addition, Polley *et al*. (1999) note that water-stressed honey mesquite trees subjected to an atmospheric CO_2 concentration of 700 ppm produced 37 percent more root biomass than water-stressed control seedlings growing at 370 ppm.

Elevated levels of atmospheric CO_2 also tend to reduce the area of open stomatal pore space on leaf surfaces, thus reducing plant stomatal conductance. This phenomenon, in turn, reduces the amount of water lost to the atmosphere via transpiration. Tognetti *et al*. (1998), for example, determined that stomatal conductances of mature oak trees growing near natural CO_2 springs in central Italy were significantly lower than those of similar trees growing further away from the springs during periods of severe summer drought.

CO_2-induced increases in root development together with CO_2-induced reductions in stomatal conductance often contribute to the maintenance of a more favorable plant water status during times of drought. In the case of three Mediterranean shrubs, Tognetti *et al*. (2002) found that leaf water potential, which is a good indicator of plant water status, was consistently higher (less negative and, hence, less stressful) under twice-ambient CO_2 concentrations. Similarly, leaf water potentials of water-stressed mesquite seedlings grown at 700 ppm CO_2 were 40 percent higher than those of their water-stressed counterparts growing in ambient air (Polley *et al*., 1999), which is comparable to values of -5.9 and -3.4 MPa observed in water-stressed evergreen shrubs (*Larrea tridentata*) exposed to 360 and 700 ppm CO_2, respectively (Hamerlynck *et al*., 2000).

Palanisamy (1999) observed water-stressed *Eucalyptus* seedlings grown at 800 ppm CO_2 display greater net photosynthetic rates than their ambiently grown and water-stressed counterparts. Runion *et al*. (1999) observed the CO_2-induced photosynthetic stimulation of water-stressed pine seedlings grown at 730 ppm CO_2 to be nearly 50 percent greater than that of similar water-stressed pine seedlings grown at 365 ppm CO_2. Similarly, Centritto *et al*. (1999a) found that water-stressed cherry trees grown at 700 ppm CO_2 displayed net photosynthetic rates that were 44 percent greater than those of water-stressed trees grown at 350 ppm CO_2. And Anderson and Tomlinson (1998) found that a 300-ppm increase in the air's CO_2 concentration boosted photosynthetic rates in well-watered and water-stressed red oak seedlings by 34 and 69 percent, respectively, demonstrating that the CO_2-induced percentage enhancement in net photosynthesis in this species was essentially twice as great in water-stressed seedlings as in well-watered ones.

Sometimes, plants suffer drastically when subjected to extreme water stress. However, the addition of CO_2 to the atmosphere often gives them an edge over ambiently growing plants. Tuba *et al*. (1998), for example, reported that leaves of a water-stressed woody shrub exposed to an atmospheric CO_2 concentration of 700 ppm continued to maintain positive rates of net carbon fixation for a period that lasted three times longer than that observed for leaves of equally water-stressed control plants growing in ambient air. Similarly, Fernandez *et al*. (1998) discovered that herb and tree species growing near natural CO_2 vents in Venezuela continued to maintain positive rates of net photosynthesis during that location's dry season, while the same species growing some distance away from the CO_2 source displayed net losses of carbon during this stressful time. Likewise, Fernandez *et al*. (1999) noted that after four weeks of drought, the deciduous Venezuelan shrub *Ipomoea carnea* continued to exhibit positive carbon gains under elevated CO_2 conditions, whereas ambiently growing plants displayed net carbon losses. Polley *et al*. (2002) reported that seedlings of five woody species grown at twice-ambient CO_2 concentrations survived 11 days longer (on average) than control seedlings when subjected to maximum drought conditions. Thus, in some cases of water stress, enriching the air with CO_2 can mean the difference between life or death.

Arp *et al*. (1998) reported that six perennial plants common to the Netherlands increased their biomass under CO_2-enriched conditions even when suffering from lack of water. In other cases, the CO_2-induced percentage biomass increase is sometimes even greater for water-stressed plants than it is for well-watered plants. Catovsky and Bazzaz (1999), for example, reported that the CO_2-induced biomass increase for paper birch was 27 percent and 130 percent for well-watered and water-stressed seedlings, respectively. Similarly, Schulte *et al*. (1998) noted that the CO_2-induced biomass increase of oak seedlings was greater under water-limiting conditions than under well-watered conditions (128 percent vs. 92 percent), as did Centritto *et al*. (1999b) for basal trunk area in cherry seedlings (69 percent vs. 22 percent).

Finally, Knapp *et al*. (2001) developed tree-ring index chronologies from western juniper stands in Oregon, USA, finding that the trees recovered better from the effects of drought in the 1990's, when the air's CO_2 concentration was around 340 ppm, than they did from 1900-1930, when the atmospheric CO_2 concentration was around 300 ppm. In a loosely related study, Osborne *et al*. (2002) looked at the warming and reduced precipitation experienced in Mediterranean shrublands over the last century and concluded that primary productivity should have been negatively impacted in those areas. However, when the concurrent increase in atmospheric CO_2 concentration was factored into their mechanistic model, a 25 percent increase in primary productivity was projected.

In summary, the peer-reviewed scientific literature indicates that the ongoing rise in the air's CO_2 content will likely lead to substantial increases in photosynthetic rates and biomass production in earth's woody species in the years and decades ahead, even in the face of stressful conditions imposed by less-than-optimal availability of soil moisture.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/growthwaterwood.php.

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7.4. Acclimation

Plants grown in elevated CO_2 environments often exhibit some degree of photosynthetic acclimation or down regulation, which is typically characterized by long-term rates of photosynthesis that are somewhat lower than what would be expected on the basis of measurements made during short-term exposure to CO_2-enriched air. These downward adjustments result from modest long-term decreases in the activities and/or amounts of the primary plant carboxylating enzyme rubisco. Acclimation is said to be present when the photosynthetic rates of long-term CO_2-enriched plants are found to be lower than those of long-term *non*-CO_2-enriched plants when the normally CO_2-enriched plants are measured during brief exposures to ambient CO_2 concentrations. In this section, we review research that has been published on acclimation in agricultural, desert, grassland and woody species.

Additional information on this topic, including reviews on acclimation not discussed here, can be found at http://www.co2science.org/subject/a/subject_a.php under the heading Acclimation.

7.4.1. Agricultural Species

Several studies have examined the effects of elevated CO_2 on acclimation in agricultural crops. Ziska (1998), for example, reported that soybeans grown at an atmospheric CO_2 concentration of 720 ppm initially exhibited photosynthetic rates that were 50 percent greater than those observed in control plants grown at 360 ppm. However, after the onset of photosynthetic acclimation, CO_2-enriched plants displayed subsequent photosynthetic rates that were only 30 percent greater than their ambiently grown counterparts. In another study, Theobald *et al*. (1998) grew spring wheat at twice-ambient atmospheric CO_2 concentrations and determined that elevated CO_2 reduced the amount of rubisco required to sustain enhanced rates of photosynthesis, which led to a significant increase in plant photosynthetic nitrogen-use efficiency. CO_2-induced increases in photosynthetic nitrogen-use efficiency have also been reported in spring wheat by Osborne *et al*. (1998).

In an interesting study incorporating both hydroponically and pot-grown wheat plants, Farage *et al*. (1998) demonstrated that low nitrogen fertilization does not lead to photosynthetic acclimation in elevated CO_2 environments, as long as the nitrogen supply keeps pace with the relative growth rate of the plants. Indeed, when spring wheat was grown at an atmospheric CO_2 concentration of 550 ppm in a free-air CO_2 enrichment (FACE) experiment with optimal soil nutrition and unlimited rooting volume, Garcia *et al*. (1998) could find no evidence of photosynthetic acclimation.

CO_2-induced photosynthetic acclimation often results from insufficient plant sink strength, which can lead to carbohydrate accumulation in source leaves and the triggering of photosynthetic end product feedback inhibition, which reduces net photosynthetic rates. Indeed, Gesch *et al*. (1998) reported that rice plants—which have relatively limited potential for developing additional carbon sinks—grown at an atmospheric CO_2 concentration of 700 ppm exhibited increased leaf carbohydrate contents, which likely reduced *rbcS* mRNA levels and rubisco protein content. Similarly, Sims *et al*. (1998) reported that photosynthetic acclimation was induced in CO_2-enriched soybean plants from the significant accumulation of nonstructural carbohydrates in their leaves. However, in growing several different *Brassica* species at 1,000 ppm CO_2, Reekie *et al*. (1998) demonstrated that CO_2-induced acclimation was avoided in species having well-developed carbon sinks (broccoli and cauliflower) and only appeared in those lacking significant sink strength (rape and mustard). Thus, acclimation does not appear to be a direct consequence of atmospheric CO_2 enrichment but rather an indirect effect of low sink strength, which results in leaf carbohydrate accumulation that can trigger acclimation.

In some cases, plants can effectively increase their sink strength, and thus reduce the magnitude of CO_2-induced acclimation, by forming symbiotic relationships with certain species of soil fungi. Under such conditions, photosynthetic down regulation is not triggered as rapidly, or as frequently, by end product feedback inhibition, as excess carbohydrates are mobilized out of source leaves and sent belowground to symbiotic fungi. Indeed, Louche-Tessandier *et al*. (1999) report that photosynthetic acclimation in CO_2-enriched potatoes was less apparent when plants were simultaneously colonized by a mycorrhizal fungus. Thus, CO_2-induced acclimation appears to be closely related to the source:sink balance that exists within plants, being triggered when sink strength falls below, and source strength rises above, critical thresholds in a species-dependent manner.

Acclimation is generally regarded as a process that reduces the amount of rubisco and/or other photosynthetic proteins, which effectively increases the amount of nitrogen available for enhancing sink development or stimulating other nutrient-limited processes. In the study of Watling *et al*. (2000), for example, the authors reported a 50 percent CO_2-induced reduction in the concentration of PEP-carboxylase, the primary carboxylating enzyme in C_4 plants, within sorghum leaves. Similarly, Maroco *et al*. (1999) documented CO_2-induced decreases in both PEP-carboxylase and rubisco in leaves of the C_4 crop maize.

In some cases, however, acclimation to elevated CO_2 is manifested by an "up-regulation" of certain enzymes. When Gesch *et al*. (2002) took rice plants from ambient air and placed them in air containing 700 ppm, for example, they noticed a significant increase in the activity of sucrose-phosphate synthase (SPS), which is a key enzyme involved in the production of sucrose. Similarly, Hussain *et al*. (1999) reported that rice plants grown at an atmospheric CO_2 concentration of 660 ppm displayed 20 percent more SPS activity during the growing season than did ambiently grown rice plants. Such increases in the activity of this enzyme could allow CO_2-enriched plants to avoid the onset of photosynthetic acclimation by synthesizing and subsequently exporting sucrose from source leaves into sink tissues before they accumulate and trigger end product feedback inhibition.

In an interesting experiment, Gesch *et al*. (2000) took ambiently growing rice plants and placed them in an atmospheric CO_2 concentration of 175 ppm, which reduced photosynthetic rates by 45 percent. However, after five days exposure to this sub-ambient CO_2 concentration, the plants manifested an up-regulation of rubisco, which stimulated photosynthetic rates by 35 percent. Thus, plant acclimation responses can involve both an increase or decrease in specific enzymes, depending on the atmospheric CO_2 concentration.

In summary, many peer-reviewed studies suggest that as the CO_2 content of the air slowly but steadily rises, agricultural species may not necessarily exhibit photosynthetic acclimation, even under conditions of low soil nitrogen. If a plant can maintain a balance between its sources and sinks for carbohydrates at the whole-plant level, acclimation should not be necessary. Because earth's atmospheric CO_2 content is rising by an average of only 1.5 ppm per year, most plants should be able to either (1) adjust their relative growth rates by the small amount that would be needed to prevent low nitrogen-induced acclimation from ever occurring, or (2) expand their root systems by the small amount that would be needed to supply the extra nitrogen required to take full advantage of the CO_2-induced increase in leaf carbohydrate production. In the event a plant cannot initially balance its sources and sinks for carbohydrates at the whole-plant level, CO_2-induced acclimation represents a beneficial secondary mechanism for achieving that balance through redistributing limiting resources away from the plant's photosynthetic machinery to strengthen sink development or enhance other nutrient-limiting processes.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/acclimationag.php.

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7.4.2. Chaparral and Desert Species

Roberts *et al.* (1998) conducted a FACE experiment in southern California, USA, exposing *Adenostoma fassciculatum* shrubs to atmospheric CO_2 concentrations of 360 and 550 ppm while they studied the nature of gas-exchange in this chaparral species. After six months of CO_2 fumigation, photosynthetic acclimation occurred. However, because of reductions in stomatal conductance and transpirational water loss, the CO_2-enriched shrubs exhibited leaf water potentials that were less negative (and, hence, less stressful) than those of control plants. This CO_2-induced water conservation phenomenon should enable this woody perennial to better withstand the periods of drought that commonly occur in this southern California region, while the photosynthetic down regulation it exhibits should allow it to more equitably distribute the limiting resources it possesses among different essential plant physiological processes.

Huxman and Smith (2001) measured seasonal gas exchange during an unusually wet El Niño year in an annual grass (*Bromus madritensis* ssp. *rubens*) and a perennial forb (*Eriogonum inflatum*) growing within FACE plots established in the Mojave Desert, USA, which they maintained at atmospheric CO_2 concentrations of 350 and 550 ppm. The elevated CO_2 consistently increased net photosynthetic rates in the annual grass without inducing photosynthetic acclimation. In fact, even as seasonal photosynthetic rates declined post-flowering, the reduction was much less in the CO_2-enriched plants. However, elevated CO_2 had no consistent effect on stomatal conductance in this species. By contrast, *Eriogonum* plants growing at 550 ppm CO_2 exhibited significant photosynthetic acclimation, especially late in the season, which led to similar rates of net photosynthesis in these plants in both CO_2 treatments. But in this species, elevated CO_2 reduced stomatal conductance over most of the growing season. Although the two desert plants exhibited different stomatal and photosynthetic responses to elevated CO_2, both experienced significant CO_2-induced increases in water use efficiency and biomass production, thus highlighting the existence of different, but equally effective, species-specific mechanisms for responding positively to atmospheric CO_2 enrichment in a desert environment.

In another study conducted at the Mojave Desert FACE site, Hamerlynck *et al*. (2002) determined that plants of the deciduous shrub *Lycium andersonii* grown in elevated CO_2 displayed photosynthetic acclimation, as maximum rubisco activity in the plants growing in the CO_2-enriched air was 19 percent lower than in the plants growing in ambient air. Also, the elevated CO_2 did not significantly impact rates of photosynthesis. Leaf stomatal conductance, on the other hand, was consistently about 27 percent lower in the plants grown in the CO_2-enriched air; and during the last month of the spring growing season, the plants in the elevated CO_2 plots displayed leaf water potentials that were less negative than those exhibited by the control plants growing in ambient air. Hence, as the CO_2 content of the air increases, *Lycium andersonii* will likely respond by exhibiting significantly enhanced water use efficiency, which should greatly increase its ability to cope with the highly variable precipitation and temperature regimes of the Mojave Desert. The acclimation observed within the shrub's photosynthetic apparatus should allow it to reallocate more resources to producing and sustaining greater amounts of biomass. Thus, it is likely that future increases in the air's CO_2 content will favor a "greening" of the American Mojave Desert.

In summary, the few studies of the acclimation phenomenon that have been conducted on chaparral and desert plants indicate that although it can sometimes be complete, other physiological changes, such as the reductions in stomatal conductance that typically produce large increases in water use efficiency, often more than compensate for the sometimes small to negligible increases in photosynthesis.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/acclimationdesert.php.

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7.4.3. Grassland Species

In nearly every reported case of photosynthetic acclimation in CO_2-enriched plants, rates of photosynthesis displayed by grassland species grown and measured at elevated CO_2 concentrations are typically greater than those exhibited by control plants grown and measured at ambient CO_2 concentrations (Davey *et al*., 1999; Bryant *et al*., 1998).

As mentioned in prior sections, CO_2-induced photosynthetic acclimation often results from insufficient plant sink strength, which can lead to carbohydrate accumulation in source leaves and the triggering of photosynthetic end-product feedback inhibition, which reduces rubisco activity and rates of net photosynthesis (Roumet *et al*., 2000). As one example of this phenomenon, Rogers *et al*. (1998) reported that perennial ryegrass grown at an atmospheric CO_2 concentration of 600 ppm and low soil nitrogen exhibited leaf carbohydrate contents and rubisco activities that were 100 percent greater and 25 percent less, respectively, than those observed in control plants grown at 360 ppm CO_2, prior to a cutting event. Following the cutting, which effectively reduced the source:sink ratio of the plants, leaf carbohydrate contents in CO_2-enriched plants decreased and rubisco activities increased, completely ameliorating the photosynthetic acclimation in this species. However, at high soil nitrogen, photosynthetic acclimation to elevated CO_2 did not occur. Thus, photosynthetic acclimation appears to result from the inability of plants to develop adequate sinks at low soil nitrogen, and is not necessarily induced directly by atmospheric CO_2 enrichment.

In some cases, plants can effectively increase their sink strength and thus reduce the magnitude of CO_2-induced acclimation by forming symbiotic relationships with certain species of soil fungi. Under such conditions, photosynthetic down regulation is not triggered as rapidly, or as frequently, by end-product feedback inhibition, as excess carbohydrates are mobilized out of source leaves and sent belowground to symbiotic fungi. Staddon *et al.* (1999) reported that photosynthetic acclimation was not induced in CO_2-enriched *Plantago lanceolata* plants that were inoculated with a mycorrhizal fungus, while it was induced in control plants that were not inoculated with the fungus. Thus, CO_2-induced acclimation appears to be closely related to the source:sink balance that exists within plants, and is triggered when sink strength falls below, and source strength rises above, certain critical thresholds in a species-dependent manner.

As the CO_2 content of the air slowly but steadily rises, these peer-reviewed studies suggest that grassland species may not exhibit photosynthetic acclimation if they can maintain a balance between their sources and sinks for carbohydrates at the whole-plant level. But in the event this balancing act is not initially possible, acclimation represents a beneficial secondary mechanism for achieving that balance by redistributing limiting resources away from the plant's photosynthetic machinery to strengthen its sink development and/or nutrient-gathering activities.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/acclimationgrass.php.

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7.4.4. Tree Species

Trees grown for long periods of time in elevated CO_2 environments often, but not always (Marek *et al*., 2001; Stylinski *et al*., 2000; Bartak *et al*., 1999; Schortemeyer *et al*., 1999), exhibit some degree of photosynthetic acclimation or down regulation, which is typically characterized by modestly reduced rates of photosynthesis (compared to what might be expected on the basis of short-term exposure to CO_2-enriched air) that result from a long-term decrease in the activity and/or amount of the primary plant carboxylating enzyme rubisco (Kubiske *et al*., 2002; Egli *et al*., 1998). This acclimation response in plants accustomed to growing in CO_2-enriched air is characterized by short-term reductions in their rates of net photosynthesis when measured during short-term exposure to ambient air relative to net photosynthesis rates of comparable plants that have always been grown in ambient air.

Jach and Ceulemans (2000) grew one-year-old Scots pine seedlings for two additional years at twice-ambient atmospheric CO_2 concentrations and reported that the elevated CO_2 increased the trees' mean rate of net photosynthesis by 64 percent. However, when measured during a brief return to ambient CO_2 concentrations, the normally CO_2-enriched seedlings exhibited an approximate 21 percent reduction in average net photosynthesis rate relative to that of seedlings that had always been exposed to ambient air. Similarly, Spunda *et al*. (1998) noted that a 350-ppm increase in the air's CO_2 concentration boosted rates of net photosynthesis in fifteen-year-old Norway spruce trees by 78 percent; but when net photosynthesis in the normally CO_2-enriched trees was measured at a temporary atmospheric CO_2 concentration of 350 ppm, an 18 percent reduction was observed relative to what was observed in comparable trees that had always been grown in ambient air. After reviewing the results of 15 different atmospheric CO_2 enrichment studies of European forest species growing in field environments maintained at twice-ambient CO_2 concentrations, Medlyn *et al*. (1999) found that the mean photosynthetic acclimation effect in the CO_2-enriched trees was characterized by an average reduction of 19 percent in their rates of net photosynthesis when measured at temporary ambient CO_2 concentrations relative to the mean rate of net photosynthesis exhibited by those trees that had always been exposed to ambient air. Nonetheless, in nearly every reported case of CO_2-induced photosynthetic acclimation in trees, the photosynthetic rates of trees growing and measured in CO_2-enriched air have still been much greater than those exhibited by trees growing and measured in ambient air.

CO_2-induced photosynthetic acclimation, when it occurs, often results from insufficient plant sink strength, which can lead to carbohydrate accumulation in source leaves and the triggering of photosynthetic end-product feedback inhibition, which results in reduced rates of net photosynthesis. Pan *et al*. (1998), for example, reported that apple seedlings grown at an atmospheric CO_2 concentration of 1600 ppm had foliar starch concentrations 17-fold greater than those observed in leaves of seedlings grown at 360 ppm CO_2, suggesting that this phenomenon likely triggered the reductions in leaf net photosynthesis rates they observed. Similarly, Rey and Jarvis (1998) reported that the accumulation of starch within leaves of CO_2-enriched silver birch seedlings (100 percent above ambient) may have induced photosynthetic acclimation in that species. Also, in the study of Wiemken and Ineichen (2000), a 300-ppm increase in the air's CO_2 concentration induced seasonal acclimation in young spruce trees, where late-summer, fall and winter rates of net photosynthesis declined in conjunction with 40 to 50 percent increases in foliar glucose levels.

In some cases, trees can effectively increase their sink strength, and thus reduce the magnitude of CO_2-induced photosynthetic acclimation, by forming symbiotic relationships with certain species of soil fungi. Under such conditions, photosynthetic down regulation is not triggered as rapidly, or as frequently, by end-product feedback inhibition, as excess carbohydrates are mobilized out of the trees' source leaves and sent belowground to support the growth of symbiotic fungi. Jifon *et al*. (2002), for example, reported that the degree of CO_2-induced photosynthetic acclimation in sour orange tree seedlings was significantly reduced by the presence of mycorrhizal fungi, which served as sinks for excess carbohydrates synthesized by the CO_2-enriched seedlings.

During acclimation to elevated CO_2, the amounts and activities of rubisco and/or other photosynthetic proteins are often reduced, which effectively increases the amount of nitrogen available for enhancing sink development or stimulating other nutrient-limited processes. As an example of this phenomenon operating in trees, in the study of Blaschke *et al*. (2001), the authors reported that a doubling of the atmospheric CO_2 concentration reduced foliar rubisco concentrations by 15 and 30 percent in two mature oak species growing near CO_2-emitting springs. Similarly, a 200-ppm increase in the air's CO_2 content reduced foliar rubisco concentrations in young aspen and birch seedlings by 39 percent (Takeuchi *et al*., 2001) and 24 percent (Tjoelker *et al*., 1998), respectively. Also, in two *Pinus radiata* studies, seedlings fumigated with air containing 650 ppm CO_2 displayed 30 to 40 percent reductions in rubisco concentration and rubisco activity relative to measurements made on seedlings grown in ambient air (Griffin *et al*., 2000; Turnbull *et al*., 1998). Other studies of CO_2-enriched Norway spruce and Scots pines have documented CO_2-induced reductions in foliar chlorophyll contents of 17 percent (Spunda *et al*., 1998) and 26 percent (Gielen *et al*., 2000), respectively. And in the study of Gleadow *et al*. (1998), elevated CO_2 led to acclimation in eucalyptus seedlings, which mobilized nitrogen away from rubisco and into prunasin, a sugar-based defense compound that deters herbivory.

In another interesting experiment, Polle *et al*. (2001) germinated acorns from oak trees exposed to ambient and CO_2-enriched air and subsequently grew them at ambient and twice-ambient atmospheric CO_2 concentrations. They discovered that seedlings derived from acorns produced on CO_2-enriched trees exhibited less-pronounced photosynthetic acclimation to elevated CO_2 than did seedlings derived from acorns produced on ambiently grown trees, suggesting the possibility of generational adaptation to higher atmospheric CO_2 concentrations over even longer periods of time.

In summary, these many peer-reviewed scientific studies suggest that as the air's CO_2 content slowly but steadily rises, trees may be able to avoid photosynthetic acclimation if they maintain a proper balance between carbohydrate sources and sinks at the whole-tree level, which they may well be able to do in response to the current rate of rise of the air's CO_2 concentration (a mere 1.5 ppm per year). If a tree cannot *initially* balance its sources and sinks of carbohydrates, however, acclimation is an important and effective means of achieving that balance through redistributing essential resources away from the tree's photosynthetic machinery in an effort to strengthen sink development, enhance various nutrient-limited processes, and increase nutrient acquisition by, for example, stimulating the development of roots and their symbiotic fungal partners. And if those adjustments are not entirely successful, it is still the case that the acclimation process is hardly ever 100 percent complete (in the studies reviewed here it was on the order of 20 percent), so that tree growth is almost always significantly enhanced in CO_2-enriched air in nearly every real-world setting.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/a/acclimationtree.php.

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7.5. Competition

Do higher levels of atmospheric CO_2 favor some plants over others? Could this result in ecological changes that could be judged "bad" because of their effects on wildlife or plants that are beneficial to mankind? This section seeks to answer these questions by surveying research on the effects of CO_2 enhancement on C_3 versus C_4 plants, and weeds versus crops.

Additional information on this topic, including reviews on competition not discussed here, can be found at http://www.co2science.org/ subject/c/subject _c.php under the heading Competition.

7.5.1. C_3 vs C_4 Plants

C_3 plants typically respond better to atmospheric CO_2 enrichment than do C_4 plants in terms of increasing their rates of photosynthesis and biomass production. Hence, it has periodically been suggested that in a world of rising atmospheric CO_2 concentration, C_3 plants may out-compete C_4 plants and displace them, thereby decreasing the biodiversity of certain ecosystems. However, the story is much more complex that what is suggested by this simple scenario.

Wilson *et al*. (1998) grew 36 species of perennial grass common to tallgrass prairie ecosystems with and without arbuscular mycorrhizal fungi, finding that the dry matter production of the C_3 species that were colonized by the fungi was the same as that of the non-inoculated C_3 species, but that the fungal-colonized C_4 species produced, on average, 85 percent *more* dry matter than the non-inoculated C_4 species. This finding is of pertinence to the relative responsiveness of C_3 and C_4 plants to atmospheric CO_2 enrichment; for elevated levels of atmospheric CO_2 tend to enhance the mycorrhizal colonization of plant roots, which is known to make soil minerals and water more available for plant growth. Hence, this CO_2-induced fungal-mediated growth advantage, which from this study appears to be more readily available to C_4 plants, could well counter the inherently greater biomass response of C_3 plants relative to that of C_4 plants, leveling the playing field relative to their competition for space in any given ecosystem.

Another advantage that may come to C_4 plants as a consequence of the ongoing rise in the air's CO_2 content was elucidated by BassiriRad *et al*. (1998), who found that elevated CO_2 enhanced the ability of the perennial C_4 grass *Bouteloua eriopoda* to increase its uptake of NO_3^- and PO_4^{3-} considerably more than the perennial C_3 shrubs *Larrea tridentata* and *Prosopis glandulosa*. In an eight-year study of the effects of twice-ambient atmospheric CO_2 concentrations on a pristine tallgrass prairie in Kansas, Owensby *et al*. (1999) found that the elevated CO_2 did not affect the basal coverage of its C_4 species or their relative contribution to the composition of the ecosystem.

The antitranspirant effect of atmospheric CO_2 enrichment (Pospisilova and Catsky, 1999) is often more strongly expressed in C_4 plants than in C_3 plants and typically allows C_4 plants to better cope with water stress. In a study of the C_3 dicot *Abutilon theophrasti* and the C_4 dicot *Amaranthus retroflexus*, for example, Ward *et al*. (1999) found that *Amaranthus retroflexus* exhibited a greater relative recovery from drought than did the C_3 species, which suggests, in their words, that "the C_4 species would continue to be more competitive than the C_3 species in regions receiving more frequent and severe droughts," which basically characterizes regions where C_4 plants currently exist.

Two years later, Morgan *et al*. (2001) published the results of an open-top chamber study of a native shortgrass steppe ecosystem in Colorado, USA, where they had exposed the enclosed ecosystems to atmospheric CO_2 concentrations of 360 and 720 ppm for two six-month growing seasons. In spite of an average air temperature increase of 2.6°C, which was caused by the presence of the open-top chambers, the elevated CO_2 increased above-ground biomass production by an average of 38 percent in both years of the study; and when 50 percent of the standing green plant biomass was defoliated to simulate grazing halfway through the growing season, atmospheric CO_2 enrichment still increased above-ground biomass by 36 percent. It was also found that the communities enriched with CO_2 tended to have greater amounts of moisture in their soils than communities exposed to ambient air; and this phenomenon likely contributed to the less negative and, therefore, less stressful plant water potentials that were measured in the CO_2-enriched plants. Last, the elevated CO_2 did not preferentially stimulate the growth of C_3 species over that of C_4 species in these communities. Elevated CO_2 did not significantly affect the percentage composition of C_3 and C_4 species in these grasslands; they maintained their original level of vegetative biodiversity.

This would also appear to be the conclusion of the study of Wand *et al*. (1999), who in a massive review of the scientific literature published between 1980 and 1997 analyzed nearly 120 individual responses of C_3 and C_4 grasses to elevated CO_2. On average, they found photosynthetic enhancements of 33 and 25 percent, respectively, for C_3 and C_4 plants, along with biomass enhancements of 44 and 33 percent, respectively, for a doubling of the air's CO_2 concentration. These larger-than-expected growth responses in the C_4 species led them to conclude that "it may be premature to predict that C_4 grass species will lose their competitive advantage over C_3 grass species in elevated CO_2."

Further support for this conclusion comes from the study of Campbell *et al*. (2000), who reviewed research work done between 1994 and 1999 by a worldwide network of 83 scientists associated with the Global Change and Terrestrial Ecosystems (GCTE) Pastures and Rangelands Core Research Project 1, which resulted in the publication of over 165 peer-reviewed scientific journal articles. After analyzing this body of research, they concluded that the "growth of C_4 species is about as responsive to CO_2 concentration as [is that of] C_3 species when water supply restricts growth, as is usual in grasslands containing C_4 species." The work of this group of scientists also provides no evidence for the suggestion that C_3 plants may out-compete C_4 plants and thereby replace them in a high-CO_2 world of the future.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/b/biodivc3vsc4.php.

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7.5.2. N-Fixers vs. Non-N-Fixers

Will nitrogen-fixing (N-fixing) plants benefit more from atmospheric CO_2 enrichment than non-N-fixers and thus obtain a competitive advantage over them that could lead to some non-N-fixers being excluded from certain plant communities, thereby decreasing the biodiversity of those ecosystems?

In a two-year glasshouse study of simulated low-fertility ecosystems composed of grassland species common to Switzerland, Stocklin and Korner (1999) found that atmospheric CO_2 enrichment gave nitrogen-fixing legumes an initial competitive advantage over non-N-fixers. However, it would be expected that, over time, a portion of the extra nitrogen fixed by these legumes would become available to neighboring non-N-fixing species, which would then be able to use it to their own advantage, thereby preserving the species richness of the ecosystem over the long haul. Indeed, in a four-year study of an established (non-simulated) high grassland ecosystem located in the Swiss Alps, Arnone (1999) found no difference between the minimal to non-existent growth responses of N-fixing and non-N-fixing species to elevated levels of atmospheric CO_2.

In a study of mixed plantings of the grass *Lolium perenne* and the legume *Medicago sativa*, Matthies and Egli (1999) found that elevated CO_2 did not influence the competition between the two plants, either directly or indirectly via its effects upon the root hemiparasite *Rhinanthus alectorolophus*. In a study of mixed plantings of two grasses and two legumes, Navas *et al*. (1999) observed that plant responses to atmospheric CO_2 enrichment are more dependent upon neighboring plant density than they are upon neighboring plant identity.

In the few studies of this question that have been conducted to date, therefore, it would appear that there is little evidence to suggest that N-fixing legumes will out-compete non-N-fixing plants.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/b/biodivnfixers.php.

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7.5.3. Weeds vs. Non-Weeds

Elevated CO_2 typically stimulates the growth of nearly all plant species in monoculture, including those deemed undesirable by humans, i.e., weeds. Consequently, it is important to determine how future increases in the air's CO_2 content may influence relationships between weeds and non-weeds when they grow competitively in mixed-species stands.

Dukes (2002) grew model serpentine grasslands common to California, USA, in competition with the invasive forb *Centaurea solstitiali*s at atmospheric CO_2 concentrations of 350 and 700 ppm for one year, determining that elevated CO_2 increased the biomass proportion of this weedy species in the community by a mere 1.2 percent, while total community biomass increased by 28 percent. Similarly, Gavazzi *et al*. (2000) grew loblolly pine seedlings for four months in competition with both C_3 and C_4 weeds at atmospheric CO_2 concentrations of 260 and 660 ppm, reporting that elevated CO_2 increased pine biomass by 22 percent while eliciting no response from either type of weed.

In a study of pasture ecosystems near Montreal, Canada, Taylor and Potvin (1997) found that elevated CO_2 concentrations did not influence the number of native species returning after their removal (to simulate disturbance), even in the face of the introduced presence of the C_3 weed *Chenopodium album*, which normally competes quite effectively with several slower-growing crops in ambient air. In fact, atmospheric CO_2 enrichment did not impact the growth of this weed in any measurable way.

Ziska *et al*. (1999) also studied the C_3 weed *C. album*, along with the C_4 weed *Amaranthus retroflexus*, in glasshouses maintained at atmospheric CO_2 concentrations of 360 and 720 ppm. They determined that elevated CO_2 significantly increased the photosynthetic rate and total dry weight of the C_3 weed, but that it had no effect on the C_4 weed. Also, they found that the growth response of the C_3 weed to a doubling of the air's CO_2 content was approximately 51 percent, which is about the same as the average 52 percent growth response tabulated by Idso (1992), and that obtained by Poorter (1993) for rapidly growing wild C_3 species (54 percent), which finding suggests there is no enhanced dominance of the C_3 weed over other C_3 plants in a CO_2-enriched environment.

Wayne *et al*. (1999) studied another agricultural weed, field mustard (*Brassica kaber*), which was sown in pots at six densities, placed in atmospheric CO_2 concentrations of 350 and 700 ppm, and sequentially harvested during the growing season. Early in stand development, elevated CO_2 increased above-ground weed biomass in a density-dependent manner, with the greatest stimulation of 141 percent occurring at the lowest density (corresponding to 20 plants per square meter) and the smallest stimulation of 59 percent occurring at the highest density (corresponding to 652 plants per square meter). However, as stands matured, the density-dependence of the CO_2-induced growth response disappeared, and CO_2-enriched plants exhibited an average above-ground biomass that was 34 percent greater than that of ambiently grown plants across a broad range of plant densities. This final growth stimulation was similar to that of most other herbaceous plants exposed to atmospheric CO_2 enrichment (30 to 50 percent biomass increases for a doubling of the air's CO_2 content), evidence once again that atmospheric CO_2 enrichment confers no undue advantage upon weeds at the expense of other plants.

In a study of a weed that affects both plants and animals, Caporn *et al*. (1999) examined bracken (*Pteridium aquilinum*), which poses a serious weed problem and potential threat to human health in the United Kingdom and other regions, growing specimens for 19 months in controlled environment chambers maintained at atmospheric CO_2 concentrations of 370 and 570 ppm and normal or high levels of soil fertility. They found that the high CO_2 treatment consistently increased rates of net photosynthesis by 30 to 70 percent, depending on soil fertility and time of year. However, elevated CO_2 did not increase total plant dry mass or the dry mass of any plant organ, including rhizomes, roots and fronds. In fact, the only significant effect of elevated CO_2 on bracken growth was observed in the normal nutrient regime, where elevated CO_2 reduced mean frond area.

Finally, in a study involving two parasitic species (*Striga hermonthica* and *Striga asiatica*), Watling and Press (1997) reported that total parasitic biomass per host plant at an atmospheric CO_2 concentration of 700 ppm was 65 percent less than it was in ambient air. And in a related study, Dale and Press (1999) observed that the presence of a parasitic plant (*Orobanche minor*) reduced its host's biomass by 47 percent in ambient air of 360 ppm CO_2, but by only 20 percent in air of 550 ppm CO_2.

These several studies suggest that, contrary to what is claimed by the IPCC, the ongoing rise in the air's CO_2 content will not favor the growth of weedy species over that of crops and native plants. In fact, it may provide non-weeds greater protection against weed-induced decreases in their productivity and growth. Future increases in the air's CO_2 content may actually increase the competitiveness of non-weeds over weeds.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/b/weedsvsnonw.php.

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7.6. Respiration

Nearly all of earth's plants respond favorably to increases in the air's CO_2 concentration by exhibiting enhanced rates of net photosynthesis and biomass production during the light part of each day. In many cases, observed increases in these parameters (especially biomass production) are believed to be due, in part, to CO_2-induced reductions in carbon losses via respiration during the day and especially at night (called "dark respiration"). In this summary, we examine what has been learned about this subject from experiments conducted on various herbaceous and woody plants.

Additional information on this topic, including reviews on respiration not discussed here, can be found at http://www.co2science.org/subject/r/subject_r.php under the heading Respiration.

7.6.1. Herbaceous Plants

7.6.1.1. Crops

Baker *et al*. (2000) grew rice in Soil-Plant-Atmosphere Research (SPAR) units at atmospheric CO_2 concentrations of 350 and 700 ppm during daylight hours. Under these conditions, rates of dark respiration decreased in both CO_2 treatments with short-term increases in the air's CO_2 concentration at night. However, when dark respiration rates were measured at the CO_2 growth concentrations of the plants, they were not significantly different from each other.

Cousins *et al*. (2001) grew sorghum at atmospheric CO_2 concentrations of 370 and 570 ppm within a free-air CO_2 enrichment (FACE) facility near Phoenix, Arizona, USA. Within six days of planting, the photosynthetic rates of the second leaves of the CO_2-enriched plants were 37 percent greater than those of the second leaves of the ambiently grown plants. However, this CO_2-induced photosynthetic enhancement slowly declined with time, stabilizing at approximately 15 percent between 23 and 60 days after planting. In addition, when measuring photosynthetic rates at a reduced oxygen concentration of 2 percent, they observed 16 and 9 percent increases in photosynthesis for the ambient and CO_2-enriched plants, respectively. These observations suggest that the extra 200 ppm of CO_2 was reducing photorespiratory carbon losses, although this phenomenon did not account for all of the CO_2-induced stimulation of photosynthesis.

Das *et al*. (2002) grew tropical nitrogen-fixing mungbean plants in open-top chambers maintained at atmospheric CO_2 concentrations of either 350 or 600 ppm for two growing seasons, with the extra CO_2 being provided between either days 0 and 20 or days 21 and 40 after germination. This work revealed that the elevated CO_2 decreased rates of respiration by 54-62 percent, with the greatest declines occurring during the first 20 days after germination.

Wang *et al*. (2004) grew well-watered and fertilized South American tobacco plants from seed in 8.4-liter pots (one plant per pot) filled with sand and housed in controlled-environment growth chambers maintained at atmospheric CO_2 concentrations of either 365 or 730 ppm for a total of nine weeks. Over this period they found that the ratio of net photosynthesis per unit leaf area (A) to dark respiration per unit leaf area (Rd) "changed dramatically." Whereas A/Rd was the same in both treatments at the beginning of the measurement period, a month later it had doubled in the CO_2-enriched environment but had risen by only 58 percent in the ambient treatment. Speaking of this finding, the three researchers say that "if the dynamic relationship between A and Rd observed in *N. sylvestris* is applicable to other species, it will have important implications for carbon cycling in terrestrial ecosystems, since plants will assimilate CO_2 more efficiently as they mature."

Bunce (2005) grew soybeans in the field in open-top chambers maintained at atmospheric CO_2 concentrations of ambient and ambient +350 ppm at the Beltsville Agricultural Research Center in Maryland (USA), where net carbon dioxide exchange rate measurements were performed on a total of 16 days between 18 July and 11 September of 2000 and 2003, during the flowering to early pod-filling stages of the growing season. Averaged over the course of the study, he found that daytime net photosynthesis per unit leaf area was 48 percent greater in the plants growing in the CO_2-enriched air, while nighttime respiration per unit leaf area was unaffected by elevated CO_2. However, because the extra 350 ppm of CO_2 increased leaf dry mass per unit area by an average of 23 percent, respiration per unit of mass was significantly lower for the leaves of the soybeans growing in the CO_2-enriched air.

Wang and Curtis (2002) conducted a meta-analysis of the results of 45 area-based dark respiration (Rda) and 44 mass-based dark respiration (Rdm) assessments of the effects of a doubling of the air's CO_2 concentration on 33 species of plants derived from 37 scientific studies. This work revealed that the mean leaf Rda of the suite of herbaceous plants studied was significantly higher (+29 percent, $P < 0.01$) at elevated CO_2 than at ambient CO_2. However, when the herbaceous plants were separated into groups that had experienced durations of CO_2 enrichment that were either shorter or longer than 60 days, it was found that the short-term studies exhibited a mean Rda increase of 51 percent ($P < 0.05$), while the long-term studies exhibited no effect. Hence, for conditions of continuous atmospheric CO_2 enrichment, herbaceous plants would likely experience no change in leaf Rda. In addition, the two researchers found that plants exposed to elevated CO_2 for < 100 days "showed significantly less of a reduction in leaf Rdm due to CO_2 enrichment (-12%) than did plants exposed for longer periods (-35%, $P < 0.01$)." Hence, for long-term conditions of continuous atmospheric CO_2 enrichment, herbaceous crops would likely experience an approximate 35 percent decrease in leaf Rdm.

Bunce (2004) grew six different 16-plant batches of soybeans within a single controlled-environment chamber, one to a pot filled with 1.8 liters of vermiculite that was flushed daily with a complete nutrient solution. In three experiments conducted at day/night atmospheric CO_2 concentrations of 370/390 ppm, air temperatures were either 20, 25 or 30°C, while in three other experiments conducted at an air temperature of 25°C, atmospheric CO_2 concentrations were either 40, 370 or 1400 ppm. At the end of the normal 16 hours of light on the 17th day after planting, half of the plants were harvested and used for the measurement of a number of physical parameters, while measurements of the plant physiological processes of respiration, translocation and nitrate reduction were made on the other half of the plants over the following 8-hour dark period.

Plotting translocation and nitrate reduction as functions of respiration, Bunce found that "a given change in the rate of respiration was accompanied by the same change in the rate of translocation or nitrate reduction, regardless of whether the altered respiration was caused by a change in temperature or by a change in atmospheric CO_2 concentration." As a result, and irrespective of whatever mechanisms may have been involved in eliciting the responses observed, Bunce concluded that "the parallel responses of translocation and nitrate reduction for both the temperature and CO_2 treatments make it unlikely that the response of respiration to one variable [CO_2] was an artifact while the response to the other [temperature] was real." Hence, there is reason to believe that the oft-observed decreases in dark respiration experienced by plants exposed to elevated levels of atmospheric CO_2, as per the review and analysis studies of Drake *et al*. (1999) and Wang and Curtis (2002), are indeed real and not the result of measurement system defects.

In light of these several findings, it can be concluded that the balance of evidence suggests that the growth of herbaceous crops is generally enhanced by CO_2-induced decreases in respiration during the dark period.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/r/respirationcrops.php.

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7.6.1.2. Other Herbaceous Plants

In this section we review the results of studies of non-crop herbaceous plants to determine if atmospheric CO_2 enrichment tends to increase or decrease (or leave unaltered) their respiration rates.

Rabha and Uprety (1998) grew India mustard plants for an entire season in open-top chambers with either ambient or enriched (600 ppm) atmospheric CO_2 concentrations and adequate or inadequate soil moisture levels. Their work revealed that the elevated CO_2 concentration reduced leaf dark respiration rates by about 25 percent in both soil moisture treatments, which suggests that a greater proportion of the increased carbohydrate pool in the CO_2-enriched plants remained within them to facilitate increases in growth and development.

Ziska and Bunce (1999) grew four C_4 plants in controlled environment chambers maintained at either full-day (24-hour) atmospheric CO_2 concentrations of 350 and 700 ppm or a nocturnal-only CO_2 concentration of 700 ppm (with 350 ppm CO_2 during the day) for about three weeks. In this particular study, 24-hour CO_2 enrichment caused a significant increase in the photosynthesis (+13 percent) and total dry mass (+21 percent) of only one of the four C_4 species (*Amaranthus retroflexus*). However, there was no significant effect of nocturnal-only CO_2 enrichment on this species, indicating that the observed increase in biomass, resulting from 24-hour atmospheric CO_2 enrichment, was not facilitated by greater carbon conservation stemming from a CO_2-induced reduction in dark respiration.

In an experiment that produced essentially the same result, Grunzweig and Korner (2001) constructed model grasslands representative of the Negev of Israel and placed them in growth chambers maintained at atmospheric CO_2 concentrations of 280, 440 and 600 ppm for five months. This study also revealed that atmospheric CO_2 enrichment had no effect on nighttime respiratory carbon losses.

Moving to the other end of the moisture spectrum, Van der Heijden *et al*. (2000) grew peat moss hydroponically within controlled environment chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm for up to six months, while simultaneously subjecting the peat moss to three different levels of nitrogen deposition. In all cases, they found that the elevated CO_2 reduced rates of dark respiration consistently throughout the study by 40 to 60 percent.

In a final multi-species study, Gonzalez-Meler *et al*. (2004) reviewed the scientific literature pertaining to the effects of atmospheric CO_2 enrichment on plant respiration from the cellular level to the level of entire ecosystems. They report finding that "contrary to what was previously thought, specific respiration rates are generally not reduced when plants are grown at elevated CO_2." Nevertheless, they note that "whole ecosystem studies show that canopy respiration does not increase proportionally to increases in biomass in response to elevated CO_2," which suggests that respiration per unit biomass is likely somewhat reduced by atmospheric CO_2 enrichment. However, they also find that "a larger proportion of respiration takes place in the root system [when plants are grown in CO_2-enriched air]," which once again obfuscates the issue.

The three researchers say "fundamental information is still lacking on how respiration and the processes supported by it are physiologically controlled, thereby preventing sound interpretations of what seem to be species-specific responses of respiration to elevated CO_2." They conclude that "the role of plant respiration in augmenting the sink capacity of terrestrial ecosystems is still uncertain."

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/r/respirationherbaceous.php.

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7.6.2. Woody Plants

7.6.2.1. Coniferous Trees

Jach and Ceulemans (2000) grew three-year old Scots pine seedlings out-of-doors and rooted in the ground in open-top chambers maintained at atmospheric CO_2 concentrations of either 350 or 750 ppm for two years. To make the experiment more representative of the natural world, they applied no nutrients or irrigation water to the soils in which the trees grew for the duration of the study. After two years of growth under these conditions, dark respiration on a needle mass basis in the CO_2-enriched seedlings was 27 percent and 33 percent lower in current-year and one-year-old needles, respectively, with the greater reduction in the older needles being thought to arise from the greater duration of elevated CO_2 exposure experienced by those needles.

Hamilton *et al.* (2001) studied the short- and long-term respiratory responses of loblolly pines in a free-air CO_2-enrichment (FACE) study that was established in 1996 on 13-year-old trees in a North Carolina (USA) plantation, where the CO_2-enriched trees were exposed to an extra 200 ppm of CO_2. This modest increase in the atmosphere's CO_2 concentration produced no significant short-term suppression of dark respiration rates in the trees' needles. Neither did long-term exposure to elevated CO_2 alter maintenance respiration, which is the amount of CO_2 respired to maintain existing plant tissues. However, growth respiration, which is the amount of CO_2 respired when constructing new tissues, was reduced by 21 percent.

McDowell *et al.* (1999) grew five-month-old seedlings of western hemlock in root boxes subjected to various root-space CO_2 concentrations (ranging from 90 to 7000 ppm) for periods of several hours to determine the effects of soil CO_2 concentration on growth, maintenance and total root respiration. In doing so, they found that although elevated CO_2 had no effect on growth respiration, it significantly impacted maintenance and total respiration. At a soil CO_2 concentration of 1585 ppm, for example, total and maintenance respiration rates of roots were 55 percent and 60 percent lower, respectively, than they were at 395 ppm. The impact of elevated CO_2 on maintenance respiration was so strong that it exhibited an exponential decline of about 37 percent for every doubling of soil CO_2 concentration. The implications of this observation are especially important because maintenance respiration comprised 85 percent of total root respiration in this study.

The results of these experiments suggest that both above and below the soil surface, coniferous trees may exhibit reductions in total respiration in a high-CO_2 world of the future. Three studies of three species, however, is insufficent evidence to reach a firm conclusion.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/r/respirationconifers.php.

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7.6.2.2. Deciduous Trees

Wang and Curtis (2001) grew cuttings of two male and two female trembling aspen trees for about five months on soils containing low and high nitrogen contents in open-top chambers maintained at atmospheric CO_2 concentrations of 380 and 765 ppm, finding that gender had little effect on dark respiration rates, but that elevated CO_2 increased them, by 6 percent and 32 percent in the low and high soil nitrogen treatments, respectively. On the other hand, Karnosky *et al*. (1999) grew both O_3-sensitive and O_3-tolerant aspen clones for one full year in free-air CO_2-enrichment (FACE) plots maintained at atmospheric CO_2 concentrations of 360 and 560 ppm, finding that the extra CO_2 decreased dark respiration rates by 24 percent.

Gielen *et al*. (2003) measured stem respiration rates of white, black and robusta poplar trees in a high-density forest plantation in the third year of a FACE experiment in which the CO_2 concentration of the air surrounding the trees was increased to a value of approximately 550 ppm. This study revealed, in their words, that “stem respiration rates were not affected by the FACE treatment,” and that “FACE did not influence the relationships between respiration rate and both stem temperature and relative growth rate.” In addition, they say they could find “no effect of the FACE treatment on Rm [maintenance respiration, which is related to the sustaining of existing cells] and Rg [growth respiration, which is related to the synthesis of new tissues].”

Hamilton *et al*. (2001) studied respiratory responses of sweetgum trees growing in the understory of a loblolly pine plantation (but occasionally reaching the top of the canopy) to an extra 200 ppm of CO_2 in a FACE study conducted in North Carolina, USA. As a result of their measurement program, they determined that the modest increase in atmospheric CO_2 concentration did not appear to alter maintenance respiration to any significant degree, but that it reduced dark respiration by an average of 10 percent and growth respiration of leaves at the top of the canopy by nearly 40 percent.

In reviewing the results of these several deciduous tree studies, we see cases of both increases and decreases in respiration rates in response to atmospheric CO_2 enrichment, as well as cases of no change in respiration. More data are needed before any general conclusions may safely be drawn.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/r/respirationdeciduous.php.

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7.6.2.3. Multiple Tree Studies

Amthor (2000) measured dark respiration rates of intact leaves of nine different tree species growing naturally in an American deciduous forest. Within a specially designed leaf chamber, the CO_2 concentration surrounding individual leaves was stabilized at 400 ppm for 15 minutes, whereupon their respiration rates were measured for 30 minutes, after which the CO_2 concentration in the leaf chamber was raised to 800 ppm for 15 minutes and respiration data were again recorded for the same leaves. This protocol revealed that elevated CO_2 had little effect on leaf dark respiration rates. The extra 400 ppm of

CO_2 within the measurement cuvette decreased the median respiration rate by only 1.5 percent across the nine tree species. This observation led Amthor to state that the "rising atmospheric CO_2 concentration has only a small direct effect on tree leaf respiration in deciduous forests;" and he calculated that it can be "more than eliminated by a 0.22°C temperature increase." Upon this premise, he concluded that "future direct effects of increasing CO_2 in combination with warming could stimulate tree leaf respiration in their sum," and that this consequence "would translate into only slight, if any, effects on the carbon balance of temperate deciduous forests in a future atmosphere containing as much as [800 ppm] CO_2."

Amthor's conclusion is debatable, for it is based upon the extrapolation of the short-term respiratory responses of individual leaves, exposed to elevated CO_2 for only an hour or two, to that of entire trees, many of which will experience rising CO_2 levels for a century or more during their lifetimes. Trees are long-lived organisms that should not be expected to reveal the nature of their long-term responses to elevated atmospheric CO_2 concentrations on as short a time scale as 15 minutes. Indeed, their respiratory responses may change significantly with the passage of time as they acclimate and optimize their physiology and growth patterns to the gradually rising CO_2 content of earth's atmosphere, as evidenced by the findings of the following two studies.

Wang and Curtis (2002) conducted a meta-analysis of the results of 45 area-based dark respiration (Rda) and 44 mass-based dark respiration (Rdm) assessments of the effects of an approximate doubling of the air's CO_2 concentration on 33 species of plants (both herbaceous and woody) derived from 37 scientific publications. This effort revealed that the mean leaf Rda of the woody plants they analyzed was unaffected by elevated CO_2. However, there was an effect on mean leaf Rdm, and it was determined to be time-dependent. The woody plants exposed to elevated CO_2 for < 100 days, in the reviewing scientists' words, "showed significantly less of a reduction in leaf Rdm due to CO_2 enrichment (-12%) than did plants exposed for longer periods (-35%, $P < 0.01$)." Hence, for conditions of continuous long-term atmospheric CO_2 enrichment, the results of Wang and Curtis' analysis suggest woody plants may experience an approximate 35 percent decrease in leaf Rdm.

Drake *et al.* (1999) also conducted a comprehensive analysis of the peer-reviewed scientific literature to determine the effects of elevated atmospheric CO_2 concentrations on plant respiration rates. They found that atmospheric CO_2 enrichment typically decreased respiration rates in mature foliage, stems, and roots of CO_2-enriched plants relative to rates measured in plants grown in ambient air; and when normalized on a biomass basis, they determined that a doubling of the atmosphere's CO_2 concentration would likely reduce plant respiration rates by an average of 18 percent. To determine the potential effects of this phenomenon on annual global carbon cycling, which the twelve researchers say "will enhance the quantity of carbon stored by forests," they input a 15 percent CO_2-induced respiration reduction into a carbon sequestration model, finding that an additional 6 to 7 Gt of carbon would remain sequestered within the terrestrial biosphere each year, thus substantially strengthening the terrestrial carbon sink.

Davey *et al.* (2004) reached a different conclusion. "Averaged across many previous investigations, doubling the CO_2 concentration has frequently been reported to cause an instantaneous reduction of leaf dark respiration measured as CO_2 efflux." However, as they continue, "no known mechanism accounts for this effect, and four recent studies [Amthor (2000); Anthor *et al.* (2001); Jahnke (2001); Jahnke and Krewitt (2002)] have shown that the measurement of respiratory CO_2 efflux is prone to experimental artifacts that could account for the reported response."

Using a technique that avoids the potential artifacts of prior attempts to resolve the issue, Davey *et al.* employed a high-resolution dual channel oxygen analyzer in an open gas exchange system to measure the respiratory O_2 uptake of nine different species of plants in response to a short-term increase in atmospheric CO_2 concentration, as well as the response of seven species to long-term elevation of the air's CO_2 content in four different field experiments. In doing so, they found that "over six hundred separate measurements of respiration failed to reveal any decrease in respiratory O_2 uptake with an instantaneous increase in CO_2." Neither could they detect any response to a five-fold increase in the air's CO_2 concentration nor to the total removal of CO_2 from the air. They also note that "this lack of response of respiration to elevated CO_2 was independent of treatment method, developmental stage, beginning or end of night, and the CO_2 concentration at which the plants had been grown." In the long-term field studies, however, there was a respiratory response;

but it was small (7 percent on a leaf mass basis), and it was positive, not negative.

In light of these contradicgtory results, the most reasonable conclusion is that atmospheric CO_2 enrichment may either increase or decrease woody-plant respiration, but not to any great degree, and that in the mean, the net result for the conglomerate of earth's trees would likely be something of little impact.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/r/respirationtrees.php.

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7.7. Carbon Sequestration

As the CO_2 content of the air continues to rise, nearly all of earth's plants respond by increasing their photosynthetic rates and producing more biomass. This results in more carbon being captured and stored, or sequestered, in plant fibers and soil, which counterbalances some of the CO_2 emissions produced by mankind's use of fossil fuels.

In this section we begin with a research review of what is known about forest and forest-species responses to atmospheric CO_2 enrichment and subsequent carbon sequestration. Then we survey research on how temperatures affect sequestration and whether CO_2 enhancement offsets the rate at which carbon is re-released from soil (decomposition).

7.7.1. CO_2 Enhancement and Carbon Sequestration

7.7.1.1 Forests

The planting and preservation of forests has long been acknowledged to be an effective and environmentally friendly (indeed, *enhancing*) means for slowing climate-model-predicted CO_2-induced global warming. This prescription for moderating potential climate change is based on two well-established and very straightforward facts: (1) the carbon trees use to construct their tissues comes from the air, and (2) its extraction from the atmosphere slows the rate of rise of the air's CO_2 content.

In an open-top chamber experiment conducted in Switzerland, Nitschelm *et al*. (1997) reported that a 71 percent increase in the atmospheric CO_2 concentration above white clover monocultures led to a 50 percent increase in soil organic carbon content. Related studies on wheat and soybean agroecosystems (Islam *et al*., 1999) provided similar results, as did a free-air CO_2 enrichment (FACE) experiment on cotton, which documented a 10 percent increase in soil organic carbon content in plots receiving 550 ppm CO_2 relative to those receiving 370 ppm (Leavitt *et al*., 1994). These phenomena will allow long-lived perennial species characteristic of forest ecosystems to sequester large amounts of carbon within their wood for extended periods of time (Chambers *et al*., 1998).

In reviewing studies that have been conducted on individual trees, it is clear that elevated levels of atmospheric CO_2 increase photosynthesis and growth in both broad-leaved and coniferous species. When broad-leaved trembling aspen (*Populus tremuloides*) were exposed to twice-ambient levels of atmospheric CO_2 for 2.5 years, for example, Pregitzer *et al*. (2000) reported 17 and 65 percent increases in fine root biomass at low and high levels of soil nitrogen, respectively; while Zak *et al*. (2000) observed 16 and 38 percent CO_2-induced increases in total tree biomass when subjected to the same respective levels of soil nitrogen.

Similar results have been reported for coniferous trees. When branches of Sitka spruce (*Picea sitchensis*) were fumigated with air of 700 ppm CO_2 for four years, rates of net photosynthesis in current and second-year needles were 100 and 43 percent higher, respectively, than photosynthetic rates of needles exposed to ambient air (Barton and Jarvis, 1999). In addition, ponderosa pine (*Pinus ponderosa*) grown at 700 ppm CO_2 for close to 2.5 years exhibited rates of net photosynthesis in current-year needles that were 49 percent greater than those of needles exposed to air containing 350 ppm CO_2 (Houpis *et al*., 1999).

Elevated CO_2 also enhances carbon sequestration by reducing carbon losses arising from plant respiration. Karnosky *et al*. (1999) reported that aspen seedlings grown for one year at 560 ppm CO_2 displayed dark respiration rates that were 24 percent lower than rates exhibited by trembling aspen grown at 360 ppm CO_2. Also, elevated CO_2 has been shown to decrease maintenance respiration, which it did by 60 percent in western hemlock seedlings exposed to an atmospheric CO_2 concentration of nearly 1600 ppm (McDowell *et al*., 1999).

In a thorough review of these topics, Drake *et al*. (1999) concluded that, on average, a doubling of the atmospheric CO_2 concentration reduces plant respiration rates by approximately 17 percent. This finding contrasts strikingly with the much smaller effects reported by Amthor (2000), who found an average reduction in dark respiration of only 1.5 percent for nine deciduous tree species exposed to 800 ppm CO_2. The period of CO_2 exposure in his much shorter experiments, however, was a mere 15 minutes. If the air's CO_2 content doubles, plants will likely sequester something on the order of 17 percent more carbon than ambiently grown plants, solely as a consequence of CO_2-induced reductions in respiration. And it is good to remember that this stored carbon is in addition to that sequestered as a result of CO_2-induced increases in plant photosynthetic rates.

Based upon several different types of empirical data, a number of researchers have concluded that current rates of carbon sequestration are robust and that future rates will increase with increasing atmospheric CO_2 concentrations. In the study of Fan *et al*. (1998) based on atmospheric measurements, for example, the broad-leaved forested region of North America between 15 and 51°N latitude was calculated to possess a current carbon sink that can annually remove all the CO_2 emitted into the air from fossil fuel combustion in both Canada and the United States. On another large scale, Phillips *et al*. (1998) used data derived from tree basal area to show that average forest biomass in the tropics has increased substantially over the past 40 years and that growth in the Neotropics alone (south and central South America, the Mexican lowlands, the Carribean islands, and southern Florida) can account for 40 percent of the missing carbon of the entire globe. And in looking to the future, White *et al*. (2000) have calculated that coniferous and mixed forests north of 50°N latitude will likely expand their northern and southern boundaries by about 50 percent due to the combined effects of increasing atmospheric CO_2, rising temperature, and nitrogen deposition.

The latter of these factors, nitrogen deposition, is an important variable. As indicated in the study of White *et al*., it can play an interactive role with increasing atmospheric CO_2 to increase plant growth and carbon sequestration. However, the magnitude of that role is still being debated. Nadelhoffer *et al*. (1999), for example, concluded that nitrogen deposition from human activities is "unlikely to be a major contributor" to the large CO_2 sink that exists in northern temperate forests. Houghton *et al*. (1998), however, feel that nitrogen deposition holds equal weight with CO_2 fertilization in the production of terrestrial carbon sinks; and Lloyd (1999) demonstrated that when CO_2 and nitrogen increase together, modeled forest productivity is greater than that predicted by the sum of the individual contributions of these two variables. Thus, anthropogenic nitrogen deposition can have anywhere from small to large positive effects on carbon sequestration, as well as everything in between.

In conclusion, as the air's CO_2 content continues to rise, the ability of earth's forests to sequester carbon should also rise. With more CO_2 in the atmosphere, trees will likely exhibit greater rates of photosynthesis and reduced rates of respiration. Together, these observations suggest that biologically fixed carbon will experience greater residency times within plant tissues. And if this carbon is directed into wood production, which increases substantially with atmospheric CO_2 enrichment, some of it can be kept out of circulation for a *very* long time, possibly even a millennium or more.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/c/carbonforests.php.

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7.7.1.2. Old Forests

In addition to enhancing the growth and production of young forests, available research indicates that rising atmospheric CO_2 concentrations will also increase the productivity and growth of older forests. For most of the past century it was believed that old-growth forests, such as those of Amazonia, should be close to dynamic equilibrium. Just the opposite, however, has been repeatedly observed over the past two decades.

In one of the first studies to illuminate this reality, Phillips and Gentry (1994) analyzed the turnover rates—which are close correlates of net productivity (Weaver and Murphy, 1990)—of 40 tropical forests from all around the world. They found that the growth rates of these already highly productive forests had been rising ever higher since at least 1960, and that they had experienced an apparent acceleration in growth rate sometime after 1980. Commenting on these findings, Pimm and Sugden (1994) reported that the consistency and simultaneity of the forest growth trends that Phillips and Gentry had documented on several continents led them to conclude that "enhanced productivity induced by increased CO_2 is the most plausible candidate for the cause of the increased turnover."

A few years later, Phillips *et al.* (1998) analyzed forest growth rate data for the period 1958 to 1996 for several hundred plots of mature tropical trees scattered around the world, finding that tropical forest biomass, as a whole, increased substantially over the period of record. In fact, the increase in the Neotropics was equivalent to approximately 40 percent of the missing terrestrial carbon sink of the entire globe. Consequently, they concluded that tropical forests "may be helping to buffer the rate of increase in atmospheric CO_2, thereby reducing the impacts of global climate change." And, again, they identified the aerial fertilization effect of the ongoing rise in the air's CO_2 content as one of the primary factors likely to be responsible for this phenomenon.

More recently, Laurance *et al.* (2004a) reported accelerated growth in the 1990s relative to the 1980s for the large majority (87 percent) of tree genera in 18 one-hectare plots spanning an area of about 300 km^2 in central Amazonia, while Laurance *et al.* (2004b) observed similarly accelerated tree community dynamics in the 1990s relative to the 1980s. In addition, Baker *et al.* (2004) reported there has been a net increase in biomass in old-growth Amazonian forests in recent decades at a rate of 1.22 ± 0.42 Mg ha^{-1} yr^{-1}, slightly greater than that originally estimated by Phillips *et al.* And once again, it was suggested, in the words of Laurance *et al.* (2005), that these "pervasive changes in central Amazonian tree communities were most likely caused by global- or regional-scale drivers, such as increasing atmospheric CO_2 concentrations (Laurance *et al.*, 2004a,b)."

Expanding upon this theme, Laurance *et al.* (2005) say 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)." They note, however, that they have been challenged in this conclusion by Nelson (2005), and they thus go on to consider his arguments in some detail, methodically dismantling them one by one.

Evidence of increasing dynamism and productivity of intact tropical forests continued, with Lewis *et al.*, (2004a) reporting that among 50 old-growth plots scattered across tropical South America, "stem recruitment, stem mortality, and biomass growth, and loss, *all* increased significantly." In summarizing these and other findings, Lewis (2006) reports that 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," all of which rates of increase are greater than the previously documented increases in the rates of these phenomena. What is more, Lewis says that "preliminary analyses also suggest the African and Australian forests are showing structural changes similar to South American forests."

So why should we care about growth trends of old forests? People who seek to address the issue solely on the basis of forced reductions in anthropogenic CO_2 emissions claim that carbon sequestration by forests is viable only when forests are young and growing vigorously. (Pearce, 1999) As forests age, as claimed by the IPCC, they gradually lose their carbon-sequestering prowess, such that forests more than one hundred years old become essentially useless for removing CO_2 from the air, as they claim such ancient and decrepit stands yearly lose as much CO_2 via respiration as they take in via photosynthesis.

Although demonstrably erroneous, with repeated telling the twisted tale actually begins to sound reasonable. After all, doesn't the metabolism of every living thing slow down as it gets older? We grudgingly admit that it does—even with trees—but some trees live a remarkably long time. In Panama (Condit *et al*., 1995), Brazil (Chambers *et al*., 1998; Laurance *et al*., 2004; Chambers *et al*., 2001), and many parts of the southwestern United States (Graybill and Idso, 1993), for example, individuals of a number of different species have been shown to live for nearly one and a half millennia. At a hundred years of age, these super-slurpers of CO_2 are mere youngsters. And in their really old age, their appetite for the vital gas, though diminished, is not lost. In fact, Chambers *et al*. (1998) indicate that the long-lived trees of Brazil continue to experience protracted slow growth even at 1,400 years of age. And protracted slow growth (evident in yearly increasing trunk diameters) of very old and *large* trees can absorb a huge amount of CO_2 out of the air each year, especially when, as noted by Chanbers *et al*. (1998) with respect to the Brazilian forests in the central Amazon, about 50 percent of their above-ground biomass is contained in less than the largest 10 percent of their trees. Consequently, since the life span of these massive long-lived trees is considerably greater than the projected life span of the entire "Age of Fossil Fuels," their cultivation and preservation represents an essentially permanent, though only partial, solution to the perceived problem of the anthropogenic global warming.

Another important fact about forests and their ability to sequester carbon over long periods of time is that the forest itself is the unit of primary importance when it comes to determining the amount of carbon that can be sequestered on a unit area of land. Cary *et al*. (2001) note most models of forest carbon sequestration wrongly assume that "age-related growth trends of individual trees and even-aged, monospecific stands can be extended to natural forests." When they compared the predictions of such models against real-world data they gathered from northern Rocky Mountain subalpine forests that ranged in age from 67 to 458 years, for example, they found that above-ground net primary productivity in 200-year-old natural stands was almost twice as great as that of modeled stands, and that the difference between the two increased linearly throughout the entire sampled age range.

So what's the explanation for the huge discrepancy? Cary *et al.* suggest that long-term recruitment and the periodic appearance of additional late-successional species (increasing biodiversity) may have significant effects on stand productivity, infusing the primary unit of concern, i.e., the ever-evolving forest super-organism, with greater vitality than would have been projected on the basis of characteristics possessed by the unit earlier in its life. They also note that by not including effects of size- or age-dependent decreases in stem and branch respiration per unit of sapwood volume in models of forest growth, respiration in older stands can be over-estimated by a factor of two to five.

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

Another study relevant to the ability of forests to act as long-term carbon sinks was conducted by Luo *et al*. (2003), who analyzed data obtained from the Duke Forest FACE experiment, in which three 30-meter-diameter plots within a 13-year-old forest (composed primarily of loblolly pines with sweetgum and yellow poplar trees as sub-dominants, together with numerous other trees, shrubs, and vines that occupy still smaller niches) began to be enriched with an extra 200 ppm of CO_2 in August 1996, while three similar plots were maintained at the ambient atmospheric CO_2 concentration. A number of papers describing different facets of this still-ongoing long-term study have been published; and as recounted by Luo *et al*., they have revealed the existence of a CO_2-induced "sustained photosynthetic stimulation at leaf and canopy levels [Myers *et al*., 1999; Ellsworth, 2000; Luo *et al*., 2001; Lai *et al*., 2002], which resulted in sustained stimulation of wood biomass increment [Hamilton *et al.*, 2002] and a larger carbon accumulation in the forest floor at elevated CO_2 than at ambient CO_2 [Schlesinger and Lichter, 2001]."

Based upon these findings and what they imply about rates of carbon removal from the atmosphere and its different residence times in plant, litter, and soil carbon pools, Luo *et al.* developed a model for studying the sustainability of forest carbon sequestration. Applying this model to a situation where the atmospheric CO_2 concentration gradually rises from a value of 378 ppm in 2000 to a value of 710 ppm in 2100, they calculated that the carbon sequestration rate of the Duke Forest would rise from an initial value of 69 g m^{-2} yr^{-1} to a final value of 201 g m^{-2} yr^{-1}, which is a far cry from the scenario promulgated by those who claim earth's forests will have released much of the carbon they had previously absorbed as early as the year 2050 (Pearce, 1999).

Another study that supports the long-term viability of carbon sequestration by forests was conducted by Paw U *et al.* (2004), who also note that old-growth forests have generally been considered to "represent carbon sources or are neutral (Odum, 1963, 1965)," stating that "it is generally assumed that forests reach maximum productivity at an intermediate age and productivity declines in mature and old-growth stands (Franklin, 1988), presumably as dead woody debris and other respiratory demands increase." More particularly, they report that a number of articles have suggested that "old-growth conifer forests are at equilibrium with respect to net ecosystem productivity or net ecosystem exchange (DeBell and Franklin, 1987; Franklin and DeBell, 1988; Schulze *et al.*, 1999), as an age-class end point of ecosystem development."

To see if these claims had any merit, Paw U *et al.* used an eddy covariance technique to estimate the CO_2 exchange rate of the oldest forest ecosystem (500 years old) in the AmeriFlux network of carbon-flux measurement stations—the Wind River old-growth forest in southwestern Washington, USA, which is composed mainly of Douglas fir and western hemlock—over a period of 16 months, from May 1998 to August 1999. Throughout this period, the 14 scientists report "there were no monthly averages with net release of CO_2," and that the cumulative net ecosystem exchange showed "remarkable sequestration of carbon, comparable to many younger forests." They concluded that "in contrast to frequently stated opinions, old-growth forests can be significant carbon sinks," noting that "the old-growth forests of the Pacific Northwest can contribute to optimizing carbon sequestration strategies while continuing to provide ecosystem services essential to supporting biodiversity."

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

"Contrary to expectation," as they describe it, Binkley *et al.* report that "live tree mass in 2003 [186 Mg ha^{-1}] was significantly greater than in 1976 [149 Mg ha^{-1}] ($P = 0.02$), refuting the hypothesis that live tree mass declined." In fact, they found that the annual net increment of live tree mass was about 1.37 Mg ha^{-1} yr^{-1} from age 96 to age 123 years, which is only 12 percent less than the mean annual increment of live tree mass experienced over the forest's initial 96 years of existence (149 Mg ha^{-1} / 96 yr = 1.55 Mg ha^{-1} yr^{-1}). Consequently, in response to the question they posed when embarking on their study—"Do old forests gain or lose carbon?"—Binkley *et al.* concluded that "old aspen forests continue to accrue live stem mass well into their second century, despite declining current annual increments," which, we might add, are not all that much smaller than those the forests exhibited in their younger years.

Similar results have been obtained by Hollinger *et al.* (1994) for a 300-year-old *Nothofagus* site in New Zealand, by Law *et al.* (2001) for a 250-year-old ponderosa pine site in the northwestern United States, by Falk *et al.* (2002) for a 450-year-old Douglas fir/western hemlock site in the same general area, and by Knohl *et al.* (2003) for a 250-year-old deciduous forest in Germany. In commenting on these findings, the latter investigators say they found "unexpectedly high carbon uptake rates during 2 years for an unmanaged 'advanced' beech forest, which is in contrast to the widely spread hypothesis that 'advanced' forests are insignificant as carbon sinks." For the forest they studied, as they describe it, "assimilation is clearly not balanced by respiration, although this site shows typical characteristics of an 'advanced' forest at a comparatively late stage of development."

These observations about forests are remarkably similar to recent findings regarding humans; i.e., that nongenetic interventions, even late in life, can put one on a healthier trajectory that extends productive lifespan. So what is the global "intervention" that has put the planet's trees on the healthier trajectory of being able to sequester significant amounts of carbon in their old age, when past theory (which was obviously based on past observations) decreed they should be in a state of no-net-growth or even negative growth? The answer is probably CO_2 enhancement.

For any tree of age 250 years or more, the greater portion of its life (at least two-thirds of it) has been spent in an atmosphere of reduced CO_2 content. Up until 1920, for example, the air's CO_2 concentration had never been above 300 ppm throughout the lives of such trees, whereas it is currently 375 ppm or 25 percent higher. And for older trees, even greater portions of their lives have been spent in air of even lower CO_2 concentration. Hence, the "intervention" that has given new life to old trees would appear to be the aerial fertilization effect produced by the CO_2 that resulted from the Industrial Revolution and is being maintained by its ever-expanding aftermath (Idso, 1995).

Based on these many observations, as well as the results of the study of Greenep *et al*. (2003), which strongly suggest, in their words, that "the capacity for enhanced photosynthesis in trees growing in elevated CO_2 is unlikely to be lost in subsequent generations," it would appear that earth's forests will remain strong sinks for atmospheric carbon well into the distant future. A wealth of scientific data confirms the reality of the ever-increasing productivity of earth's older forests, especially those of Amazonia, concomitant with the rise in the air's CO_2 content. An even greater wealth of laboratory and field data demonstrates that rising forest productivity is what one would expect to observe in response to the stimulus provided by the ongoing rise in the atmosphere's CO_2 concentration.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/f/forestold.php.

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7.7.2. Decomposition

What is the fate of the extra carbon that is stored within plant tissues as a consequence of atmospheric CO_2 enrichment? Is it rapidly returned to the atmosphere following tissue senescence and decomposition? Or is it locked away for long periods of time? Experiments and real-world observations reveal that atmospheric CO_2 enrichment typically reduces, or has no effect upon, decomposition rates of senesced plant material.

7.7.2.1. Processes and Properties

Atmospheric CO_2 enrichment stimulates photosynthesis and growth in nearly all plants, typically producing more non-structural carbohydrates, which can be used to manufacture more carbon-based secondary compounds (CBSCs) or phenolics. This observation is important because phenolics tend to inhibit the decomposition of the organic matter in which they are found (Freeman *et al*., 2001). If elevated levels of atmospheric CO_2 lead to the production of more of these decay-resistant substances, one would expect the ongoing rise in the air's CO_2 content to lead to the enhanced sequestration of plant-litter-derived carbon in the world's soils, producing a negative feedback phenomenon that would tend to slow the rate of rise of the air's CO_2 content and thereby moderate CO_2-induced global warming.

For a long time, research on this matter was rather muddled. Many studies reported the expected increases in CBSC concentrations with experimentally created increases in the air's CO_2 content. Others, however, could find no significant plant phenolic content changes; a few even detected CO_2-induced decreases in CBSC concentrations. Penuelas *et al*. (1997) finally brought order to the issue when they identified the key role played by soil nitrogen.

In analyzing the results of several different studies, Penuelas *et al*. noticed that when soil nitrogen supply was less than adequate, some of the CBSC responses to a doubling of the air's CO_2 content were negative, i.e., a portion of the studies indicated that plant CBSC concentrations declined as the air's CO_2 content rose. When soil nutrient supply was more than adequate, however, the responses were almost all positive, with plant CBSC concentrations rising in response to a doubling of the air's CO_2 concentration. In addition, when the CO_2 content of the air was tripled, *all* CBSC responses, under both low and high soil nitrogen conditions, were positive.

The solution to the puzzle was thus fairly simple. With a tripling of the air's CO_2 content, nearly all plants exhibited increases in CBSC production; but with only a doubling of the atmospheric CO_2 concentration, adequate nitrogen is needed to ensure a positive CBSC response.

What makes these observations exciting is that atmospheric CO_2 enrichment, in addition to enhancing plant growth, typically stimulates nitrogen fixation in both woody (Olesniewicz and Thomas, 1999) and non-woody (Niklaus *et al*., 1998; Dakora and Drake, 2000) legumes. As the air's CO_2 content continues to rise, earth's nitrogen-fixing plants should become ever more proficient in this important enterprise. In addition, some of the extra nitrogen thus introduced into earth's ecosystems will likely be shared with non-nitrogen-fixing plants. Also, since the microorganisms responsible for nitrogen fixation are found in nearly all natural ecosystems (Gifford, 1992), and since atmospheric CO_2 enrichment can directly stimulate the nitrogen-fixing activities of these microbes (Lowe and Evans, 1962), it can be appreciated that the ongoing rise in the air's CO_2 content will likely provide more nitrogen for the production of more CBSCs in all of earth's plants. And with ever-increasing concentrations of decay-resistant materials being found throughout plant tissues, the plant-derived organic matter that is incorporated into soils should remain there for ever longer periods of time.

On the other hand, in a meta-analysis of the effects of atmospheric CO_2 enrichment on leaf-litter chemistry and decomposition rate that was based on a total of 67 experimental observations, Norby *et al.* (2001) found that elevated atmospheric CO_2 concentrations—mostly between 600 and 700 ppm—reduced leaf-litter nitrogen concentration by about 7 percent. But in experiments where plants were grown under as close to natural conditions as possible, such as in open-top chambers, free-air CO_2 enrichment (FACE) plots, or in the proximity of CO_2-emitting springs, there were no significant effects of elevated CO_2 on leaf-litter nitrogen content.

In addition, based on a total of 46 experimental observations, Norby *et al.* determined that elevated atmospheric CO_2 concentrations increased leaf-litter lignin concentrations by an average of 6.5 percent. However, these increases in lignin content occurred in woody but not in herbaceous species. And again, the lignin concentrations of leaf litter were not affected by elevated CO_2 when plants were grown in open-top chambers, FACE plots, or in the proximity of CO_2-emitting springs.

In an analysis of a total of 101 observations, Norby *et al.* found elevated CO_2 had no consistent effect on leaf-litter decomposition rate in any type of experimental setting. As the air's CO_2 content continues to rise, it will likely have little to no impact on leaf-litter chemistry and rates of leaf-litter decomposition. Since there will be more leaf litter produced in a high-CO_2 world of the future, however, that fact alone will ensure that more carbon is sequestered in the world's soils for longer periods of time.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/d/decompprocesses.php.

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7.7.2.2. Agricultural Crops

In the study by Booker *et al*. (2000), leaves from defoliated cotton plants grown at an atmospheric CO_2 concentration of 720 ppm displayed significantly greater amounts of starch and soluble sugars and significantly lower concentrations of nitrogen than the leaves of plants grown in ambient air. These changes in the quality of the leaf litter produced under high CO_2 likely affected its subsequent decomposition rate, which was 10 to 14 percent slower than that observed for leaf litter collected from plants grown in air of normal CO_2 concentration. Likewise, when crop residues from soybean and sorghum plants that were raised in twice-ambient CO_2 environments were mixed with soils to study their decomposition rates, Torbert *et al*. (1998) noted they lost significantly less carbon – up to 40 percent less – than similarly treated crop residues from ambiently grown crops.

In contrast to the aforementioned studies, neither Van Vuuren *et al*. (2000), for spring wheat, nor Henning *et al*. (1996), for soybean and sorghum, found any significant differences in the decomposition rates of the residues of crops grown under conditions of high or normal atmospheric CO_2 concentration.

As the air's CO_2 content continues to rise, therefore, and agricultural crops grow more robustly and return greater amounts of litter to the soil, it is likely that greater amounts of carbon will be sequestered in the soil in which they grew, as crop residue decomposition rates are significantly decreased or remain unchanged.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/d/decompositionagri.php.

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7.7.2.3. Grassland Species

In the study of Nitschelm *et al*. (1997), white clover exposed to an atmospheric CO_2 concentration of 600 ppm for one growing season channeled 50 percent more newly fixed carbon compounds into the soil than similar plants exposed to ambient air. In addition, the clover's roots decomposed at a rate that was 24 percent slower than that observed for roots of control plants, as has also been reported for white clover by David *et al*. (2001). These observations suggest that soil carbon sequestration under white clover ecosystems will be greatly enhanced as the air's CO_2 content continues to rise, as was also shown for moderately fertile sandstone grasslands (Hu *et al*., 2001).

Similar results have been observed with mini-ecosystems comprised entirely of perennial ryegrass. Van Ginkel *et al*. (1996), for example, demonstrated that exposing this species to an atmospheric CO_2 concentration of 700 ppm for two months caused a 92 percent increase in root growth and 19 percent and 14 percent decreases in root decomposition rates one and two years, respectively, after incubating ground roots within soils. This work was later followed up by Van Ginkel and Gorissen (1998), who showed a 13 percent reduction in the decomposition rates of CO_2-enriched perennial ryegrass roots in both disturbed and undisturbed root profiles. This and other work led the authors to calculate that CO_2-induced reductions in the decomposition of perennial ryegrass litter, which enhances soil carbon sequestration, could well be large enough to remove over half of the anthropogenic CO_2 emissions that may be released in the next century (Van Ginkel *et al*., 1999).

In some cases, atmospheric CO_2 enrichment has little or no significant effect on litter quality and subsequent rates of litter decomposition, as was the case in the study of Hirschel *et al*. (1997) for lowland calcareous and high alpine grassland species. Similar non-effects of elevated CO_2 on litter decomposition have also been reported in a California grassland (Dukes and Field, 2000).

In light of these experimental findings, it would appear that as the air's CO_2 concentration increases, litter decomposition rates of grassland species will likely decline, increasing the amount of carbon sequestered in grassland soils. Since this phenomenon is augmented by the aerial fertilization effect of atmospheric CO_2 enrichment, which leads to the production of greater amounts of litter, there is thus a double reason for expecting more carbon to be removed from the atmosphere by earth's grasslands in the future.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/d/decompositiongrass.php.

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7.7.2.4. Woody Plants

The sequestering of carbon in the soils upon which woody plants grow has the potential to provide a powerful brake on the rate of rise of the air's CO_2 content if the plant litter that is incorporated into those soils does not decompose more rapidly in a CO_2-enriched atmosphere than it does in current ambient air. It is important to determine if this latter constraint is true or false. In this section we review this question with respect to litter produced by conifers and deciduous trees.

Scherzel *et al.* (1998) exposed seedlings of two eastern white pine genotypes to elevated concentrations of atmospheric CO_2 and O_3 in open-top chambers for four full growing seasons, finding no changes in the decomposition rates of the litter of either genotype to the concentration increases of either of these two gases. Likewise, Kainulainen *et al.* (2003) could find no evidence that the litter of 22-year-old Scots pine trees that had been exposed to elevated concentrations of CO_2 and O_3 for three full years decomposed any faster or slower than litter produced in ambient air. In addition, Finzi and Schlesinger (2002) found that the decomposition rate of litter from 13-year-old loblolly pine trees was unaffected by elevated CO_2 concentrations maintained for a period of two full years in a FACE study.

In light of these observations, plus the fact that Saxe *et al.* (1998) have determined that a doubling of the air's CO_2 content leads to more than a doubling of the biomass production of coniferous species, it logically follows that the ongoing rise in the atmosphere's CO_2 concentration is increasing carbon sequestration rates in the soils upon which conifers grow and producing a significant negative feedback phenomenon that slows the rate of rise of the air's CO_2 content.

What about deciduous trees? Scherzel *et al.* (1998) exposed seedlings of yellow poplar trees to elevated concentrations of atmospheric CO_2 and O_3 in open-top chambers for four full growing seasons, finding that rates of litter decomposition were similar for all treatments for the first five months of the study. Thereafter, however, litter produced in the elevated O_3 and CO_2 treatment decomposed at a significantly slower rate, such that after two years had passed, the litter from the elevated O_3 and CO_2 treatment contained approximately 12 percent more biomass than the litter from any other treatment.

Cotrufo *et al*. (1998) grew two-year-old ash and sycamore seedlings for one growing season in closed-top chambers maintained at atmospheric CO_2 concentrations of 350 and 600 ppm. The high-CO_2 air increased lignin contents in the litter produced from both tree species, which likely contributed to the decreased litter decomposition rates observed in the CO_2-enriched chambers. After one year of incubation, for example, litter bags from the CO_2-enriched trees of both species had about 30 percent more dry mass remaining in them than litter bags from the ambient trees. In addition, woodlouse arthropods consumed 16 percent *less* biomass when fed litter generated from seedlings grown at 600 ppm CO_2 than when fed litter generated from seedlings grown in ambient air.

De Angelis *et al*. (2000) constructed large open-top chambers around 30-year-old mixed stands of naturally growing Mediterranean forest species (dominated by *Quercus ilex*, *Phillyrea augustifolia*, and *Pistacia lentiscus*) near the coast of central Italy. Half of the chambers were exposed to ambient air of 350 ppm CO_2, while half were exposed to air of 710 ppm CO_2; and after three years, the lignin and carbon concentrations of the leaf litter of all three species were increased by 18 and 4 percent, respectively, while their nitrogen concentrations were reduced by 13 percent. These changes resulted in a 20 percent CO_2-induced increase in the carbon-to-nitrogen ratio of the leaf litter, which parameter is commonly used to predict decomposition rates, where larger ratios are generally associated with less rapid decomposition than smaller ratios. This case was no exception, with 4 percent less decomposition occurring in the leaf litter gathered from beneath the CO_2-enriched trees than in the litter collected from beneath the trees growing in ambient air.

Cotrufo and Ineson (2000) grew beech seedlings for five years in open-top chambers fumigated with air containing either 350 or 700 ppm CO_2. Subsequently, woody twigs from each CO_2 treatment were collected and incubated in native forest soils for 42 months, after which they determined there was no significant effect of the differential CO_2 exposure during growth on subsequent woody twig decomposition, although the mean decomposition rate of the CO_2-enriched twigs was 5 percent less than that of the ambient-treatment twigs.

Conway *et al*. (2000) grew two-year-old ash tree seedlings in solardomes maintained at atmospheric CO_2 concentrations of 350 and 600 ppm, after which naturally senesced leaves were collected, inoculated with various fungal species, and incubated for 42 days. They found the elevated CO_2 significantly reduced the amount of nitrogen in the senesced leaves, thus giving the CO_2-enriched leaf litter a higher carbon-to-nitrogen ratio than the litter collected from the seedlings growing in ambient air. This change likely contributed to the observed reductions in the amount of fungal colonization present on the senesced leaves from the CO_2-enriched treatment, which would be expected to result in reduced rates of leaf decomposition.

King *et al*. (2001) grew aspen seedlings for five months in open-top chambers receiving atmospheric CO_2 concentrations of 350 and 700 ppm. At the end of this period, naturally senesced leaf litter was collected, analyzed, and allowed to decompose under ambient conditions for 111 days. Although the elevated CO_2 slightly lowered leaf litter nitrogen content, it had no effect on litter sugar, starch, or tannin concentrations. With little to no CO_2-induced effects on leaf litter quality, there was no CO_2-induced effect on litter decomposition.

Dilustro *et al*. (2001) erected open-top chambers around portions of a regenerating oak-palmetto scrub ecosystem in Florida, USA and maintained them at CO_2 concentrations of either 350 or 700 ppm, after which they incubated ambient- and elevated-CO_2-produced fine roots for 2.2 years in the chamber soils, which were nutrient-poor and often water-stressed. They found the elevated CO_2 did not significantly affect the decomposition rates of the fine roots originating from either the ambient or CO_2-enriched environments.

Of these seven studies of deciduous tree species, five are suggestive of slight reductions in litter decomposition rates under CO_2-enriched growth conditions, while two show no effect. With deciduous trees exhibiting large growth enhancements in response to atmospheric CO_2 enrichment, we can expect to see large increases in the amounts of carbon they sequester in the soils on which they grow as the air's CO_2 content continues to rise. And this phenomenon should slow the rate of rise of the atmosphere's CO_2 concentration and thereby reduce the impetus for CO_2-induced global warming.

To summarize, scientific theory and empirical research show that the ongoing rise in the air's CO_2 content will not materially alter the rate of decomposition of the world's soil organic matter. This means the rate at which carbon is sequestered in the world's soils should continue to increase, a joint function of the rate at which the productivity of earth's plants is increased by the aerial fertilization effect of the rising atmospheric CO_2 concentration and the rate of expansion of the planet's vegetation into drier regions of the globe that is made possible by the concomitant CO_2-induced increase in vegetative water use efficiency.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/d/decompconifers.php and http://www.co2science.org/subject/d/decompdeciduous.php.

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7.7.3. Temperature and Carbon Sequestration

7.7.3.1. General

It must noted, as stated by Agren and Bosatta (2002), that "global warming has long been assumed to lead to an increase in soil respiration and, hence, decreasing soil carbon stores." Indeed, this dictum was accepted as gospel for many years, for a number of laboratory experiments seemed to suggest that nature would not allow more carbon to be sequestered in the soils of a warming world. As one non-laboratory experiment after another has recently demonstrated, however, such is not the case, and theory has been forced to change to accommodate reality.

The old-school view of things began to unravel in 1999 when two studies presented evidence refuting the long-standing orthodoxy. Abandoning the laboratory for the world of nature, Fitter *et al*. (1999) heated natural grass ecosystems by 3°C and found that the temperature increase had "no direct effect on the soil carbon store." That same year, Liski *et al*. (1999) showed that carbon storage in the soils of both high- and low-productivity boreal forests in Finland actually increased with rising temperatures along a natural temperature gradient.

The following year, Johnson *et al*. (2000) warmed natural Arctic tundra ecosystems by nearly 6°C for eight full years and found no significant effect on ecosystem respiration. Likewise, Giardina and Ryan (2000) analyzed organic carbon decomposition data derived from the forest soils of 82 different sites on five continents, reporting that "despite a 20°C gradient in mean annual temperature, soil carbon mass loss ... was insensitive to temperature."

Thornley and Cannell (2001) ventured forth with what they called "a hypothesis" concerning the matter. Specifically, they proposed the idea that warming may increase the rate of certain physico-chemical processes that transfer organic carbon from less-stable to more-stable soil organic matter pools, thereby enabling the better-protected organic matter to avoid, or more strongly resist, decomposition. Then, they developed a dynamic soil model in which they demonstrated that if their thinking were correct, long-term soil carbon storage would appear to be insensitive to a rise in temperature, even if the respiration rates of all soil carbon pools rose in response to warming, as they indeed do.

Agren and Bosatta's 2002 paper is an independent parallel development of much the same concept, although they describe the core idea in somewhat different terms, and they upgrade the concept from what Thornley and Cannell call a "hypothesis" to what they refer to as the "continuous-quality theory." *Quality*, in this context, refers to the degradability of soil organic matter; and *continuous quality* suggests there is a wide-ranging continuous spectrum of soil organic carbon "mini-pools" that possess differing degrees of resistance to decomposition.

The continuous quality theory states that soils from naturally higher temperature regimes will contain relatively more organic matter in carbon pools that are more resistant to degradation and are consequently characterized by lower rates of decomposition, which has been observed experimentally to be the case by Grisi *et al*. (1998). In addition, it states that this shift in the distribution of soil organic matter qualities—i.e., the higher-temperature-induced creation of more of the more-difficult-to-decompose organic matter—will counteract the decomposition-promoting influence of the higher temperatures, so that the overall decomposition rate of the totality of organic matter in a higher-temperature soil is either unaffected or reduced.

Rising CO_2 levels tend to maintain (Henning *et al*., 1996) or decrease (Torbert *et al*., 1998; Nitschelm *et al*., 1997) CO_2 fluxes from agricultural soils. Consequently, these phenomena tend to increase the carbon contents of most soils in CO_2-enriched atmospheres. However, it is sometimes suggested that rising air temperatures, which can accelerate the breakdown of soil organic matter and increase biological respiration rates, could negate this CO_2-induced enhancement of carbon sequestration, possibly leading to an even greater release of carbon back to the atmosphere.

Casella and Soussana (1997) grew perennial ryegrass in controlled environments receiving ambient and elevated (700 ppm) atmospheric CO_2 concentrations, two levels of soil nitrogen, and ambient and elevated (+3°C) air temperatures for a period of two years, finding that "a relatively large part of the additional photosynthetic carbon is stored below-ground during the two first growing seasons after exposure to elevated CO_2, thereby increasing significantly the below-ground carbon pool." At the low and high levels of soil nitrogen supply, for example, the elevated CO_2 increased soil carbon storage by 32 and 96 percent, respectively, "with no significant increased temperature effect." The authors thus concluded that in spite of predicted increases in temperature, "this stimulation of the below-ground carbon sequestration in temperate grassland soils could exert a negative feed-back on the current rise of the atmospheric CO_2 concentration."

Much the same conclusion was reached by Van Ginkel *et al*. (1999). After reviewing prior experimental work that established the growth and decomposition responses of perennial ryegrass to both atmospheric CO_2 enrichment and increased temperature, these researchers concluded that, at both low and high soil nitrogen contents, CO_2-induced increases in plant growth and CO_2-induced decreases in plant decomposition rate are more than sufficient to counteract any enhanced soil respiration rate that might be caused by an increase in air temperature. In addition, after reconstructing carbon storage in the terrestrial vegetation of Northern Eurasia as far back as 125,000 years ago, Velichko *et al*. (1999) determined that plants in this part of the world were more productive and efficient in sequestering carbon at higher temperatures than they were at lower temperatures. Similarly, Allen *et al*., (1999) used sediment cores from a lake in southern Italy and from the Mediterranean Sea to conclude that, over the past 102,000 years, warmer climates have been better for vegetative productivity and carbon sequestration than have cooler climates.

In conclusion, research conducted to date strongly suggests that the CO_2-induced enhancement of vegetative carbon sequestration will not be reduced by any future rise in air temperature, regardless of its cause. The rest of this section looks more closely at research regarding forests and peatlands.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/c/carbonco2xtemp.php.

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7.7.3.2. Forests

Liski *et al*. (1999) studied soil carbon storage across a temperature gradient in a modern-day Finnish boreal forest, determining that carbon sequestration in the soil of this forest increased with temperature. In deciduous forests of the eastern United States, White *et al*. (1999) also determined that persistent increases in growing season length (due to rising air temperatures) may lead to long-term increases in carbon storage, which tend to counterbalance the effects of increasing air temperature on respiration rates.

A data-driven analysis by Fan *et al*. (1998) suggests that the carbon-sequestering abilities of North America's forests between 15 and 51°N latitude are so robust that they can yearly remove from the atmosphere all of the CO_2 annually released to it by fossil fuel consumption in both the United States and Canada (and this calculation was done during a time touted as having the warmest temperatures on record). Moreover, Phillips *et al*. (1998) have shown that carbon sequestration in tropical forests has increased substantially over the past 42 years, in spite of any temperature increases that may have occurred during that time.

Similarly, King *et al*. (1999) showed that aspen seedlings increased their photosynthetic rates and biomass production as temperatures rose from 10 to 29°C, putting to rest the idea that high-temperature-induced increases in respiration rates would cause net losses in carbon fixation. White *et al*. (2000) showed that rising temperatures increased the growing season by about 15 days for 12 sites in deciduous forests located within the United States, causing a 1.6 percent increase in net ecosystem productivity per day. Thus, rather than exerting a negative influence on forest carbon sequestration, if air temperatures rise in the future they will likely have a positive effect on carbon storage in forests and their associated soils.

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7.7.3.3. Peatlands

Putative CO_2-induced global warming has long been predicted to turn boreal and tundra biomes into major sources of carbon emissions. Until just a few short years ago it was nearly universally believed that rising air temperatures would lead to the thawing of extensive areas of permafrost and the subsequent decomposition of their vast stores of organic matter, which, it was thought, would release much of the peatlands' tightly held carbon, enabling it to make its way back to the atmosphere as CO_2.

Improved soil drainage and increased aridity were also envisioned to help the process along, possibly freeing enough carbon at a sufficiently rapid rate to rival the amount released to the atmosphere as CO_2 by all anthropogenic sources combined. The end result was claimed to be a tremendous positive feedback to the ongoing rise in the air's CO_2 content, which was envisioned to produce a greatly amplified atmospheric greenhouse effect that would lead to catastrophic global warming.

This scenario was always too bad to be true. Why? Because it did not begin to deal with the incredible complexity of the issue, several important neglected aspects of which have been briefly described by Weintraub and Schimel (2005).

One of the first cracks in the seemingly sound hypothesis was revealed by the study of Oechel *et al.* (2000), wherein long-term measurements of net ecosystem CO_2 exchange rates in wet-sedge and moist-tussock tundra communities of the Alaskan Arctic indicated that these ecosystems were gradually changing from carbon sources to carbon sinks. The transition occurred between 1992 and 1996, at the apex of a regional warming trend that culminated with the highest summer temperature and surface water deficit of the previous four decades.

How did this dramatic and unexpected biological transformation happen? The answer of the scientists who documented the phenomenon was "a previously undemonstrated capacity for ecosystems to metabolically adjust to long-term changes in climate." Just as people can change their behavior in response to environmental stimuli, so can plants. And this ecological acclimation process is only one of several newly recognized phenomena that have caused scientists to radically revise the way they think about global change in Arctic regions.

Camill *et al.* (2001) investigated (1) changes in peat accumulation across a regional gradient of mean annual temperature in Manitoba, Canada, (2) net above-ground primary production and decomposition for major functional plant groups of the region, and (3) soil cores from several frozen and thawed bog sites that were used to determine long-term changes in organic matter accumulation following the thawing of boreal peatlands. In direct contradiction of earlier thinking on the subject, but in confirmation of the more recent findings of Camill (1999a,b), the researchers discovered that above-ground biomass and decomposition "were more strongly controlled by local succession than regional climate." In other words, they determined that over a period of several years, natural changes in plant community composition generally "have stronger effects on carbon sequestration than do simple increases in temperature and aridity." Their core-derived assessments of peat accumulation over the past two centuries demonstrated that rates of biological carbon sequestration can almost double following the melting of permafrost, in harmony with the findings of Robinson and Moore (2000) and Turetsky *et al.* (2000), who found rates of organic matter accumulation in other recently thawed peatlands to have risen by 60-72 percent.

Griffis and Rouse (2001) drew upon the findings of a number of experiments conducted over the past quarter-century at a subarctic sedge fen near Churchill, Manitoba, Canada, in order to develop an empirical model of net ecosystem CO_2 exchange there. The most fundamental finding of this endeavor was that "carbon acquisition is greatest during wet and warm conditions," such as is generally predicted for the world as a whole by today's most advanced climate models. However, since regional climate change predictions are not very dependable, the two scientists investigated the consequences of a 4°C increase in temperature accompanied by both a 30 percent increase and decrease in precipitation; and "in all cases," as they put it, "the equilibrium response showed substantial increases in carbon acquisition." One of the reasons behind this finding, as explained by Griffis and Rouse, is that "arctic ecosystems photosynthesize below their temperature optimum over the majority of the growing season," so that increasing temperatures enhance plant growth rates considerably more than they increase plant decay rates.

In summing up their findings, Griffis and Rouse say "warm surface temperatures combined with wet soil conditions in the early growing season increase above-ground biomass and carbon acquisition throughout the summer season." Indeed, they note that "wet spring conditions can lead to greater CO_2 acquisition through much of the growing period even when drier conditions persist." They thus conclude that if climate change plays out as described by current climate models—i.e., if the world becomes warmer and wetter—"northern wetlands should therefore become larger sinks for atmospheric CO_2."

In a somewhat different type of study, Mauquoy *et al.* (2002) analyzed three cores obtained from a raised peat bog in the UK (Walton Moss) and a single core obtained from a similar bog in Denmark (Lille Vildmose) for macro- and micro-fossils (pollen), bulk density, loss on ignition, carbon/nitrogen ratios, and humification, while they were ^{14}C dated by accelerator mass spectrometry. Among a variety of other things, it was determined, in their words, that "the lowest carbon accumulation values for the Walton Moss monoliths between ca. cal AD 1300 and 1800 and between ca. cal AD 1490 and 1580 for Lille Vildmose occurred during the course of Little Ice Age deteriorations," which finding they describe as being much the same as the observation "made by Oldfield *et al.* (1997) for a Swedish 'aapa' mire between ca. cal AD 1400 and 1800." They also report that carbon accumulation before this, in the Medieval Warm Period, was higher, as was also the case following the Little Ice Age, as the earth transitioned to the Modern Warm Period. Consequently, whereas the IPCC claims that warming will hasten the release of carbon from ancient peat bogs, these real-world data demonstrate that just the opposite is more likely.

In a somewhat similar study, but one that concentrated more on the role of nitrogen than of temperature, Turunen *et al.* (2004) derived recent (0-150 years) and long-term (2,000-10,000 years) apparent carbon accumulation rates for several ombrotrophic peatlands in eastern Canada with the help of ^{210}Pb- and ^{14}C-dating of soil-core materials. This work revealed that the average long-term apparent rate of C accumulation at 15 sites was 19 ± 8 g C m^{-2} yr^{-1}, which is comparable to long-term rates observed in Finnish bogs by Tolonen and Turunen (1996) and Turunen *et al.* (2002). Recent C accumulation rates at 23 sites, on the other hand, were much higher, averaging 73 ± 17 g C m^{-2} yr^{-1}, which results, in their words, are also "similar to results from Finland (Tolonen and Turunen, 1996; Pitkanen *et al*., 1999) and for boreal *Sphagnum* dominated peat deposits in North America (Tolonen *et al*., 1988; Wieder *et al*., 1994; Turetsky *et al*., 2000)." Noting that recent rates of C accumulation are "strikingly higher" than long-term rates, Turunen *et al*. suggested that increased N deposition "leads to larger rates of C and N accumulation in the bogs, as has been found in European forests (Kauppi *et al*., 1992; Berg and Matzner, 1997), and could account for some of the missing C sink in the global C budget."

Returning to the role of temperature, Payette *et al.* (2004) quantified the main patterns of change in a subarctic peatland on the eastern coast of Canada's Hudson Bay, which were caused by permafrost decay between 1957 and 2003, based on detailed surveys conducted in 1973, 1983, 1993 and 2003. This work revealed there was continuous permafrost thawing throughout the period of observation, such that "about 18 percent of the initial frozen peatland surface was melted in 1957," while thereafter "accelerated thawing occurred with only 38 percent, 28 percent and 13 percent of the original frozen surface still remaining in 1983, 1993 and 2003, respectively." This process, in their words, was one of "terrestrialization" via the establishment of fen/bog vegetation, which nearly always results in either no net loss of carbon or actual carbon sequestration. As a result, Payette *et al.* concluded that "contrary to current expectations, the melting of permafrost caused by recent climate change does *not* [our italics] transform the peatland to a carbon-source ecosystem." Instead, they say that "rapid terrestrialization exacerbates carbon-sink conditions and tends to balance the local carbon budget."

In a study of experimental warming of Icelandic plant communities designed to see if the warming of high-latitude tundra ecosystems would result in significant losses of species and reduced biodiversity, Jonsdottir *et al.* (2005) conducted a field experiment to learn how vegetation might respond to moderate warming at the low end of what is predicted by most climate models for a doubling of the air's CO_2 content. Specifically, they studied the effects of 3-5 years of modest surface warming (1°-2°C) on two widespread but contrasting tundra plant communities, one of which was a nutrient-deficient and species-poor moss heath and the other of which was a species-rich dwarf shrub heath. At the conclusion of the study, no changes in community structure were detected in the moss heath. In the dwarf shrub heath, on the other hand, the number of deciduous and evergreen dwarf shrubs increased more than 50 percent, bryophytes decreased by 18 percent, and canopy height increased by 100 percent, but with the researchers reporting they "detected no changes in species richness or other diversity measures in either community and the abundance of lichens did not change." Although Jonsdottir *et al.*'s study was a relatively short-term experiment as far as ecosystem studies go, its results indicate a rise in temperature need not have a negative effect on the species diversity of high-latitude tundra ecosystems and may have a positive influence on plant growth.

In a study that included an entirely new element of complexity, Cole *et al.* (2002) constructed 48 small microcosms from soil and litter they collected near the summit of Great Dun Fell, Cumbria, England. Subsequent to "defaunating" this material by reducing its temperature to -80°C for 24 hours, they thawed and inoculated it with native soil microbes, after which half of the microcosms were incubated in the dark at 12°C and half at 18°C for two weeks, in order to establish near-identical communities of the soils' natural complement of microflora in each microcosm. The former of these temperatures was chosen to represent mean August soil temperature at a depth of 10 cm at the site of soil collection, while the latter was picked to be "close to model predictions for soil warming that might result from a doubling of CO_2 in blanket peat environments."

Next, 10 seedlings of *Festuca ovina*, an indigenous grass of blanket peat, were planted in each of the microcosms, while 100 enchytraeid worms were added to each of half of the mini-ecosystems, producing four experimental treatments: ambient temperature, ambient temperature plus enchytraeid worms, elevated temperature, and elevated temperature plus enchytraeid worms. Then, the 48 microcosms—sufficient to destructively harvest three replicates of each treatment four different times throughout the course of the 64-day experiment—were arranged in a fully randomized design and maintained at either 12° or 18°C with alternating 12-hour light and dark periods, while being given distilled water every two days to maintain their original weights.

So what did the researchers learn? First, they found that elevated temperature reduced the ability of the enchytraeid worms to enhance the loss of carbon from the microcosms. At the normal ambient temperature, the presence of the worms enhanced dissolved organic carbon (DOC) loss by 16 percent, while at the elevated temperature expected for a doubling of the air's CO_2 content they had no effect on DOC. In addition, Cole *et al.* note that "warming may cause drying at the soil surface, forcing enchytraeids to burrow to deeper subsurface horizons;" and since the worms are known to have little influence on soil carbon dynamics below a depth of about 4 cm (Cole *et al.*, 2000), the researchers concluded that this additional consequence of warming would further reduce the ability of enchytraeids to enhance carbon loss from blanket peatlands. In summing up their findings, Cole *et al.* concluded that "the soil biotic response to warming in this study was negative," in that it resulted in a reduced loss of carbon to the atmosphere.

But what about the effects of elevated CO_2 itself on the loss of DOC from soils? Freeman *et al.* (2004) note that riverine transport of DOC has increased markedly in many places throughout the world over the past few decades (Schindler *et al.*, 1997; Freeman *et al.*, 2001; Worrall *et al.*, 2003); they suggest this phenomenon may be related to the historical increase in the air's CO_2 content.

The researchers' first piece of evidence for this conclusion came from a three-year study of monoliths (11-cm diameter x 20-cm deep cores) taken from three Welsh peatlands—a bog that received nutrients solely from rainfall, a *fen* that gained more nutrients from surrounding soils and groundwater, and a riparian peatland that gained even more nutrients from nutrient-laden water transported from other terrestrial ecosystems via drainage streams—which they exposed to either ambient air or air enriched with an extra 235 ppm of CO_2 within a solardome facility. This study revealed that the DOC released by monoliths from the three peatlands was significantly enhanced—by 14 percent in the bog, 49 percent in the fen, and 61 percent in the riparian peatland—by the additional CO_2 to which they were exposed, which is the order of response one would expect from what we know about the stimulation of net primary productivity due to atmospheric CO_2 enrichment, i.e., it is low in the face of low soil nutrients, intermediate when soil nutrient concentrations are intermediate, and high when soil nutrients are present in abundance. Consequently, Freeman *et al.* concluded that the DOC increases they observed "were induced by increased primary production and DOC exudation from plants," which conclusion logically follows from their findings.

Nevertheless, and to further test their hypothesis, they followed the translocation of labeled ^{13}C through the plant-soil systems of the different peat monoliths for about two weeks after exposing them to ~99 percent-pure $^{13}CO_2$ for a period of five hours. This exercise revealed that (1) the plants in the ambient-air and CO_2-enriched treatments assimilated 22.9 and 35.8 mg of ^{13}C from the air, respectively, (2) the amount of DOC that was recovered from the leachate of the CO_2-enriched monoliths was 0.6 percent of that assimilated, or 0.215 mg (35.8 mg x 0.006 = 0.215 mg), and (3) the proportion of DOC in the soil solution of the CO_2-enriched monoliths that was derived from recently assimilated CO_2 (the ^{13}C labeled CO_2) was 10 times higher than that of the control.

This latter observation suggests that the amount of DOC recovered from the leachate of the ambient-air monoliths was only about a tenth as much as that recovered from the leachate of the CO_2-enriched monoliths, which puts the former amount at about 0.022 mg. Hence, what really counts, i.e., the net sequestration of ^{13}C experienced by the peat monoliths over the two-week period (which equals the amount that went into them minus the amount that went out), comes to 22.9 mg minus 0.022 mg = 22.878 mg for the ambient-air monoliths and 35.8 mg minus 0.215 mg = 35.585 mg for the CO_2-enriched monoliths. In the end, therefore, even though the CO_2-enriched monoliths lost 10 times more ^{13}C via root exudation than did the ambient-air monoliths, they still sequestered about 55 percent more ^{13}C overall, primarily in living-plant tissues.

In light of this impressive array of pertinent findings, it would appear that continued increases in the air's CO_2 concentration and temperature would not result in losses of carbon from earth's peatlands. Quite to the contrary, these environmental changes—if they persist—would likely work together to enhance carbon capture by these particular ecosystems.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/c/carbonpeat.php.

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7.8. Other Benefits

Other benefits to plants of CO_2 enhancement documented in this section include superior nitrogen-use efficiency, increased nutrient acquisition, greater resistance to pathogens and parasitic plants, greater root development, greater seed and tannin production, and improved performance of transgenic plants. In addition to these benefits to plants, CO_2 enrichment benefits all life on earth by reducing plant emissions of isoprene, a chemical responsible for the production of tropospheric ozone.

7.8.1. Nitrogen-Use Efficiency

Long-term exposure to elevated atmospheric CO_2 concentrations often, but not always, elicits photosynthetic acclimation or down regulation in plants, which is typically accompanied by reduced amounts of rubisco and/or other photosynthetic proteins that are typically present in excess amounts in plants grown in ambient air. As a consequence, foliar nitrogen concentrations often decrease with atmospheric CO_2 enrichment, as nitrogen is mobilized out of leaves and into other areas of the plant to increase its availability for enhancing sink development or stimulating other nutrient-limited processes.

In reviewing the literature in this area, one quickly notices that in spite of the fact that photosynthetic acclimation has occurred, CO_2-enriched plants nearly always display rates of photosynthesis that are greater than those of control plants exposed to ambient air. Consequently, photosynthetic nitrogen-use efficiency, i.e., the amount of carbon converted into sugars during the photosynthetic process per unit of leaf nitrogen, often increases dramatically in CO_2-enriched plants.

In the study of Davey *et al.* (1999), for example, CO_2-induced reductions in foliar nitrogen contents and concomitant increases in photosynthetic rates led to photosynthetic nitrogen-use efficiencies in the CO_2-enriched (to 700 ppm CO_2) grass *Agrostis capillaris* that were 27 and 62 percent greater than those observed in control plants grown at 360 ppm CO_2 under moderate and low soil nutrient conditions, respectively. Similarly, elevated CO_2 enhanced photosynthetic nitrogen-use efficiencies in *Trifolium repens* by 66 and 190 percent under moderate and low soil nutrient conditions, respectively, and in *Lolium perenne* by 50 percent, regardless of soil nutrient status. Other researchers have found comparable CO_2-induced enhancements of photosynthetic nitrogen-use efficiency in wheat (Osborne *et al*., 1998) and in *Leucadendron* species (Midgley *et al*., 1999).

In some cases, researchers report nitrogen-use efficiency in terms of the amount of biomass produced per unit of plant nitrogen. Niklaus *et al*. (1998), for example, reported that intact swards of CO_2-enriched calcareous grasslands grown at 600 ppm CO_2 attained total biomass values that were 25 percent greater than those of control swards exposed to ambient air while extracting the same amount of nitrogen from the soil as ambiently grown swards. Similar results have been reported for strawberry by Deng and Woodward (1998), who noted that the growth nitrogen-use efficiencies of plants grown at 560 ppm CO_2 were 23 and 17 percent greater than those of ambiently grown plants simultaneously subjected to high and low soil nitrogen availability, respectively.

In conclusion, the scientific literature indicates that as the air's CO_2 content continues to rise, earth's plants will likely respond by reducing the amount of nitrogen invested in rubisco and other photosynthetic proteins, while still maintaining enhanced rates of photosynthesis, which consequently should increase their photosynthetic nitrogen-use efficiencies. As overall plant nitrogen-use efficiency increases, it is likely plants will grow ever better on soils containing less-than-optimal levels of nitrogen, a point addressed in more detail in Section 7.3.7 of this report.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/n/nitrogenefficiency.php.

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7.8.2. Nutrient Acquisition

Most species of plants respond to increases in the air's CO_2 content by displaying enhanced rates of photosynthesis and biomass production. Oftentimes, the resulting growth stimulation is preferentially expressed belowground, thereby causing significant increases in fine-root numbers and surface area. This phenomenon tends to increase total nutrient uptake under CO_2-enriched conditions, which further stimulates plant growth and development. In this summary, we review how the acquisition of plant nutrients—primarily nitrate and phosphate—is affected by atmospheric CO_2 enrichment. The effects of elevated CO_2 on nitrogen fixation are addressed elsewhere (Sections 7.3.7 and 7.8.1) and more research on the effects of CO_2 enhancement on roots appears in Section 7.8.5.

Smart *et al*. (1998) noted there were no differences on a per-unit-biomass basis in the total amounts of nitrogen within CO_2-enriched and ambiently grown wheat seedlings after three weeks of exposure to atmospheric CO_2 concentrations of 360 and 1,000 ppm. Nevertheless, the CO_2-enriched seedlings exhibited greater rates of soil nitrate extraction than did the ambiently grown plants. Similarly, BassiriRad *et al*. (1998) reported that a doubling of the atmospheric CO_2 concentration doubled the uptake rate of nitrate in the C_4 grass *Bouteloua eriopoda*. However, they also reported that elevated CO_2 had no effect on the rate of nitrate uptake in *Prosopis*, and that it decreased the rate of nitrate uptake by 55 percent in *Larrea*. Nonetheless, atmospheric CO_2 enrichment increased total biomass in these two species by 55 and 69 percent, respectively. Thus, although the uptake rate of this nutrient was depressed under elevated CO_2 conditions in the latter species, the much larger CO_2-enriched plants likely still extracted more total nitrate from the soil than did the ambiently grown plants of the experiment.

Nasholm *et al*. (1998) determined that trees, grasses and shrubs can all absorb significant amounts of organic nitrogen from soils. Thus, plants do not have to wait for the mineralization of organic nitrogen before they extract the nitrogen they need from soils to support their growth and development. Hence, the forms of nitrogen removed from soils by plants (nitrate vs. ammonium) and their abilities to remove different forms may not be as important as was once thought.

With respect to the uptake of phosphate, Staddon *et al*. (1999) reported that *Plantago lanceolata* and *Trifolium repens* plants grown at 650 ppm CO_2 for 2.5 months exhibited total plant phosphorus contents that were much greater than those displayed by plants grown at 400 ppm CO_2, due to the fact that atmospheric CO_2 enrichment significantly enhanced plant biomass. Similarly, Rouhier and Read (1998) reported that enriching the air around *Plantago lanceolata* plants with an extra 190 ppm of CO_2 for a period of three months led to increased uptake of phosphorus and greater tissue phosphorus concentrations than were observed in plants growing in ambient air.

Greater uptake of phosphorus also can occur due to CO_2-induced increases in root absorptive surface area or enhancements in specific enzyme activities. In addressing the first of these phenomena, BassiriRad *et al*. (1998) reported that a doubling of the atmospheric CO_2 concentration significantly increased the belowground biomass of *Bouteloua eriopoda* and doubled its uptake rate of phosphate. However, elevated CO_2 had no effect on uptake rates of phosphate in *Larrea* and *Prosopis*. Because the CO_2-enriched plants grew so much bigger, they still removed more phosphate from the soil on a per-plant basis. With respect to the second phenomenon, phosphatase—the primary enzyme responsible for the conversion of organic phosphate into usable inorganic forms—had its activity increased by 30 to 40 percent in wheat seedlings growing at twice-ambient CO_2 concentrations (Barrett *et al*., 1998).

In summary, as the CO_2 content of the air increases, experimental data to date suggest that much of earth's vegetation will likely extract enhanced amounts of mineral nutrients from the soils in which they are rooted.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/n/nutrientacquis.php.

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7.8.3. Pathogens

As the air's CO_2 content continues to rise, it is natural to wonder—and important to determine—how this phenomenon may impact plant-pathogen interactions. One thing we know about the subject is that atmospheric CO_2 enrichment nearly always enhances photosynthesis, which commonly leads to increased plant production of carbon-based secondary compounds, including lignin and various phenolics, both of which substances tend to increase plant resistance to pathogen attack.

Enlarging upon this topic, Chakraborty and Datta (2003) report that "changes in plant physiology, anatomy and morphology that have been implicated in increased resistance or [that] can potentially enhance host resistance at elevated CO_2 include: increased net photosynthesis allowing mobilization of resources into host resistance (Hibberd *et al*., 1996a.); reduced stomatal density and conductance (Hibberd *et al*., 1996b); greater accumulation of carbohydrates in leaves; more waxes, extra layers of epidermal cells and increased fibre content (Owensby, 1994); production of papillae and accumulation of silicon at penetration sites (Hibberd *et al*., 1996a); greater number of mesophyll cells (Bowes, 1993); and increased biosynthesis of phenolics (Hartley *et al*., 2000), among others."

Chakraborty and Datta found another way atmospheric CO_2 enrichment may tip the scales in favor of plants in a study of the aggressiveness of the fungal anthracnose pathogen *Colletotrichum gloeosporioides*. They inoculated two isolates of the pathogen onto two cultivars of the tropical pasture legume *Stylosanthes scabra* (Fitzroy, which is susceptible to the fungal pathogen, and Seca, which is more resistant) over the course of 25 sequential infection cycles at ambient (350 ppm) and elevated (700 ppm) atmospheric CO_2 concentrations in controlled environment chambers. This protocol revealed that "at twice-ambient CO_2 the overall level of aggressiveness of the two [pathogen] isolates was significantly reduced on both [host] cultivars." In addition, they say that "as shown previously (Chakraborty *et al*., 2000), the susceptible Fitzroy develops a level of resistance to anthracnose at elevated CO_2, but resistance in Seca remains largely unchanged." Simultaneously, however, pathogen fecundity was found to increase at twice-ambient CO_2. Of this finding, they report that their results "concur with the handful of studies that have demonstrated increased pathogen fecundity at elevated CO_2 (Hibberd *et al*., 1996a; Klironomos *et al*., 1997; Chakraborty *et al*., 2000)." How this happened in the situation they investigated, as they describe it, is that the overall increase in fecundity at high CO_2 "is a reflection of the altered canopy environment," wherein "the 30 percent larger *S. scabra* plants at high CO_2 (Chakraborty *et al*., 2000) makes the canopy microclimate more conducive to anthracnose development."

In view of the opposing changes induced in pathogen behavior by elevated levels of atmospheric CO_2 in this specific study—reduced aggressiveness but increased fecundity—it is difficult to know the outcome of atmospheric CO_2 enrichment for the pathogen-host relationship. More research, especially under realistic field conditions, will be needed to clarify the situation; and, of course, different results are likely to be observed for different pathogen-host associations. Results also could differ under different climatic conditions. Nevertheless, the large number of ways in which elevated CO_2 has been demonstrated to increase plant resistance to pathogen attack suggests that plants may well gain the advantage over pathogens as the air's CO_2 content continues to climb in the years ahead.

McElrone *et al*. (2005) "assessed how elevated CO_2 affects a foliar fungal pathogen, *Phyllosticta minima*, of *Acer rubrum* [red maple] growing in the understory at the Duke Forest free-air CO_2 enrichment experiment in Durham, North Carolina, USA … in the 6th, 7th, and 8th years of the CO_2 exposure." Surveys conducted in those years, in their words, "revealed that elevated CO2 [to 200 ppm above ambient] significantly reduced disease incidence, with 22%, 27% and 8% fewer saplings and 14%, 4%, and 5% fewer leaves infected per plant in the three consecutive years, respectively." In addition, they report that the elevated CO_2 "also significantly reduced disease severity in infected plants in all years (e.g. mean lesion area reduced 35%, 50%, and 10% in 2002, 2003, and 2004, respectively)."

With respect to identifying the underlying mechanism or mechanisms that produced these beneficent consequences, thinking it could have been a direct deleterious effect of elevated CO_2 on the fungal pathogen, McElrone *et al*. performed some side experiments in controlled environment chambers. However, they found that the elevated CO_2 benefited the fungal pathogen as well as the red maple saplings, observing that "exponential growth rates of *P. minima* were 17% greater under elevated CO2." And they obtained similar results when they repeated the *in vitro* growth analysis two additional times in different growth chambers.

Taking another tack when "scanning electron micrographs verified that conidia germ tubes of *P. minima* infect *A. rubrum* leaves by entering through the stomata," the researchers turned their attention to the pathogen's mode of entry into the saplings' foliage. In this investigation they found that both stomatal size and density were unaffected by atmospheric CO_2 enrichment, but that "stomatal conductance was reduced by 21-36% under elevated CO_2, providing smaller openings for infecting germ tubes." They concluded that reduced disease severity under elevated CO_2 was likely due to altered leaf chemistry, as elevated CO_2 increased total leaf phenolic concentrations by 15 percent and tannin concentrations by 14 percent.

Because the phenomena they found to be important in reducing the amount and severity of fungal pathogen infection (leaf spot disease) of red maple have been demonstrated to be operative in most other plants as well, McElrone *et al.* say these CO_2-enhanced leaf defensive mechanisms "may be prevalent in many plant pathosystems where the pathogen targets the stomata." They state their results "provide concrete evidence for a potentially generalizable mechanism to predict disease outcomes in other pathosystems under future climatic conditions."

Malmstrom and Field (1997) grew individual oat plants for two months in pots within phytocells maintained at CO_2 concentrations of 350 and 700 ppm, while a third of each CO_2 treatment's plants were infected with the barley yellow dwarf virus (BYDV), which plagues more than 150 plant species worldwide, including all major cereal crops. They found that the elevated CO_2 stimulated net photosynthesis rates in all plants, but with the greatest increase occurring in diseased individuals (48 percent vs. 34 percent). In addition, atmospheric CO_2 enrichment decreased stomatal conductance by 34 percent in healthy plants, but by 50 percent in infected ones, thus reducing transpirational water losses more in infected plants. Together, these two phenomena contributed to a CO_2-induced doubling of the instantaneous water-use efficiency of healthy control plants, but to a much larger 2.7-fold increase in diseased plants. Thus, although BYDV infection did indeed reduce overall plant biomass production, the growth response to elevated CO_2 was greatest in the diseased plants. After 60 days of CO_2 enrichment, for example, total plant biomass increased by 36 percent in infected plants, while it increased by only 12 percent in healthy plants. In addition, while elevated CO_2 had little effect on root growth in healthy plants, it increased root biomass in infected plants by up to 60 percent. In their concluding remarks, therefore, Malmstrom and Field say that CO_2 enrichment "may reduce losses of infected plants to drought" and "may enable diseased plants to compete better with healthy neighbors."

Tiedemann and Firsching (2000) grew spring wheat from germination to maturity in controlled environment chambers maintained at either ambient (377 ppm) or enriched (612 ppm) atmospheric CO_2 concentrations and either ambient (20 ppb) or enriched (61 ppb) atmospheric ozone (O_3) concentrations, while half of the plants in each of the four resulting treatments were inoculated with a leaf rust-causing pathogen. These procedures revealed that the percent of leaf area infected by rust in inoculated plants was largely unaffected by atmospheric CO_2 enrichment but strongly reduced by elevated O_3. With respect to photosynthesis, elevated CO_2 increased rates in inoculated plants by 20 and 42 percent at ambient and elevated O_3 concentrations, respectively. Although inoculated plants produced lower yields than non-inoculated plants, atmospheric CO_2 enrichment still stimulated yield in infected plants, increasing it by fully 57 percent at high O_3. Consequently, the beneficial effects of elevated CO_2 on wheat photosynthesis and yield continued to be expressed in the presence of both O_3 and pathogenic stresses.

In another joint CO_2/O_3 study, Percy *et al.* (2002) grew the most widely distributed North American tree species—trembling aspen—in twelve 30-m-diameter free-air CO^2 enrichment (FACE) rings near Rhinelander, Wisconsin, USA in air maintained at ambient CO_2 and O_3 concentrations, ambient O_3 and elevated CO2 (560 ppm during daylight hours), ambient CO_2 and elevated O_3 (46.4-55.5 ppb during daylight hours), and elevated CO_2 and O_3 over the period of each growing season from 1998 through 2001. Throughout this experiment they assessed a number of the young trees' growth characteristics, as well as their responses to poplar leaf rust (*Melampsora medusae*), which they say "is common on aspen and belongs to the most widely occurring group of foliage diseases." Their work revealed that elevated CO_2 alone did not alter rust occurrence, but that elevated O_3 alone increased it by nearly fourfold. When applied together, however, elevated CO_2 reduced the enhancement of rust development caused by elevated O_3 from nearly fourfold to just over twofold.

Jwa and Walling (2001) grew tomato plants in hydroponic culture for eight weeks in controlled environment chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm. At week five of their study, half of the plants growing in each CO_2 concentration were infected with the fungal pathogen *Phytophthora parasitica*, which attacks plant roots and induces water stress that decreases plant growth and yield. This infection procedure reduced total plant biomass by nearly 30 percent at both atmospheric CO_2 concentrations. However, the elevated CO_2 treatment increased the total biomass of healthy and infected plants by the same percentage, so that infected tomato plants grown at 700 ppm CO_2 exhibited biomass values similar to those of healthy tomato plants grown at 350 ppm CO_2. Consequently, atmospheric CO_2 enrichment completely counterbalanced the negative effects of *Phytophthora parasitica* infection on tomato productivity.

Pangga *et al*. (2004) grew well-watered and fertilized pencilflower (cultivar Fitzroy) seedlings—an important legume crop susceptible to anthracnose disease caused by *Colletotrichum gloeosporioides*—within a controlled environment facility maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm, where they inoculated six-, nine- and twelve-week-old plants with conidia of *C. gloeosporioides*. Then, ten days after inoculation, they counted the anthracnose lesions on the plants and classified them as either resistant or susceptible. In doing so, they found that "the mean number of susceptible, resistant, and total lesions per leaf averaged over the three plant ages was significantly ($P<0.05$) greater at 350 ppm than at 700 ppm CO_2, reflecting the development of a level of resistance in susceptible cv. Fitzroy at high CO_2." With respect to plants inoculated at twelve weeks of age, they say that those grown "at 350 ppm had 60 and 75 percent more susceptible and resistant lesions per leaf, respectively, than those [grown] at 700 ppm CO_2." The Australian scientists say their work "clearly shows that at 350 ppm overall susceptibility of the canopy increases with increasing age because more young leaves are produced on secondary and tertiary branches of the more advanced plants." However, "at 700 ppm CO_2, infection efficiency did not increase with increasing plant age despite the presence of many more young leaves in the enlarged canopy," which finding, in their words, "points to reduced pathogen efficiency or an induced partial resistance to anthracnose in Fitzroy at 700 ppm CO_2."

Finally, according to Plessl *et al*. (2007), "potato late blight caused by the oomycete *Phytophthora infestans* (Mont.) de Bary is the most devastating disease of potato worldwide," adding that "infection occurs through leaves and tubers followed by a rapid spread of the pathogen finally causing destructive necrosis." In an effort to ascertain the effects of atmospheric CO_2 enrichment on this pathogen, Plessl *et al*. grew individual well watered and fertilized plants of the potato cultivar Indira in 3.5-liter pots filled with a 1:2 mixture of soil and "Fruhstorfer T-Erde" in controlled-environment chambers maintained at atmospheric CO_2 concentrations of either 400 or 700 ppm. Four weeks after the start of the experiment, the first three fully developed pinnate leaves were cut from the plants and inoculated with zoospores of *P. infestans* in Petri dishes containing water-agar, after which their symptoms were evaluated daily via comparison with control leaves that were similarly treated but unexposed to the pathogen.

Results of the German researchers analysis revealed that the 300 ppm increase in CO_2 "dramatically reduced symptom development," including extent of necrosis (down by 44 percent four days after inoculation and 65 percent five days after inoculation), area of sporulation (down by 100 percent four days after inoculation and 61 percent five days after inoculation), and sporulation intensity (down by 73 percent four days after inoculation and 17 percent five days after inoculation). Plessl *et al.* conclude that their results "clearly demonstrated that the potato cultivar Indira, which under normal conditions shows a high susceptibility to *P. infestans*, develops resistance against this pathogen after exposure to 700 ppm CO_2," noting that "this finding agrees with results from Ywa *et al*. (1995), who reported an increased tolerance of tomato plants to *Phytophthora* root rot when grown at elevated CO_2." These similar observations bode well for both potato and tomato cultivation in a CO_2-enriched world of the future.

In conclusion, the balance of evidence obtained to date demonstrates an enhanced ability of plants to withstand pathogen attacks in CO_2-enriched as opposed to ambient-CO_2 air. As the atmosphere's CO_2 concentration continues to rise in the years to come, earth's vegetation should fare ever better in its battle against myriad debilitating plant diseases.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/p/pathogens.php.

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7.8.4. Parasitic Plants

Parasitic plants obtain energy, water and nutrients from their host plants and cause widespread reductions in harvestable crop yields around the globe. Hence, it is important to understand how rising atmospheric CO_2 levels may impact the growth of parasitic plants and the relationships between them and their hosts.

Matthies and Egli (1999) grew *Rhinanthus alectorolophus* (a widely distributed parasitic plant of Central Europe) for a period of two months on the grass *Lolium perenne* and the legume *Medicago sativa* in pots placed within open-top chambers maintained at atmospheric CO_2 concentrations of 375 and 590 ppm, half of which pots were fertilized to produce an optimal soil nutrient regime and half of which were unfertilized. At low nutrient supply, they found that atmospheric CO_2 enrichment decreased mean parasite biomass by an average of 16 percent, while at high nutrient supply it increased parasite biomass by an average of 123 percent. Nevertheless, the extra 215 ppm of CO_2 increased host plant biomass in both situations: by 29 percent under high soil nutrition and by 18 percent under low soil nutrition.

Dale and Press (1999) infected white clover (*Trifolium repens*) plants with *Orobanche minor* (a parasitic weed that primarily infects leguminous crops in the United Kingdom and the Middle East) and exposed them to atmospheric CO_2 concentrations of either 360 or 550 ppm for 75 days in controlled-environment growth cabinets. The elevated CO_2 in this study had no effect on the total biomass of parasite per host plant, nor did it impact the number of parasites per host plant or the time to parasitic attachment to host roots. On the other hand, whereas infected host plants growing in ambient air produced 47 percent less biomass than uninfected plants growing in ambient air, infected plants growing at 550 ppm CO_2 exhibited final dry weights that were only 20 percent less than those displayed by uninfected plants growing in the CO_2-enriched air, indicative of a significant CO_2-induced partial alleviation of parasite-induced biomass reductions in the white clover host plants.

Watling and Press (1997) infected several C_4 sorghum plants with *Striga hermonthica* and *Striga asiatica* (parasitic C_3 weeds of the semi-arid tropics that infest many grain crops) and grew them, along with uninfected control plants, for approximately two months in controlled-environment cabinets maintained at atmospheric CO_2 concentrations of 350 and 700 ppm. In the absence of parasite infection, the extra 350 ppm of CO_2 increased sorghum biomass by approximately 36 percent. When infected with *S. hermonthica*, however, the sorghum plants grown at ambient and elevated CO_2 concentrations only produced 32 and 43 percent of the biomass displayed by their respective uninfected controls. Infection with *S. asiatica* was somewhat less stressful and led to host biomass production that was about half that of uninfected controls in both ambient and CO_2-enriched air. The end result was that the doubling of the air's CO_2 content employed in this study increased sorghum biomass by 79 percent and 35 percent in the C_4 sorghum plants infected with *S. hermonthica* and *S. asiatica*, respectively.

Hwangbo *et al*. (2003) grew Kentucky Bluegrass (*Poa pratensis* L.) with and without infection by the C_3 chlorophyllous parasitic angiosperm *Rhinanthus minor* L. (a facultative hemiparasite found in natural and semi-natural grasslands throughout Europe) for eight weeks in open-top chambers maintained at ambient and elevated (650 ppm) CO_2 concentrations. At the end of the study, the parasite's biomass (when growing on its host) was 47 percent greater in the CO_2-enriched chambers, while its host exhibited only a 10 percent CO_2-induced increase in biomass in the parasite's absence but a nearly doubled 19 percent increase when infected by it.

Watling and Press (2000) grew upland rice (*Oryza sativa* L.) in pots in controlled-environment chambers maintained at 350 and 700 ppm CO_2 in either the presence or absence of the root parasite *S. hermonthica* for a period of 80 days after sowing, after which time the plants were harvested and weighed. In ambient air, the presence of the parasite reduced the biomass of the rice to only 35 percent of what it was in the absence of the parasite; whereas in air enriched with CO_2 the presence of the parasite reduced the biomass of infected plants to but 73 percent of what it was in the absence of the parasite.

In summary, these several observations suggest that the rising CO_2 content of the air can have wide and variable effects on parasitic plants, ranging from negative to positive growth responses, depending upon soil nutrition and host plant specificity. With respect to the infected host plants, elevated CO_2 generally tends to reduce the negative effects of parasitic infection, so that infected host plants continue to exhibit positive growth responses to elevated CO_2. It is likely that whatever the scenario with regard to parasitic infection, host plants will fare better under higher atmospheric CO_2 conditions than they do currently.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/p/parasites.php.

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7.8.5. Roots

In reviewing the scientific literature pertaining to atmospheric CO_2 enrichment effects on belowground plant growth and development, Weihong *et al*. (2000) briefly summarize what is known about this subject. They report that atmospheric CO_2 enrichment typically enhances the growth rates of roots, especially those of fine roots, and that CO_2-induced increases in root production eventually lead to increased carbon inputs to soils, due to enhanced root turnover and exudation of various organic carbon compounds, which can potentially lead to greater soil carbon sequestration. In addition, they note that increased soil carbon inputs stimulate the growth and activities of soil microorganisms that utilize plant-derived carbon as their primary energy source; and they report that subsequently enhanced activities of fungal and bacterial plant symbionts often lead to increased plant nutrient acquisition.

In a much more narrowly focused study, Crookshanks *et al*. (1998) sprouted seeds of the small and fast-growing *Arabidopsis thaliana* plant on agar medium in Petri dishes and grew the resulting immature plants in controlled environment chambers maintained at atmospheric CO_2 concentrations of either 355 or 700 ppm. Visual assessments of root growth were made after emergence of the roots from the seeds, while microscopic investigations of root cell properties were also conducted. The scientists learned that the CO_2-enriched plants directed a greater proportion of their newly produced biomass into root, as opposed to shoot, growth. In addition, the young plants produced longer primary roots and more and longer lateral roots. These effects were found to be related to the CO_2-induced stimulation of mitotic activity, accelerated cortical cell expansion, and increased cell wall plasticity.

Gouk *et al*. (1999) grew an orchid plantlet, Mokara Yellow, in plastic bags flushed with 350 and 10,000 ppm CO_2 for three months to study the effects of elevated CO_2 on this epiphytic CAM species. They determined that the super-elevated CO_2 of their experiment enhanced the total dry weight of the orchid plantlets by more than two-fold, while increasing the growth of existing roots and stimulating the induction of new roots from internodes located on the orchid stems. Total chlorophyll content was also increased by elevated CO_2—by 64 percent in young leaves and by 118 percent in young roots. This phenomenon permitted greater light harvesting during photosynthesis and likely led to the tissue starch contents of the CO_2-enriched plantlets rising nearly 20-fold higher than those of the control-plantlets. In spite of this large CO_2-induced accumulation of starch, however, no damage or disruption of chloroplasts was evident in the leaves and roots of the CO_2-enriched plants.

A final question that has periodically intrigued researchers is whether plants take up carbon through their roots in addition to through their leaves. Although a definitive answer eludes us, various aspects of the issue have been described by Idso (1989), who we quote as follows.

“Although several investigators have claimed that plants should receive little direct benefit from dissolved CO_2 (Stolwijk *et al*., 1957; Skok *et al*., 1962; Splittstoesser, 1966), a number of experiments have produced significant increases in root growth (Erickson, 1946; Leonard and Pinckard, 1946; Geisler, 1963; Yorgalevitch and Janes, 1988), as well as yield itself (Kursanov *et al*., 1951; Grinfeld, 1954; Nakayama and Bucks, 1980; Baron and Gorski, 1986), with CO_2-enriched irrigation water. Early on, Misra (1951) suggested that this beneficent effect may be related to CO_2-induced changes in soil nutrient availability; and this hypothesis may well be correct. Arteca *et al*. (1979), for example, have observed K, Ca and Mg to be better absorbed by potato roots when the concentration of CO_2 in the soil solution is increased; while Mauney and Hendrix (1988) found Zn and Mn to be better absorbed by cotton under such conditions, and Yurgalevitch and Janes (1988) found an enhancement of the absorption of Rb by tomato roots. In all cases, large increases in either total plant growth or yield accompanied the enhanced uptake of nutrients. Consequently, as it has been suggested that CO_2 concentration plays a major role in determining the porosity, plasticity and charge of cell membranes (Jackson and Coleman, 1959; Mitz, 1979), which could thereby alter ion uptake and organic acid production (Yorgalevitch and Janes, 1988), it is possible that some such suite of mechanisms may well be responsible for the plant productivity increases often observed to result from enhanced concentrations of CO_2 in the soil solution.”

In the next two sections we survey the scientific literature on root responses to atmospheric CO_2 enrichment for crops and then trees.

Additional information on this topic, including reviews on roots not discussed here, can be found at http://www.co2science.org/subject/r/subject_r.php under the heading Roots.

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7.8.5.1. Crops

Hodge and Millard (1998) grew narrowleaf plantain (*Plantago lanceolata*) seedlings for a period of six weeks in controlled environment growth rooms maintained at atmospheric CO_2 concentrations of either 400 or 800 ppm. By the end of this period, the plants in the 800-ppm air exhibited increases in shoot and root dry matter production that were 159 percent and 180 percent greater, respectively, than the corresponding dry matter increases experienced by the plants growing in 400-ppm air, while the amount of plant carbon recovered from the potting medium (sand) was 3.2 times greater in the elevated-CO_2 treatment. Thus, these investigators found that the belowground growth stimulation provided by atmospheric CO_2 enrichment was greater than that experienced above-ground.

Wechsung *et al.* (1999) grew spring wheat (*Triticum aestivum*) in rows in a FACE study employing atmospheric CO_2 concentrations of 370 and 550 ppm and irrigation treatments that periodically replaced either 50 percent or 100 percent of prior potential evapotranspiration in an effort to determine the effects of elevated CO_2 and water stress on root growth. They found that elevated CO_2 increased in-row root dry weight by an average of 22 percent during the growing season under both the wet and dry irrigation regimes. In addition, during the vegetative growth phase, atmospheric CO_2 enrichment increased inter-row root dry weight by 70 percent, indicating that plants grown in elevated CO_2 developed greater lateral root systems than plants grown at ambient CO_2. During the reproductive growth phase, elevated CO_2 stimulated the branching of lateral roots into inter-row areas, but only when water was limiting to growth. In addition, the CO_2-enriched plants tended to display greater root dry weights at a given depth than did ambiently grown plants.

In a comprehensive review of all prior FACE experiments conducted on agricultural crops, Kimball *et al*. (2002) determined that for a 300-ppm increase in atmospheric CO_2 concentration, the root biomass of wheat, ryegrass and rice experienced an average increase of 70 percent at ample water and nitrogen, 58 percent at low nitrogen and 34 percent at low water, while clover experienced a 38 percent increase at ample water and nitrogen, plus a 32 percent increase at low nitrogen. Outdoing all of the other crops was cotton, which exhibited a 96 percent increase in root biomass at ample water and nitrogen.

Zhao *et al*. (2000) germinated pea (*Pisum sativum*) seeds and exposed the young plants to various atmospheric CO_2 concentrations in controlled environment chambers to determine if elevated CO_2 impacts root border cells, which are major contributors of root exudates in this and most other agronomic plants. They found that elevated CO_2 increased the production of root border cells in pea seedlings. In going from ambient air to air enriched to 3,000 and 6,000 ppm CO_2, border-cell numbers increased by over 50 percent and 100 percent, respectively. Hence, as the CO_2 content of the air continues to rise, peas (and possibly many other crop plants) will likely produce greater numbers of root border cells, which should increase the amounts of root exudations occurring in their rhizospheres, which further suggests that associated soil microbial and fungal activities will be stimulated as a result of the increases in plant-derived carbon inputs that these organisms require to meet their energy needs.

Van Ginkel *et al*. (1996) grew perennial ryegrass (*Lolium perenne*) plants from seed in two growth chambers for 71 days under continuous $^{14}CO_2$-labeling of the atmosphere at CO_2 concentrations of 350 and 700 ppm at two different soil nitrogen levels. At the conclusion of this part of the experiment, the plants were harvested and their roots dried, pulverized and mixed with soil in a number of one-liter pots that were placed within two wind tunnels in an open field, one of which had ambient air of 361 ppm CO_2 flowing through it, and one of which had air of 706 ppm CO_2 flowing through it. Several of the containers were then seeded with more *Lolium perenne*, others were similarly seeded the following year, and still others were kept bare for two years. Then, at the ends of the first and second years, the different degrees of decomposition of the original plant roots were assessed.

It was determined, first, that shoot and root growth were enhanced by 13 and 92 percent, respectively, by the extra CO_2 in the initial 71-day portion of the experiment, once again demonstrating the significant benefits that are often conferred upon plant roots by atmospheric CO_2 enrichment. Secondly, it was found that the decomposition of the high-CO_2-grown roots in the high-CO_2 wind tunnel was 19 percent lower than that of the low-CO_2-grown roots in the low-CO_2 wind tunnel at the end of the first year, and that it was 14 percent lower at the end of the second year in the low-nitrogen-grown plants but equivalent in the high-nitrogen-grown plants. It was also determined that the presence of living roots reduced the decomposition rate of dead roots below the dead-root-only decomposition rate observed in the bare soil treatment. Based on these findings, van Ginkel *et al*. conclude that "the combination of higher root yields at elevated CO_2 combined with a decrease in root decomposition will lead to a longer residence time of C in the soil and probably to a higher C storage."

In conclusion, as the CO_2 content of the air continues to rise, many crops will likely develop larger and more extensively branching root systems that may help them to better cope with periods of reduced soil moisture availability. This chain of events should make the soil environment even more favorable for plant growth and development in a high-CO_2 world of the future.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/r/rootscrops.php.

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7.8.5.2. Trees

Janssens *et al.* (1998) grew three-year-old Scots pine seedlings for a period of six months in open-top chambers maintained at ambient and 700 ppm atmospheric CO_2, finding that the extra CO_2 increased total root length by 122 percent and total root dry mass by 135 percent. In a similar study that employed close to the same degree of enhancement of the air's CO_2 content, Pritchard *et al.* (2001a) grew idealized ecosystems representative of regenerating longleaf pine forests of the southeastern USA for a period of 18 months in large soil bins located within open-top chambers. The above-ground parts of these seedlings experienced a growth enhancement of 20 percent. The root biomass of the trees, however, was increased by more than three times as much (62 percent).

Working with FACE technology, Pritchard *et al.* (2001b) studied 14-year-old loblolly pine trees after a year of exposure to an extra 200 ppm of CO_2, finding that total standing root length and root numbers were 16 and 34 percent greater, respectively, in the CO_2-enriched plots than in the ambient-air plots. In addition, the elevated CO_2 increased the diameter of living and dead roots by 8 and 6 percent, respectively, while annual root production was found to be 26 percent greater in the CO_2-enriched plots. For the degree of CO_2 enrichment employed in the prior two studies, this latter enhancement corresponds to a root biomass increase of approximately 45 percent.

In an open-top chamber study of a model ecosystem composed of a mixture of spruce and beech seedlings, Wiemken *et al.* (2001) investigated the effects of a 200 ppm increase in the air's CO_2 concentration that prevailed for a period of four years. On nutrient-poor soils, the extra CO_2 led to a 30 percent increase in fine-root biomass, while on nutrient-rich soils it led to a 75 percent increase. These numbers correspond to increases of about 52 percent and 130 percent, respectively, for atmospheric CO_2 enhancements on the order of those employed by Janssens *et al.* (1998) and Pritchard *et al.* (2001a).

Another interesting aspect of the Wiemken *et al.* study was their finding that the extra CO_2 increased the amount of symbiotic fungal biomass associated with the trees' fine roots by 31 percent on nutrient-poor soils and by 100 percent on nutrient-rich soils, which for the degree of atmospheric CO_2 enrichment used in the studies of Janssens *et al.* (1998) and Pritchard *et al.* (2001a) translate into increases of about 52 percent and 175 percent, respectively.

Berntsen and Bazzaz (1998) removed intact chunks of soil from the Hardwood-White Pine-Hemlock forest region of New England and placed them in plastic containers within controlled environment glasshouses maintained at either 375 or 700 ppm CO_2 for a period of two years in order to study the effects of elevated CO_2 on the regeneration of plants from seeds and rhizomes present in the soil. At the conclusion of the study, total mesocosm plant biomass (more than 95 percent of which was supplied by yellow and white birch tree seedlings) was found to be 31 percent higher in the elevated CO_2 treatment than in ambient air, with a mean enhancement of 23 percent above-ground and 62 percent belowground. The extra CO_2 also increased the mycorrhizal colonization of root tips by 45 percent in white birch and 71 percent in yellow birch; and the CO_2-enriched yellow birch seedlings exhibited 322 percent greater root length and 305 percent more root surface area than did the yellow birch seedlings growing in ambient air.

Kubiske *et al.* (1998) grew cuttings of four quaking aspen genotypes in open-top chambers for five months at atmospheric CO_2 concentrations of either 380 or 720 ppm and low or high soil nitrogen concentrations. They found, surprisingly, that the cuttings grown in elevated CO_2 displayed no discernible increases in above-ground growth. However, the extra CO_2 significantly increased fine-root length and root turnover rates at high soil nitrogen by increasing fine-root production, which would logically be expected to produce benefits (not the least of which would be a larger belowground water- and nutrient-gathering system) that would eventually lead to enhanced above-ground growth as well.

Expanding on this study, Pregitzer *et al.* (2000) grew six quaking aspen genotypes for 2.5 growing seasons in open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm with both adequate and inadequate supplies of soil nitrogen. This work demonstrated that the trees exposed to elevated CO_2 developed thicker and longer roots than the trees growing in ambient air, and that the fine-root biomass of the CO_2-enriched trees was enhanced by 17 percent in the nitrogen-poor soils and by 65 percent in the nitrogen-rich soils.

Yet another study of quaking aspen conducted by King *et al*. (2001) demonstrated that trees exposed to an atmospheric CO_2 concentration 560 ppm in a FACE experiment produced 133 percent more fine-root biomass than trees grown in ambient air of 360 ppm, which roughly equates to 233 percent more fine-root biomass for the degree of CO_2 enrichment employed in the prior study of Pregitzer *et al*. And when simultaneously exposed to air of 1.5 times the normal ozone concentration, the degree of fine-root biomass stimulation produced by the extra CO_2 was still as great as 66 percent, or roughly 115 percent when extrapolated to the greater CO_2 enrichment employed by Pregitzer *et al*.

In a final quaking aspen study, King *et al*. (1999) grew four clones at two different temperature regimes (separated by 5°C) and two levels of soil nitrogen (N) availability (high and low) for 98 days, while measuring photosynthesis, growth, biomass allocation, and root production and mortality. They found that the higher of the two temperature regimes increased rates of photosynthesis by 65 percent and rates of whole-plant growth by 37 percent, while it simultaneously enhanced root production and turnover. It was thus their conclusion that "trembling aspen has the potential for substantially greater growth and root turnover under conditions of warmer soil at sites of both high and low N-availability" and that "an immediate consequence of this will be greater inputs of C and nutrients to forest soils."

In light of these several findings pertaining to quaking aspen trees, it is evident that increases in atmospheric CO_2 concentration, air temperature and soil nitrogen content all enhance their belowground growth, which positively impacts their above-ground growth.

Turning our attention to other deciduous trees, Gleadow *et al*. (1998) grew eucalyptus seedlings for six months in glasshouses maintained at atmospheric CO_2 concentrations of either 400 or 800 ppm, fertilizing them twice daily with low or high nitrogen solutions. The elevated CO_2 of their experiment increased total plant biomass by 98 and 134 percent relative to plants grown at ambient CO_2 in the high and low nitrogen treatments, respectively. In addition, in the low nitrogen treatment, elevated CO_2 stimulated greater root growth, as indicated by a 33 percent higher root:shoot ratio.

In a more complex study, Day *et al*. (1996) studied the effects of elevated CO_2 on fine-root production in open-top chambers erected over a regenerating oak-palmetto scrub ecosystem in Florida, USA, determining that a 350-ppm increase in the atmosphere's CO_2 concentration increased fine-root length densities by 63 percent while enhancing the distribution of fine roots at both the soil surface (0-12 cm) and at a depth of 50-60 cm. These findings suggest that the ongoing rise in the atmosphere's CO_2 concentration will likely increase the distribution of fine roots near the soil surface, where the greatest concentrations of nutrients are located, and at a depth that coincides with the upper level of the site's water table, both of which phenomena should increase the trees' ability to acquire the nutrients and water they will need to support CO_2-enhanced biomass production in the years ahead.

In another study that employed CO_2, temperature and nitrogen as treatments, Uselman *et al*. (2000) grew seedlings of the nitrogen-fixing black locust tree for 100 days in controlled environments maintained at atmospheric CO_2 concentrations of 350 and 700 ppm and air temperatures of 26°C (ambient) and 30°C, with either some or no additional nitrogen fertilization, finding that the extra CO_2 increased total seedling biomass by 14 percent, the elevated temperature increased it by 55 percent, and nitrogen fertilization increased it by 157 percent. With respect to root exudation, a similar pattern was seen. Plants grown in elevated CO_2 exuded 20 percent more organic carbon compounds than plants grown in ambient air, while elevated temperature and fertilization increased root exudation by 71 and 55 percent, respectively. Hence, as the air's CO_2 content continues to rise, black locust trees will likely exhibit enhanced rates of biomass production and exudation of dissolved organic compounds from their roots. Moreover, if air temperature also rises, even by as much as 4°C, its positive effect on biomass production and root exudation will likely be even greater than that resulting from the increasing atmospheric CO_2 concentration. The same would appear to hold true for anthropogenic nitrogen deposition, reinforcing what was learned about the impacts of these three environmental factors on the growth of quaking aspen trees.

In light of these several experimental findings, it can confidently be concluded that the ongoing rise in the air's CO_2 content, together with possible concurrent increases in air temperature and nitrogen deposition, will likely help earth's woody plants increase their root mass and surface area to become ever more robust and productive.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/r/rootsconifers.php and http://www.co2science.org/subject/r/rootsdeciduous.php.

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7.8.6. Seeds

Elevated CO_2 levels are known to have effects on seeds that are different from their effects on total biomass, roots, and other dimensions examined so far. In this section we survey the scientific literature on this topic regarding crops, grasslands, and trees.

Additional information on this topic, including reviews on seeds not discussed here, can be found at http://www.co2science.org/subject/s/subject_s.php under the heading Seeds.

7.8.6.1. Crops

In a greenhouse study of the various components of seed biomass production, Palta and Ludwig (2000) grew narrow-leafed lupin in pots filled with soil within Mylar-film tunnels maintained at either 355 or 700 ppm CO_2. They found that the extra CO_2 increased (1) the final number of pods and (2) the number of pods that filled large seeds, while it (3) reduced to zero the number of pods that had small seeds, (4) reduced the number of pods with unfilled seeds from 16 to 1 pod per plant, and increased (5) pod set and (6) dry matter accumulation on the developing branches. These several CO_2-induced improvements to key physiological processes resulted in 47 to 56 percent increases in dry matter per plant, which led to increases of 44 to 66 percent in seed yield per plant.

Sanhewe *et al*. (1996) grew winter wheat in polyethylene tunnels maintained at atmospheric CO_2 concentrations of 380 and 680 ppm from the time of seed germination to the time of plant maturity, while maintaining a temperature gradient of approximately 4°C in each tunnel. In addition to the elevated CO_2 increasing seed yield per unit area, they found it also increased seed weight, but not seed survival or germination. Increasing air temperature, on the other hand, increased seed longevity across the entire range of temperatures investigated (14 to 19°C).

Thomas *et al*. (2003) grew soybean plants to maturity in sunlit controlled-environment chambers under sinusoidally varying day/night-max/min temperatures of 28/18, 32/22, 36/26, 40/30 and 44/34°C and two levels of atmospheric CO_2 concentration (350 and 700 ppm). They determined, in their words, that the effect of temperature on seed composition and gene expression was "pronounced," but that "there was no effect of CO_2." In this regard, however, they note that "Heagle *et al*. (1998) observed a positive significant effect of CO_2 enrichment on soybean seed oil and oleic acid concentration," the latter of which parameters Thomas *et al*. found to increase with rising temperature all the way from 28/18 to 44/34°C.

In another soybean study, Ziska *et al*. (2001) grew one modern and eight ancestral genotypes in glasshouses maintained at atmospheric CO_2 concentrations of 400 and 710 ppm, finding that the extra CO_2 increased photosynthetic rates by an average of 75 percent. This enhancement in photosynthetic sugar production led to increases in seed yield that averaged 40 percent for all cultivars, except for one ancestral variety that exhibited an 80 percent increase in seed yield. Hence, if plant breeders were to utilize the highly CO_2-responsive ancestral cultivar identified in this study in their breeding programs, it is possible that soybean seed yields could be made to rise even faster and higher in the days and years ahead.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/s/seedscrops.php.

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7.8.6.2. Grasslands

Steinger *et al*. (2000) collected seeds from *Bromus erectus* plants that had been grown at atmospheric CO_2 concentrations of 360 and 650 ppm and germinated some of both groups of seeds under those same two sets of conditions. They found the elevated CO_2 treatment increased individual seed mass by about 9 percent and increased seed carbon-to-nitrogen ratio by almost 10 percent. However, they also learned that these changes in seed properties had little impact on subsequent seedling growth. In fact, when the seeds produced by ambient or CO_2-enriched plants were germinated and grown in ambient air, there was no significant size difference between the two groups of resultant seedlings after a period of 19 days. Likewise, when the seeds produced from ambient or CO_2-enriched plants were germinated and grown in the high CO_2 treatment, there was also no significant difference between the sizes of the seedlings derived from the two groups of seeds. However, the CO_2-enriched seedlings produced from both groups of seeds were almost 20 percent larger than the seedlings produced from *both* groups of seeds grown in ambient air, demonstrating that the direct effects of elevated atmospheric CO_2 concentration on seedling growth and development were more important than the differences in seed characteristics produced by the elevated atmospheric CO_2 concentration in which their parent plants grew.

In another study conducted about the same time, Edwards *et al*. (2001) utilized a FACE experiment where daytime atmospheric CO_2 concentrations above a sheep-grazed pasture in New Zealand were increased by 115 ppm to study the effects of elevated CO_2 on seed production, seedling recruitment and species compositional changes. In the two years of their study, the extra daytime CO_2 increased seed production and dispersal in seven of the eight most abundant species, including the grasses *Anthoxanthum odoratum*, *Lolium perenne* and *Poa pratensis*, the legumes *Trifolium repens* and *T. subterranean*, and the herbs *Hypochaeris radicata* and *Leontodon saxatilis*. In some of these plants, elevated CO_2 increased the number of seeds per reproductive structure, while all of them exhibited CO_2-induced increases in the number of reproductive structures per unit of ground area. In addition, they determined that the CO_2-induced increases in seed production contributed in a major way to the increase in the numbers of species found within the CO_2-enriched plots.

In a five-year study of a nutrient-poor calcareous grassland in Switzerland, Thurig *et al*. (2003) used screen-aided CO_2 control (SACC) technology (Leadley *et al*., 1997) to enrich the air over half of their experimental plots with an extra 300 ppm of CO_2, finding that "the effect of elevated CO_2 on the number of flowering shoots (+24%) and seeds (+29%) at the community level was similar to above ground biomass response." In terms of species functional groups, there was a 42 percent increase in the mean seed number of graminoids and a 33 percent increase in the mean seed number of forbs, but no change in legume seed numbers. In most species, mean seed weight also tended to be greater in plants grown in CO_2-enriched air (+12 percent); and Thurig *et al*. say it is known from many studies that heavier seeds result in seedlings that "are more robust than seedlings from lighter seeds (Baskin and Baskin, 1998)."

Wang and Griffin (2003) grew dioecious white cockle plants from seed to maturity in sand-filled pots maintained at optimum moisture and fertility conditions in environmentally controlled growth chambers in which the air was continuously maintained at CO_2 concentrations of either 365 or 730 ppm. In response to this doubling of the air's CO_2 content, the vegetative mass of both male and female plants rose by approximately 39 percent. Reproductive mass, on the other hand, rose by 82 percent in male plants and by 97 percent in females. In the female plants, this feat was accomplished, in part, by increases of 36 percent and 44 percent in the number and mass of seeds per plant, and by a 15 percent increase in the mass of individual seeds, in harmony with the findings of Jablonski *et al*. (2002), which they derived from a meta-analysis of the results of 159 CO_2 enrichment experiments conducted on 79 species of agricultural and wild plants. Because dioecious plants comprise nearly half of all angiosperm families, we may expect to see a greater proportion of plant biomass allocated to reproduction in a high-CO_2 world of the future, which result should bode well for the biodiversity of earth's many ecosystems.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/s/seedsgrasslands.php.

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7.8.6.3. Trees

How does enriching the air with carbon dioxide impact the reproductive capacity of trees? LaDeau and Clark (2001) determined the reproductive response of loblolly pine trees to atmospheric CO_2 enrichment at Duke Forest in the Piedmont region of

North Carolina, USA, where in August of 1996 three 30-m-diameter FACE rings began to enrich the air around the 13-year-old trees they encircled to 200 ppm above the atmosphere's normal background concentration, while three other FACE rings served as control plots. Because the trees were not mature at the start of the experiment they did not produce any cones until a few rare ones appeared in 1998. By the fall of 1999, however, the two scientists found that, compared to the trees growing in ambient air, the CO_2-enriched trees were twice as likely to be reproductively mature, and they produced three times more cones per tree. Similarly, the trees growing in the CO_2-enriched air produced 2.4 times more cones in the fall of 2000; and from August 1999 through July 2000, they collected three times as many seeds in the CO_2-fertilized FACE rings as in the control rings.

Also working on this aspect of the Duke Forest FACE study were Hussain *et al.* (2001), who report that (1) seeds collected from the CO_2-enriched trees were 91 percent heavier than those collected from the trees growing in ambient air, (2) the CO_2-enriched seeds had a lipid content that was 265 percent greater than that of the seeds produced on the ambient-treatment trees, (3) the germination success for seeds developed under atmospheric CO_2 enrichment was more than three times greater than that observed for control seeds developed at ambient CO_2, regardless of germination CO_2 concentration, (4) seeds from the CO_2-enriched trees germinated approximately five days earlier than their ambiently produced counterparts, again regardless of germination CO_2 concentration, and (5) seedlings developing from seeds collected from CO_2-enriched trees displayed significantly greater root lengths and needle numbers than seedlings developing from trees exposed to ambient air, also regardless of growth CO_2 concentration.

The propensity for elevated levels of atmospheric CO_2 to hasten the production of more plentiful seeds on the trees of this valuable timber species bodes well for naturally regenerating loblolly pine stands of the southeastern United States, where LaDeau and Clark report the trees "are profoundly seed-limited for at least 25 years." As the air's CO_2 content continues to climb, they conclude that "this period of seed limitation may be reduced." In addition, the observations of Hussain *et al.* suggest that loblolly pine trees in a CO_2-enriched world of the future will likely display significant increases in their photosynthetic rates. Enhanced carbohydrate supplies resulting from this phenomenon will likely be used to increase seed weight and lipid content. Such seeds should consequently exhibit significant increases in germination success, and their enhanced lipid supplies will likely lead to greater root lengths and needle numbers in developing seedlings. Consequently, when CO_2-enriched loblolly pine seedlings become photosynthetically active, they will likely produce biomass at greater rates than those exhibited by seedlings growing under current CO_2 concentrations.

Five years later, LaDeau and Clark (2006a) conducted a follow-up study that revealed "carbon dioxide enrichment affected mean cone production both through early maturation and increased fecundity," so that "trees in the elevated CO_2 plots produced twice as many cones between 1998 and 2004 as trees in the ambient plots." They also determined that the trees grown in elevated CO_2 "made the transition to reproductive maturation at smaller [trunk] diameters," and that they "not only reached reproductive maturation at smaller diameters, but also at younger ages." By 2004, for example, they say that "roughly 50% of ambient trees and 75% of fumigated trees [had] produced cones." In addition, they observed that "22% of the trees in high CO_2 produced between 40 and 100 cones during the study, compared with only 9% of ambient trees."

"In this 8-year study," in the words of the two researchers, "we find that previous short-term responses indeed persist." In addition, they note that "*P. taeda* trees that produce large seed crops early in their life span tend to continue to be prolific producers (Schutlz, 1997)," and they conclude that this fact, together with their findings, suggests that "individual responses seen in this young forest may be sustained over their life span."

In a concurrent report, LaDeau and Clark (2006b) analyzed the seed and pollen responses of the loblolly pines to atmospheric CO_2 enrichment, finding that the "trees grown in high-CO_2 plots first began producing pollen while younger and at smaller sizes relative to ambient-grown trees," and that cone pollen and airborne pollen grain abundances were significantly greater in the CO_2-enriched stands. More specifically, they found that "by spring 2005, 63% of all trees growing in high CO_2 had produced both pollen and seeds *vs.* only 36% of trees in the ambient plots." The researchers say precocious pollen production "could enhance the production of viable seeds by increasing the percentage of fertilized ovules," and that "more pollen disseminated from multiple-source trees may also increase rates of gene flow among stands, and could further reduce rates of self-pollination, indirectly enhancing the production of viable seeds." They also say "pine pollen is not a dangerous allergen for the public at large."

Another major study of the reproductive responses of trees to elevated levels of atmospheric CO_2 was conducted at the Kennedy Space Center, Florida, USA, where in 1996 three species of scrub-oak (*Quercus myrtifolia*, *Q. chapmanii*, and *Q. geminata*) were enclosed within sixteen open-top chambers, half of which were maintained at 379 ppm CO_2 and half at 704 ppm. Five years later—in August, September and October of 2001—Stiling *et al*. (2004) counted the numbers of acorns on randomly selected twigs of each species, while in November of that year they counted the numbers of fallen acorns of each species within equal-size quadrates of ground area, additionally evaluating mean acorn weight, acorn germination rate, and degree of acorn infestation by weevils. They found acorn germination rate and degree of predation by weevils were unaffected by elevated CO_2, while acorn size was enhanced by a small amount: 3.6 percent for *Q. myrtifolia*, 7.0 percent for *Q. chapmanii*, and 7.7 percent for *Q. geminata*. Acorn number responses, on the other hand, were enormous, but for only two of the three species, as *Q. geminata* did not register any CO_2-induced increase in reproductive output, in harmony with its unresponsive overall growth rate. For *Q. myrtifolia*, however, Stiling *et al*. report "there were four times as many acorns per 100 twigs in elevated CO_2 as in ambient CO_2 and for *Q. chapmanii* the increase was over threefold." On the ground, the enhancement was greater still, with the researchers reporting that "the number of *Q. myrtifolia* acorns per meter squared in elevated CO_2 was over seven times greater than in ambient CO_2 and for *Q. chapmanii*, the increase was nearly sixfold."

Stiling *et al*. say these results lead them to believe "there will be large increases in seedling production in scrub-oak forests in an atmosphere of elevated CO_2," noting that "this is important because many forest systems are 'recruitment-limited' (Ribbens *et al*., 1994; Hubbell *et al*., 1999)," which conclusion echoes that of LaDeau and Clark with respect to loblolly pines.

A third major study of CO_2 effects on seed production in trees has been conducted at the FACE facility near Rhinelander, Wisconsin (USA), where young paper birch (*Betula papyrifera* Marsh.) seedlings were planted in 1997 and have been growing since 1998 in open-top chambers maintained at atmospheric CO_2 concentrations of either 360 or 560 ppm, as well as at atmospheric ozone (O_3) concentrations of either ambient or 1.5 times ambient. There, Darbah *et al*. (2007) collected many types of data pertaining to flowering, seed production, seed germination and new seedling growth and development over the 2004-2006 growing seasons; and as they describe it, "elevated CO_2 had significant positive effect[s] on birch catkin size, weight, and germination success rate." More specifically, they note that "elevated CO_2 increased germination rate of birch by 110%, compared to ambient CO_2 concentrations, decreased seedling mortality by 73%, increased seed weight by 17% [and] increased [new seedling] root length by 59%."

In conclusion, research on a variety of tree species finds that CO_2 enhancement increases the production of viable seeds and seedlings, meaning these species should flourish as CO_2 levels conntinue to rise. Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/s/seedstrees.php.

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7.8.7. Tannins

Condensed tannins are naturally occurring secondary carbon compounds produced in the leaves of a number of different plants that often act to deter herbivorous insects. How do condensed tannin concentrations in the leaves and roots of trees respond to atmospheric CO_2 enrichment?

Additional information on this topic, including reviews on tannins not discussed here, can be found at http://www.co2science.org/subject/t/subject_t.php under the heading Tannins.

7.8.7.1. Aspen Trees

King *et al*. (2001) grew aspen seedlings for five months in open-top chambers maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm. At the end of this period, naturally senesced leaf litter was collected and analyzed; and it was found that the elevated CO_2 of this particular study had no effect on leaf litter tannin concentration.

A substantially different result was obtained in an earlier study of aspen leaves that was conducted by McDonald *et al*. (1999), who grew aspen seedlings in controlled environment greenhouses that were maintained at either ambient (387 ppm) or elevated (696 ppm) CO_2 concentrations under conditions of either low or high light availability (half and full sunlight, respectively) for 31 days after the mean date of bud break. In this case it was determined that under low light conditions, the CO_2-enriched seedlings exhibited an increase of approximately 15 percent in leaf condensed tannin concentration, while under high light conditions the CO_2-induced increase in leaf condensed tannin concentration was 175 percent.

In a much more complex study than either of the two preceding ones, Agrell *et al*. (2005) examined the effects of ambient and elevated concentrations of atmospheric CO_2 (360 ppm and 560 ppm, respectively) and O_3 (35-60 ppb and 52-90 ppb, respectively) on the foliar chemistry of more mature aspen trees of two different genotypes (216 and 259) growing out-of-doors at the Aspen Free Air CO_2 Enrichment (FACE) facility near Rhinelander, Wisconsin, USA, as well as the impacts of these effects on the host plant preferences of forest tent caterpillar larvae.

In reporting the results of the study, Agrell *et al*. say that "the only chemical component showing a somewhat consistent covariation with larval preferences was condensed tannins," noting that "the tree becoming relatively less preferred as a result of CO_2 or O_3 treatment was in general also the one for which average levels of condensed tannins were most positively (or least negatively) affected by that treatment." The mean condensed tannin concentrations of the aspen 216 and 259 genotypes were 25 percent and 57 percent higher, respectively, under the elevated CO_2 and O_3 combination treatment compared to the ambient CO_2 and O_3 combination treatment.

In light of these findings, it is logical to presume that as atmospheric concentrations of CO_2 and O_3 continue to rise, the increase in condensed tannin concentration likely to occur in the foliage of aspen trees should lead to their leaves becoming less preferred for consumption by the forest tent caterpillar.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/tanninsaspen.php.

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7.8.7.2. Birch Trees

How do condensed tannin concentrations in the leaves and roots of paper birch (*Betula papyrifera* Marsh.) and silver birch (*Betula pendula* Roth) trees respond to atmospheric CO_2 enrichment with and without concomitant increases in atmospheric temperature and ozone concentrations? We here briefly summarize the findings of several studies that have broached one or more parts of this question.

McDonald *et al*. (1999) grew paper birch seedlings in controlled environment greenhouses that were maintained at either ambient (387 ppm) or elevated (696 ppm) CO_2 concentrations under conditions of either low or high light availability (half and full sunlight, respectively) for 31 days after the mean date of bud break. In doing so, they determined that under low light conditions the CO_2-enriched seedlings exhibited an increase of approximately 15 percent in leaf condensed tannin concentration, while under high light conditions the CO_2-induced tannin increase was a whopping 175 percent.

Peltonen *et al*. (2005) studied the impacts of doubled atmospheric CO_2 and O_3 concentrations on the accumulation of 27 phenolic compounds, including soluble condensed tannins, in the leaves of two European silver birch clones in seven-year-old soil-grown trees that were exposed in open-top chambers for three growing seasons to ambient and twice-ambient atmospheric CO_2 and O_3 concentrations singly and in combination. This work, which was carried out in central Finland, revealed that elevated CO_2 increased the concentration of soluble condensed tannins in the leaves of the trees by 19 percent. In addition, they found that the elevated CO_2 protected the leaves from elevated O_3 because, as they describe it, "all the O_3-derived effects on the leaf phenolics and traits were prevented by elevated CO_2."

Kuokkanen *et al*. (2003) grew two-year-old silver birch seedlings in ambient air of 350 ppm CO_2 or air enriched to a CO_2 concentration of 700 ppm under conditions of either ambient temperature or ambient temperature plus 3°C for one full growing season in the field in closed-top chambers at the Mekrijarvi Research Station of the University of Joensuu in eastern Finland. Then, during the middle of the summer, when carbon-based secondary compounds of birch leaves are fairly stable, they picked several leaves from each tree and determined their condensed tannin concentrations, along with the concentrations of a number of other physiologically important substances. This work revealed that the concentration of total phenolics, condensed tannins and their derivatives significantly increased in the leaves produced in the CO_2-enriched air, as has also been observed by Lavola and Julkunen-Titto (1994), Williams *et al*. (1994), Kinney *et al*. (1997), Bezemer and Jones (1998) and Kuokkanen *et al*. (2001). In fact, the extra 350 ppm of CO_2 nearly tripled condensed tannin concentrations in the ambient-temperature air, while it increased their concentrations in the elevated-temperature air by a factor in excess of 3.5.

In a study of roots, Parsons *et al*. (2003) grew two-year-old paper birch saplings in well-watered and fertilized 16-L pots from early May until late August in glasshouse rooms maintained at either 400 or 700 ppm CO_2. This procedure revealed that the concentration of condensed tannins in the fine roots of the saplings was increased by 27 percent in the CO_2-enriched treatment; and in regard to this finding, the researchers say "the higher condensed tannin concentrations that were present in the birch fine roots may offer these tissues greater protection against soil-borne pathogens and herbivores."

Parsons *et al*. (2004) collected leaf litter samples from early September to mid-October beneath paper birch trees growing in ambient and CO_2-enriched (to 200 ppm above ambient) FACE plots in northern Wisconsin, USA, which were also maintained under ambient and O_3-enriched (to 19 ppb above ambient) conditions, after which the leaf mass produced in each treatment was determined, sub-samples of the leaves were assessed for a number of chemical constituents. The researchers learned that condensed tannin concentrations were 64 percent greater in the CO_2-enriched plots. Under CO_2- and O_3-enriched conditions, condensed tannin concentrations were 99 percent greater.

In conclusion, it appears that elevated concentrations of atmospheric CO_2 tend to increase leaf and fine-root tannin concentrations of birch trees, and that this phenomenon tends to protect the trees' foliage from predation by voracious insect herbivores and protect the trees' roots from soil-borne pathogens and herbivores.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/tanninsbirch.php.

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7.8.7.3. Oak Trees

Dury *et al*. (1998) grew four-year-old pedunculate oak trees (*Quercus robur* L.) in pots within greenhouses maintained at ambient and twice-ambient atmospheric CO_2 concentrations in combination with ambient and elevated (ambient plus 3°C) air temperatures for approximately one year. This work revealed that elevated CO_2 had only minor and contrasting direct effects on leaf palatability: a temporary increase in foliar phenolic concentrations and decreases in leaf toughness and nitrogen content. The elevated temperature treatment, on the other hand, significantly reduced leaf palatability, because oak leaf toughness increased as a consequence of temperature-induced increases in condensed tannin concentrations. As a result, the researchers concluded that “a 3°C rise in temperature might be expected to result in prolonged larval development, increased food consumption, and reduced growth” for herbivores feeding on oak leaves in a CO_2-enriched and warmer world of the future.

Cornelissen *et al*. (2003) studied fluctuating asymmetry in the leaves of two species of schlerophyllous oaks—myrtle oak (*Quercus myrtifolia*) and sand live oak (*Quercus geminata*)—that dominate a native scrub-oak community at the Kennedy Space Center, Titusville, Florida (USA). Fluctuating asymmetry is the term used to describe small variations from perfect symmetry in otherwise bilaterally symmetrical characters in an organism (Moller and Swaddle, 1997), which asymmetry is believed to arise as a consequence of developmental instabilities experienced during ontogeny that may be caused by various stresses, including both genetic and environmental factors (Moller and Shykoff, 1999).

Based on measurements of (1) distances from the leaf midrib to the left and right edges of the leaf at its widest point and (2) leaf areas on the left and right sides of the leaf midrib, Cornelissen *et al*. determined that “asymmetric leaves were less frequent in elevated CO_2, and, when encountered, they were less asymmetric than leaves growing under ambient CO_2.” In addition, they found that “*Q. myrtifolia* leaves under elevated CO_2 were 15.0% larger than in ambient CO_2 and *Q. geminata* leaves were 38.0 percent larger in elevated CO_2 conditions.” They also determined that “elevated CO_2 significantly increased tannin concentration for both *Q. myrtifolia* and *Q. geminata* leaves” and that “asymmetric leaves contained significantly lower concentrations of tannins than symmetric leaves for both *Q. geminata* and *Q. myrtifolia*.” Specifically, they found induced incfreases in tanning concentrations of approximately 35 percent for *Q. myrtifolia* and 43 percent for *Q. geminata*. In commenting on their primary findings of reduced percentages of leaves experiencing asymmetry in the presence of elevated levels of atmospheric CO_2 and the lesser degree of asymmetry exhibited by affected leaves in the elevated CO_2 treatment, Cornelissen *et al*. say that "a possible explanation for this pattern is the fact that, by contrast to other environmental stresses, which can cause negative effects on plant growth, the predominant effect of elevated CO_2 on plants is to promote growth with consequent reallocation of resources (Docherty *et al*., 1996)." Another possibility they discuss "is the fact that CO_2 acts as a plant fertilizer," and, as a result, that "elevated CO_2 ameliorates plant stress compared with ambient levels of CO_2."

In a subsequent study conducted at the Kennedy Space Center's scrub-oak community, Hall *et al*. (2005b) evaluated foliar quality and herbivore damage in three oaks (*Q. myrtifolia*, *Q. chapmanii* and *Q. geminata*) plus the nitrogen-fixing legume *Galactia elliottii* at three-month intervals from May 2001 to May 2003, at which times samples of undamaged leaves were removed from each of the four species in all chambers and analyzed for various chemical constituents, while 200 randomly selected leaves of each species in each chamber were scored for the presence of six types of herbivore damage. Analyses of the data thereby obtained indicated that for condensed tannins, hydrolyzable tannins, total phenolics and lignin, in all four species there were always greater concentrations of all four leaf constituents in the CO_2-enriched leaves, with across-species mean increases of 6.8 percent for condensed tannins, 6.1 percent for hydrolyzable tannins, 5.1 percent for total phenolics and 4.3 percent for lignin. In addition, there were large CO_2-induced decreases in all leaf damage categories among all species: chewing (-48 percent), mines (-37 percent), eye spot gall (-45 percent), leaf tier (-52 percent), leaf mite (-23 percent) and leaf gall (-16 percent). Hall *et al*. thus concluded that the changes they observed in leaf chemical constituents and herbivore damage "suggest that damage to plants may decline as atmospheric CO_2 levels continue to rise."

Last, and largely overlapping the investigation of Hall *et al*. (2005b), was the study of Hall *et al*. (2005a), who evaluated the effects of the Kennedy Space Center experiment's extra 350 ppm of CO_2 on litter quality, herbivore activity, and their interactions, over the three-year-period 2000-2002. This endeavor indicated, in their words, that "changes in litter chemistry from year to year were far larger than effects of CO_2 or insect damage, suggesting that these may have only minor effects on litter decomposition." The one exception to this finding was that "condensed tannin concentrations increased under elevated CO_2 regardless of species, herbivore damage, or growing season," rising by 11 percent in 2000, 18 percent in 2001 and 41 percent in 2002 as a result of atmospheric CO_2 enrichment, as best we can determine from the researchers' bar graphs. Also, the five scientists report that "lepidopteran larvae can exhibit slower growth rates when feeding on elevated CO_2 plants (Fajer *et al*., 1991) and become more susceptible to pathogens, parasitoids, and predators (Lindroth, 1996; Stiling *et al*., 1999)," noting further that at their field site, "which hosts the longest continuous study of the effects of elevated CO_2 on insects, herbivore populations decline markedly under elevated CO_2 (Stiling *et al*., 1999, 2002, 2003; Hall *et al*., 2005b)."

In conclusion, it would appear CO_2-enriched air produces a large and continuous enhancement of condensed tannin concentrations in oak tree foliage, which causes marked declines in herbivore populations observed in CO_2-enriched open-top-chamber studies.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/tanninsoak.php.

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7.8.8. Transgenic Plants

Toxins produced by *Bacillus thuringiensis* (Bt) supplied to crops via foliar application have been used as a means of combating crop pests for well over half a century. More recently, the Bt gene for producing the toxin has been artificially inserted in some species of plants, producing transgenic plants that are pest resistant. The effectiveness of this management technique depends primarily upon the amount of Bt-produced toxins that are ingested by targeted insects. Another kind of transgenic plant is wheat that has been made heat resistant by the introduction into its gene code of heat shock protein (HSP) or plastidial EF-Tu (protein synthesis elongation factor). How does atmospheric CO_2 enrichment affect transgenic plants?

If soil nitrogen levels are low, foliar nitrogen concentrations in plants grown in enhanced CO_2 environments are generally reduced from what they are at the current atmospheric CO_2 concentration, which suggests that insects would have to eat more foliage to get their normal requirement of nitrogen for proper growth and development in CO_2-enriched air. But by eating more foliage, the insects would also ingest more Bt-produced toxins, and they would be more severely impacted by those substances.

To test this hypothesis, Coviella and Trumble (2000) grew cotton plants in each of six Teflon-film chambers in a temperature-controlled greenhouse, where three of the chambers were maintained at an atmospheric CO_2 concentration of 370 ppm, and three were maintained at 900 ppm CO_2. In addition, half of the plants in each chamber received high levels of nitrogen (N) fertilization, while half received low levels (30 vs. 130 mg N/kg soil/week). After 45 days of growth under these conditions, leaves were removed from the plants and dipped in a Bt solution, after which known amounts of treated leaf material were fed to *Spodoptera exigua* larvae and their responses measured and analyzed.

By these means, the two researchers determined that the plants grown in the elevated CO_2 chambers did indeed have significantly lower foliar nitrogen concentrations than the plants grown in the ambient CO_2 chambers under the low N fertilization regime; but this was not the case under the high N regime. They also discovered that older larvae fed with foliage grown in elevated CO_2 with low N fertilization consumed significantly more plant material than insects fed with foliage grown in ambient CO_2; but, again, no differences were observed with high N fertilization. Last, and "consistent with the effect of higher Bt toxin intake due to enhanced consumption," they found that "insects fed on low N plants had significantly higher mortality in elevated CO_2." Yet, again, no such effect was evident in the high N treatment. Consequently, with respect to pest management using Bt-produced toxins supplied to crops via foliar application, Coviella and Trumble concluded that "increasing atmospheric CO_2 is making the foliar applications more efficacious."

Coviella *et al*. (2000), in an analogous experiment to that of Coviella and Trumble, grew cotton plants in 12 Teflon-film chambers in a temperature-controlled greenhouse, where six chambers were maintained at an atmospheric CO_2 concentration of 370 ppm and six were maintained at 900 ppm CO_2. Half of the cotton plants in each of these chambers were of a transgenic line containing the Bt gene for the production of the Cry1Ac toxin, which is mildly toxic for *Spodoptera exigua*, while the other half were of a near isogenic line without the Bt gene. In addition, and as before, half of the plants in each chamber received the same low and high levels of N fertilization; and between 40 and 45 days after emergence, leaves were removed from the plants and fed to the *S. exigua* larvae, after which a number of larval responses were measured and analyzed, along with various leaf properties.

This work revealed that the low-N plants in the elevated CO_2 treatment had lower foliar N concentrations than did the low-N plants in the ambient CO_2 treatment, and that the transgenic plants from the low-N, high CO_2 treatment produced lower levels of Bt toxin than did the transgenic plants from the low-N, ambient CO_2 treatment. In addition, the high level of N fertilization only partially compensated for this latter high-CO_2 effect. In the ambient CO_2 treatment there was also a significant increase in days to pupation for insects fed transgenic plants; but this difference was not evident in elevated CO_2. In addition, pupal weight in ambient CO_2 was significantly higher in non-transgenic plants; and, again, this difference was not observed in elevated CO_2.

In discussing their findings, the three researchers wrote that "these results support the hypothesis that the lower N content per unit of plant tissue caused by the elevated CO_2 will result in lower toxin production by transgenic plants when nitrogen supply to the plants is a limiting factor." They also note that "elevated CO_2 appears to eliminate differences between transgenic and non-transgenic plants for some key insect developmental/fitness variables including length of the larval stage and pupal weight."

These findings suggest that in the case of inadvertent Bt gene transference to wild relatives of transgenic crop lines, elevated levels of atmospheric CO_2 will tend to negate certain of the negative effects the wayward genes might otherwise inflict on the natural world. Hence, the ongoing rise in the air's CO_2 content could be said to constitute an "insurance policy" against this potential outcome.

On the other hand, Coviella *et al.*'s results also suggest that transgenic crops designed to produce Bt-type toxins may become less effective in carrying out the objectives of their design as the air's CO_2 content continues to rise. Coupling this possibility with the fact that the *foliar* application of *Bacillus thuringiensis* to crops should become even more effective in a higher-CO_2 world, as found by Coviella and Trumble, one could argue that the implantation of toxin-producing genes in crops is not the way to go in the face of the ongoing rise in the air's CO_2 content, which reduces that technique's effectiveness at the same time that it increases the effectiveness of direct foliar applications.

In a study of three different types of rice—a wild type (WT) and two transgenic varieties, one with 65 percent wild-type Rubisco (AS-77) and one with 40 percent wild-type Rubisco (AS-71)—Makino *et al.* (2000) grew plants from seed for 70 days in growth chambers maintained at 360 and 1000 ppm CO_2, after which they harvested the plants and determined their biomass. In doing so, they found that the mean dry weights of the WT, AS-77 and AS-71 varieties grown in air of 360 ppm were, respectively, 5.75, 3.02 and 0.83 g, while in air of 1000 ppm CO_2, corresponding mean dry weights were 7.90, 7.40 and 5.65 g. Consequently, although the growth rates of the genetically engineered rice plants were inferior to that of the wild type when grown in normal air of 360 ppm CO_2 (with AS-71 producing less than 15 percent as much biomass as the wild type), when grown in air of 1000 ppm CO_2 they experienced greater CO_2-induced increases in growth: a 145 percent increase in the case of AS-77 and a 581 percent increase in the case of AS-71. Hence, whereas the transgenic plants were highly disadvantaged in normal air of 360 ppm CO_2 (with AS-71 plants attaining a mean dry weight of only 0.83 g while the WT plants attained a mean dry weight of 5.75 g), they were found to be pretty much on an equal footing in highly CO_2-enriched air (with AS-71 plants attaining a mean dry weight of 5.65 g while the WT plants attained a mean dry weight of 7.90 g). This finding bodes well for the application of this type of technology to rice crops in a future world of higher atmospheric CO_2 content.

Returning to cotton, Chen *et al.* (2005) grew well watered and fertilized plants of two varieties—one expressing Cry1A (c) genes from *Bacillus thurigiensis* and a non-transgenic cultivar from the same recurrent parent—in pots placed within open-top chambers maintained at either 375 or 750 ppm CO_2 in Sanhe County, Hebei Province, China, from planting in mid-May to harvest in October, throughout which period several immature bolls were collected and analyzed for various chemical characteristics, while others were stored under refrigerated conditions for later feeding to cotton bollworm larvae, whose growth characteristics were closely were monitored. In pursuing this protocol, the five researchers found that the elevated CO_2 treatment increased immature boll concentrations of condensed tannins by approximately 22 percent and 26 percent in transgenic and non-transgenetic cotton, respectively (see Tannins in Section 7.8.7. for a discussion of the significance of this observation). In addition, they found that elevated CO_2 slightly decreased the body biomass of the cotton bollworms and reduced moth fecundity. The Bt treatment was even more effective in this regard, and in the combined Bt-high-CO_2 treatment, the negative cotton bollworm responses were expressed most strongly of all. Chen *et al*. concluded that the expected higher atmospheric CO_2 concentrations of the future will "either not change or only slightly enhance the efficacy of Bt technology against cotton bollworms."

Two years later, Chen *et al*. (2007) reported growing the same two cultivars under the same conditions from the time of planting on 10 May 2004 until the plants were harvested in October, after which egg masses of the cotton bollworms were reared in a growth chamber under ambient-CO_2 conditions, while three successive generations of them were fed either transgenic or non-transgenic cotton bolls from plants grown in either ambient or twice-ambient atmospheric CO_2 concentrations, during which time a number of physiological characteristics of the cotton bollworms were periodically assessed. This work revealed, in the words of Chen *et al*., that "both elevated CO_2 and transgenic Bt cotton increased larval lifespan," but that they decreased "pupal weight, survival rate, fecundity, frass output, relative and mean relative growth rates, and the efficiency of conversion of ingested and digested food." As a result, they say that "transgenic Bt cotton significantly decreased the population-trend index compared to non-transgenic cotton for the three successive bollworm generations, *especially at elevated CO_2* [our italics]."

Based on these findings, the four researchers concluded that the negative effects of elevated CO_2 on cotton bollworm physiology and population dynamics "may intensify through successive generations," in agreement with the findings of Brooks and Whittaker (1998, 1999) and Wu *et al*. (2006). They additionally concluded that "both elevated CO_2 and transgenic Bt cotton are adverse environmental factors for cotton bollworm long-term population growth," and that the combination of the two factors may intensify their adverse impact on the population performance of the cotton bollworm, which would be good news for cotton growers.

Fu *et al*. (2008) note that "heat stress is a major constraint to wheat production and negatively impacts grain quality, causing tremendous economic losses, and may become a more troublesome factor due to global warming." Consequently, as they describe it, they "introduced into wheat the maize gene coding for plastidal EF-Tu [protein synthesis elongation factor]," in order to assess "the expression of the transgene, and its effect on thermal aggregation of leaf proteins in transgenic plants," as well as "the heat stability of photosynthetic membranes (thylakoids) and the rate of CO_2 fixation in young transgenic plants following exposure to heat stress." These operations led, in their words, "to improved protection of leaf proteins against thermal aggregation, reduced damage to thylakoid membranes and enhanced photosynthetic capability following exposure to heat stress," which results "support the concept that EF-Tu ameliorates negative effects of heat stress by acting as a molecular chaperone."

Fu *et al*. describe their work as "the first demonstration that a gene other than HSP [heat shock protein] gene can be used for improvement of heat tolerance," noting it also indicates that the improvement is possible in a species that has a complex genome, such as hexaploid wheat. They conclude by stating their results "strongly suggest that heat tolerance of wheat, and possibly other crop plants, can be improved by modulating expression of plastidal EF-Tu and/or by selection of genotypes with increased endogenous levels of this protein."

In summary, genetic alterations to crop plants enable them to better withstand the assaults of insects pests or increases in seasonal maximum air temperates. Elevated CO_2 either improves or does not change the effectiveness of genetic alternatives to achieve these objectives, while it simultaneously reduces the severity of possible negative effects that could arise from the escape of transplanted genes into the natural environment.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/t/summaries/transgenicplants.php.

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7.8.9. Isoprene

Isoprene (C_5H_8 or 2-methyl-1,3-butadiene) is a highly reactive non-methane hydrocarbon (NMHC) that is emitted in copious quantities by vegetation and is responsible for the production of vast amounts of tropospheric ozone (Chameides *et al*., 1988; Harley *et al*., 1999), which is a debilitating scourge of plant and animal life alike. Poisson *et al*. (2000) calculate that current levels of NMHC emissions—the vast majority of which are isoprene, accounting for more than twice as much as all other NMHCs combined—may increase surface ozone concentrations by up to 40 percent in the marine boundary-layer and 50-60 percent over land. They further estimate that the current tropospheric ozone content extends the atmospheric lifetime of methane—one of the world's most powerful greenhouse gases—by approximately 14 percent. Consequently, it can be appreciated that reducing isoprene emissions from vegetation is to be desired.

Although a few experiments conducted on certain plant species have suggested that elevated concentrations of atmospheric CO_2 have little to no effect on their emissions of isoprene (Buckley, 2001; Baraldi *et al*., 2004; Rapparini *et al*., 2004), a much larger number of other experiments are suggestive of substantial CO_2-induced reductions in isoprene emissions, as demonstrated by the work of Monson and Fall (1989), Loreto and Sharkey (1990), Sharkey *et al*. (1991) and Loreto *et al*. (2001).

Rosentiel *et al*. (2003) studied three 50-tree cottonwood plantations growing in separate mesocosms within the forestry section of the Biosphere 2 facility near Oracle, Arizona, USA, one of which mesocosms was maintained at an atmospheric CO_2 concentration of 430 ppm, while the other two were enriched to concentrations of 800 and 1200 ppm for one entire growing season. Integrated over that period, the total above-ground biomass of the trees in the latter two mesocosms was increased by 60 percent and 82 percent, respectively, while their production of isoprene was decreased by 21 percent and 41 percent, respectively.

Scholefield *et al*. (2004) measured isoprene emissions from *Phragmites australis* plants (one of the world's most important natural grasses) growing at different distances from a natural CO_2 spring in central Italy. At the specific locations they chose to make their measurements, atmospheric CO_2 concentrations of approximately 350, 400, 550 and 800 ppm had likely prevailed for the entire lifetimes of the plants. Across this CO_2 gradient, plant isoprene emissions dropped ever lower as the air's CO_2 concentration rose ever higher. Over the first 50-ppm CO_2 increase, isoprene emissions were reduced to approximately 65 percent of what they were at ambient CO_2, while for CO_2 increases of 200 and 450 ppm, they were reduced to only about 30 percent and 7 percent of what they were in the 350-ppm-CO_2 air. The researchers note that these reductions were likely caused by reductions in leaf isoprene synthase, which was observed to be highly correlated with isoprene emissions, leading them to conclude that "elevated CO_2 generally inhibits the expression of isoprenoid synthesis genes and isoprene synthase activity which may, in turn, limit formation of every chloroplast-derived isoprenoid." They state that the "basal emission rate of isoprene is likely to be reduced under future elevated CO_2 levels."

Centritto *et al*. (2004) grew hybrid poplar saplings for one full growing season in a FACE facility located at Rapolano, Italy, where the air's CO_2 concentration was increased by approximately 200 ppm. Their study demonstrated that "isoprene emission is reduced in elevated CO_2, in terms of both maximum values of isoprene emission rate and isoprene emission per unit of leaf area averaged across the total number of leaves per plant," which in their case amounted to a reduction of approximately 34 percent. When isoprene emission was summed over the entire plant profile, however, the reduction was not nearly so great (only 6 percent), because of the greater number of leaves on the CO_2-enriched saplings. "However," as they state, "Centritto *et al*. (1999), in a study with potted cherry seedlings grown in open-top chambers, and Gielen *et al*. (2001), in a study with poplar saplings exposed to FACE, showed that the stimulation of total leaf area in response to elevated CO_2 was a transient effect, because it occurred only during the first year of growth." Hence, they concluded "it may be expected that with similar levels of leaf area, the integrated emission of isoprene would have been much lower in elevated CO_2." Indeed, they say that their data, "as well as that reported by Scholefield *et al*. (2004), in a companion experiment on *Phragmites* growing in a nearby CO_2 spring, mostly confirm that isoprene emission is inversely dependent on CO_2 [concentration] when this is above ambient, and suggests that a lower fraction of C will be re-emitted in the atmosphere as isoprene by single leaves in the future."

Working at another FACE facility, the Aspen FACE facility near Rhinelander, Wisconsin, USA, Calfapietra *et al*. (2008) measured emissions of isoprene from sun-exposed upper-canopy leaves of an O_3-tolerant clone and an O_3-sensitive clone of trembling aspen (*Populus tremuloides* Michx.) trees that were growing in either normal ambient air, air enriched with an extra 190-200 ppm CO_2, air with 1.5 times the normal ozone concentration, or air simultaneously enriched with the identical concentrations of both of these atmospheric trace gases. Results of their analysis showed that for the trees growing in air of ambient ozone concentration, the extra 190 ppm of CO_2 decreased the mean isoprene emission rate by 11.7 percent in the O_3-tolerant aspen clone and by 22.7 percent in the O_3-sensitive clone, while for the trees growing in air with 1.5 times the ambient ozone concentration, the extra CO_2 also decreased the mean isoprene emission rate by 10.4 percent in the O_3-tolerant clone and by 32.7 percent in the O_3-sensitive clone. At the same time, and in the same order, net photosynthesis rates were increased by 34.9 percent, 47.4 percent, 31.6 percent and 18.9 percent.

Possell *et al*. (2004) grew seedlings of English oak (*Quercus robur*), one to a mesocosm (16 cm diameter, 60 cm deep), in either fertilized or unfertilized soil in *solardomes* maintained at atmospheric CO_2 concentrations of either ambient or ambient plus 300 ppm for one full year, at the conclusion of which period they measured rates of isoprene emissions from the trees' foliage together with their rates of photosynthesis. In the unfertilized trees, this work revealed that the 300-ppm increase in the air's CO_2 concentration reduced isoprene emissions by 63 percent on a leaf area basis and 64 percent on a biomass basis, while in the fertilized trees the extra CO_2 reduced isoprene emissions by 70 percent on a leaf area basis and 74 percent on a biomass basis. In addition, the extra CO_2 boosted leaf photosynthesis rates by 17 percent in the unfertilized trees and 13 percent in the fertilized trees.

Possell *et al*. (2005) performed multiple three-week-long experiments with two known isoprene-emitting herbaceous species (*Mucuna pruriens* and *Arundo donax*), which they grew in controlled environment chambers that were maintained at two different sets of day/night temperatures (29/24°C and 24/18°C) and atmospheric CO_2 concentrations characteristic of glacial (180 ppm), pre-industrial (280 ppm) and current (366 ppm) conditions, where canopy isoprene emission rates were measured on the final day of each experiment. They obtained what they describe as "the first empirical evidence for the enhancement of isoprene production, on a unit leaf area basis, by plants that grew and developed in [a] CO_2-depleted atmosphere," which results, in their words, "support earlier findings from short-term studies with woody species (Monson and Fall, 1989; Loreto and Sharkey, 1990)." Then, combining their emission rate data with those of Rosenstiel *et al*. (2003) for *Populus deltoides*, Centritto *et al*. (2004) for *Populus x euroamericana* and Scholefield *et al*. (2004) for *Phragmites australis*, they developed a single downward-trending isoprene emissions curve that stretches all the way from 180 to 1200 ppm CO_2, where it asymptotically approaches a value that is an order of magnitude less than what it is at 180 ppm.

Working at the Biosphere 2 facility near Oracle, Arizona, USA, in enclosed ultraviolet light-depleted mesocosms (to minimize isoprene depletion by atmospheric oxidative reactions such as those involving OH), Pegoraro *et al*. (2005) studied the effects of atmospheric CO_2 enrichment (1200 ppm compared to an ambient concentration of 430 ppm) and drought on the emission of isoprene from cottonwood (*Populus deltoides* Bartr.) foliage and its absorption by the underlying soil for both well-watered and drought conditions. In doing so, they found that "under well-watered conditions in the agriforest stands, gross isoprene production (i.e., the total production flux minus the soil uptake) was inhibited by elevated CO_2 and the highest emission fluxes of isoprene were attained in the lowest CO_2 treatment." In more quantitative terms, it was determined that the elevated CO_2 treatment resulted in a 46 percent reduction in gross isoprene production. In addition, it was found that drought suppressed the isoprene sink capacity of the soil beneath the trees, but that "the full sink capacity of dry soil was recovered within a few hours upon rewetting."

Putting a slightly negative slant on their findings, Pegoraro *et al*. suggested that "in future, potentially hotter, drier environments, higher CO_2 may not mitigate isoprene emission as much as previously suggested." However, we note that climate models generally predict an intensification of the hydrologic cycle in response to rising atmospheric CO_2 concentrations, and that the anti-transpirant effect of atmospheric CO_2 enrichment typically leads to increases in the moisture contents of soils beneath vegetation. Also, we note that over the latter decades of the twentieth century, when the IPCC claims the earth warmed at a rate and to a level that were unprecedented over the past two millennia, soil moisture data from all around the world tended to display upward trends. Robock *et al*. (2000), for example, developed a massive collection of soil moisture data from over 600 stations spread across a variety of climatic regimes, including the former Soviet Union, China, Mongolia, India and the United States, determining that "In contrast to predictions of summer desiccation with increasing temperatures, for the stations with the longest records, summer soil moisture in the top 1 m has increased while temperatures have risen." And in a subsequent study of "45 years of gravimetrically observed plant available soil moisture for the top 1 m of soil, observed every 10 days for April-October for 141 stations from fields with either winter or spring cereals from the Ukraine for 1958-2002," Robock *et al*. (2005) discovered that these real-world observations "show a positive soil moisture trend for the entire period of observation," noting that "even though for the entire period there is a small upward trend in temperature and a downward trend in summer precipitation, the soil moisture still has an upward trend for both winter and summer cereals." Consequently, in a CO_2-enriched world of the future, we likely will have the best of both aspects of isoprene activity: less production by vegetation and more consumption by soils.

Finally, we address the issue of how well models predict the response of isoprene emission to future global change. According to Monson *et al*. (2007) such predictions "probably contain large errors," which clearly need to be corrected. The reason for the errors, write the twelve researchers who conducted the study, is that "the fundamental logic of such models is that changes in NPP [net primary production] will produce more or less biomass capable of emitting isoprene, and changes in climate will stimulate or inhibit emissions per unit of biomass." They continue, "these models tend to ignore the discovery that there are direct effects of changes in the atmospheric CO_2 concentration on isoprene emission that tend to work in the opposite direction to that of stimulated NPP," as has been indicated in the research studies described above. Their results showed, in their words, "that growth in an atmosphere of elevated CO_2 inhibited the emission of isoprene at levels that completely compensate for possible increases in emission due to increases in aboveground NPP."

In lamenting this sorry state of global-change modeling, Monson *et al*. say that, "to a large extent, the modeling has 'raced ahead' of our mechanistic understanding of how isoprene emissions will respond to the fundamental drivers of global change," and that "without inclusion of these effects in the current array of models being used to predict changes in atmospheric chemistry due to global change, one has to question the relevance of the predictions."

A year later, Arneth *et al*. (2008) used a mechanistic isoprene-dynamic vegetation model of European woody vegetation to "investigate the interactive effects of climate and CO_2 concentration on forest productivity, species composition, and isoprene emissions for the periods 1981-2000 and 2081-2100," which included a parameterization of the now-well-established direct CO_2-isoprene inhibition phenomenon we have described in the papers above. The study found that "across the model domain," the CO_2-isoprene inhibition effect "has the potential to offset the stimulation of [isoprene] emissions that could be expected from warmer temperatures and from the increased productivity and leaf area of emitting vegetation."

In view of these findings, it appears the ongoing rise in the atmosphere's CO_2 concentration will lead to ever greater reductions in atmospheric isoprene concentrations. As noted in the introductory paragraph of this section, such a consequence would be welcome news for man and nature.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/i/isoprene.php.

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7.8.10. Microorganisms

Plants grown in CO_2-enriched atmospheres nearly always exhibit increased photosynthetic rates and biomass production. Due to this productivity enhancement, more plant material is typically added to soils from root growth, turnover and exudation, as well as from leaves and stems following their abscission and falling to the ground during senescence. Such additions of carbon onto and into soils often serve as the only carbon source for supporting the development and growth of microorganisms in terrestrial habitats. Thus, it is important to understand how CO_2-induced increases in plant growth affect microorganisms, a topic omitted from discussion by the IPCC.

Several studies have shown that atmospheric CO_2 enrichment does not significantly impact soil microorganisms. Zak *et al.* (2000), for example, observed no significant differences in soil microbial biomass beneath aspen seedlings grown at 350 and 700 ppm CO_2 after 2.5 years of differential treatment. Likewise, in the cases of Griffiths *et al.* (1998) and Insam *et al.* (1999), neither research team reported any changes in microbial community structure beneath ryegrass and artificial tropical ecosystems, respectively, after subjecting them to atmospheric CO_2 enrichment.

Other studies, however, have found that elevated CO_2 can significantly affect soil microorganisms. Van Ginkel and Gorissen (1998) observed that three months of elevated CO_2 exposure (700 ppm) increased soil microbial biomass beneath ryegrass plants by 42 percent relative to that produced under ambient CO_2 conditions, as did Van Ginkel *et al.* (2000). Likewise, soil microbial biomass was reported to increase by 15 percent beneath agricultural fields subjected to a two-year wheat-soybean crop rotation (Islam *et al.*, 2000). In a study by Marilley *et al.* (1999), atmospheric CO_2 enrichment significantly increased bacterial numbers in the rhizospheres beneath ryegrass and white clover monocultures. Similarly, Lussenhop *et al.* (1998) reported CO_2-induced increases in the amounts of bacteria, protozoa, and microarthropods in soils that had supported regenerating poplar tree cuttings for five months. In addition, Hungate *et al.* (2000) reported that twice-ambient CO_2 concentrations significantly increased the biomass of active fungal organisms and flagellated protozoa beneath serpentine and sandstone grasslands after four years of treatment exposure.

In taking a closer look at the study of Marilley *et al.* (1999), it is evident that elevated CO_2 caused shifts in soil microbial populations. In soils beneath their leguminous white clover, for example, elevated CO_2 favored shifts towards *Rhizobium* bacterial species, which likely increased nitrogen availability—via nitrogen fixation—to support enhanced plant growth. However, in soils beneath non-leguminous ryegrass monocultures, which do not form symbiotic relationships with *Rhizobium* species, elevated CO_2 favored shifts towards *Pseudomonas* species, which likely acquired nutrients to support enhanced plant growth through mechanisms other than nitrogen fixation. Nonetheless, in both situations, the authors observed CO_2-induced shifts in bacterial populations that would likely optimize nutrient acquisition for specific host plant species.

In an unrelated study, Montealegre *et al.* (2000) reported that elevated CO_2 acted as a selective agent among 120 different isolates of *Rhizobium* growing beneath white clover plants. Specifically, when bacterial strains favored by ambient and elevated CO_2 concentrations were mixed together and grown with white clover at an atmospheric CO_2 concentration of 600 ppm, 17 percent more root nodules were formed by isolates previously determined to be favored by elevated CO_2.

Hu *et al.* (2001) subjected fertile sandstone grasslands to five years of twice-ambient CO_2 concentrations and found they exhibited increased soil microbial biomass while simultaneously enhancing plant nitrogen uptake. The net effect of these phenomena reduced nitrogen availability for microbial use, which consequently decreased microbial respiration and, hence, microbial decomposition. Consequently, these ecosystems displayed CO_2-induced increases in net carbon accumulation. Similarly, Williams *et al*. (2000) reported that microbial biomass carbon increased by 4 percent in a tallgrass prairie after five years exposure to twice-ambient CO_2 concentrations, which contributed to a total soil carbon enhancement of 8 percent.

In summation, as the CO_2 content of the air continues to rise, earth's vegetation will likely respond with increasing photosynthetic rates and biomass production, returning more organic carbon to the soil where it will be utilized by microbial organisms to maintain or increase their population numbers, biomass and heterotrophic activities (Weihong *et al*., 2000; Arnone and Bohlen, 1998). Shifts in microbial community structure may occur that will favor the intricate relationships that currently exist between leguminous and non-leguminous plants and the specific microorganisms upon which they depend.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/m/microorganisms.php.

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7.8.11. Worms

Perhaps the best known worm in the world is the common earthworm. How will it be affected as the air's CO_2 content continues to climb, and how will its various responses affect the biosphere? What about other worms? How will they fare in a CO_2-enriched world of the future, and what will be the results of their responses?

"Earthworms," in the words of Edwards (1988), "play a major role in improving and maintaining the fertility, structure, aeration and drainage of agricultural soils." As noted by Sharpley *et al*. (1988), "by ingestion and digestion of plant residue and subsequent egestion of cast material, earthworms can redistribute nutrients in a soil and enhance enzyme activity, thereby increasing plant availability of both soil and plant residue nutrients," as others have also demonstrated (Bertsch *et al*., 1988; McCabe *et al*., 1988; Zachmann and Molina, 1988). Kemper (1988) describes how "burrows opened to the surface by surface-feeding worms provide drainage for water accumulating on the surface during intense rainfall," noting that "the highly compacted soil surrounding the expanded burrows has low permeability to water which often allows water to flow through these holes for a meter or so before it is sorbed into the surrounding soil."

Hall and Dudas (1988) report that the presence of earthworms appears to mitigate the deleterious effects of certain soil toxins. Logsdon and Linden (1988) describe a number of other beneficial effects of earthworms, including (1) enhancement of soil aeration, since under wet conditions earthworm channels do not swell shut as many soil cracks do, (2) enhancement of soil water uptake, since roots can explore deeper soil layers by following earthworm channels, and (3) enhancement of nutrient uptake, since earthworm casts and channel walls have a more neutral pH and higher available nutrient level than bulk soil. Hence, we should care about what happens to earthworms as the air's CO_2 content rises because of the many important services they provide for earth's plant life.

Edwards (1988) says "the most important factor in maintaining good earthworm populations in agricultural soils is that there be adequate availability of organic matter," while Hendrix *et al*. (1988) and Kladivko (1988) report that greater levels of plant productivity promote greater levels of earthworm activity. Consequently, since the most ubiquitous and powerful effect of atmospheric CO_2 enrichment is its stimulation of plant productivity, which leads to enhanced organic matter delivery to soils, it logically follows that this aerial fertilization effect of the ongoing rise in the air's CO_2 content should increase earthworm populations and amplify the many beneficial services they provide for plants.

The second most significant and common effect of atmospheric CO_2 enrichment on plants is its antitranspirant effect, whereby elevated levels of atmospheric CO_2 reduce leaf stomatal apertures and slow the rate of evaporative water loss from the vast bulk of earth's vegetation. Both growth chamber studies and field experiments that have studied this phenomenon provide voluminous evidence that it often leads to increased soil water contents in many terrestrial ecosystems, which also benefits earthworm populations.

Zaller and Arnone (1997) fumigated open-top and -bottom chambers in a calcareous grassland near Basal, Switzerland with air of either 350 or 600 ppm CO_2 for an entire growing season. They found that the mean annual soil moisture content in the CO_2-enriched chambers was 10 percent greater than that observed in the ambient-air chambers, and because rates of surface cast production by earthworms are typically positively correlated with soil moisture content, they found that cumulative surface cast production after only one year was 35 percent greater in the CO_2-enriched chambers than in the control chambers. In addition, because earthworm casts are rich in organic carbon and nitrogen, the cumulative amount of these important nutrients on a per-land-area basis was found to be 28 percent greater in the CO_2-enriched chambers than it was in the ambient-air chambers. In a subsequent study of the same grassland, Zaller and Arnone (1999) found that plants growing in close proximity to the earthworm casts produced more biomass than similar plants growing further away from them. They also found that the CO_2-induced growth stimulation experienced by the various grasses was also greater for those plants growing nearer the earthworm casts.

These various observations suggest that atmospheric CO_2 enrichment sets in motion a self-enhancing cycle of positive biological phenomena, whereby increases in the air's CO_2 content (1) stimulate plant productivity and (2) reduce plant evaporative water loss, which results in (3) more organic matter entering the soil and (4) a longer soil moisture retention time and/or greater soil water contents, all of which factors lead to (5) the development of larger and more active earthworm populations, which (6) enhance many important soil properties, including fertility, structure, aeration and drainage, which improved properties (7) further enhance the growth of the plants whose CO_2-induced increase in productivity was the factor that started the whole series of processes in the first place.

More earthworms also can increase soil's ability to sequester carbon. As Jongmans *et al*. (2003) point out, "the rate of organic matter decomposition can be decreased in worm casts compared to bulk soil aggregates (Martin, 1991; Haynes and Fraser, 1998)." On the basis of these studies and their own micromorphological investigation of structural development and organic matter distribution in two calcareous marine loam soils on which pear trees had been grown for 45 years (one of which soils exhibited little to no earthworm activity and one of which exhibited high earthworm activity, due to different levels of heavy metal contamination of the soils as a consequence of the prior use of different amounts of fungicides), they concluded that "earthworms play an important role in the intimate mixing of organic residues and fine mineral soil particles and the formation of organic matter-rich micro-aggregates and can, therefore, contribute to physical protection of organic matter, thereby slowing down organic matter turnover and increasing the soil's potential for carbon sequestration." Put more simply, atmospheric CO_2 enrichment that stimulates the activity of earthworms also leads to more—and more secure—sequestration of carbon in earth's soils.

Don *et al.* (2008) studied the effects of anecic earthworms—which generally inhabit a single vertical burrow throughout their entire lives that can be as much as five meters in depth, but is generally in the range of one to two meters—on soil carbon stocks and turnover via analyses of enzyme activity, stable isotopes, nuclear magnetic resonance spectroscopy, and the ^{14}C age of their burrow linings. The results of their study indicated that "the carbon distribution in soils is changed by anecic earthworms' activity with more carbon stored in the subsoil where earthworms slightly increase the carbon stocks." In this regard they also state that "the translocation of carbon from [the] organic layer to the subsoil will decrease the carbon vulnerability to mineralization," since "carbon in the organic layer and the surface soil is much more prone to disturbances with rapid carbon loss than subsoil carbon."

Bossuyt *et al.* (2005) conducted a pair of experiments designed to investigate "at what scale and how quickly earthworms manage to protect SOM [soil organic matter]." In the first experiment, soil aggregate size distribution together with total C and ^{13}C were measured in three treatments—control soil, soil + ^{13}C-labeled sorghum leaf residue, and soil + ^{13}C-labeled residue + earthworms—after a period of 20 days incubation, where earthworms were added after the eighth day. In the second experiment, they determined the protected C and ^{13}C pools inside the newly formed casts and macro- and micro-soil-aggregates. Results indicated that the proportion of large water-stable macroaggregates was on average 3.6 times greater in the soil-residue samples that contained earthworms than in those that lacked earthworms, and that the macroaggregates in the earthworm treatment contained approximately three times more sequestered carbon. What is more, the earthworms were found to form "a significant pool of protected C in microaggregates within large macroaggregates after 12 days of incubation," thereby demonstrating the rapidity with which earthworms perform their vital function of sequestering carbon in soils when plant residues become available to them.

Cole *et al.* (2002) report that "in the peatlands of northern England, which are classified as blanket peat, it has been suggested that the potential effects of global warming on carbon and nutrient dynamics will be related to the activities of dominant soil fauna, and especially enchytraeid worms." In harmony with these ideas, Cole *et al.* say they "hypothesized" that warming would lead to increased enchytraeid worm activity, which would lead to higher grazing pressure on microbes in the soil; and since enchytraeid grazing has been observed to enhance microbial activity (Cole *et al.*, 2000), they further hypothesized that more carbon would be liberated in dissolved organic form, "supporting the view that global warming will increase carbon loss from blanket peat ecosystems."

The scientists next describe how they constructed small microcosms from soil and litter they collected near the summit of Great Dun Fell, Cumbria, England. Subsequent to "defaunating" this material by reducing its temperature to -80°C for 24 hours, they thawed and inoculated it with native soil microbes, after which half of the microcosms were incubated in the dark at 12°C and half at 18°C, the former of which temperatures was approximately equal to mean August soil temperature at a depth of 10 cm at the site of soil collection, while the latter was said by them to be "close to model predictions for soil warming that might result from a doubling of CO_2 in blanket peat environments."

Ten seedlings of an indigenous grass of blanket peat were then transplanted into each of the microcosms, while 100 enchytraeid worms were added to each of half of the mini-ecosystems. These procedures resulted in the creation of four experimental treatments: ambient temperature, ambient temperature + enchytraeid worms, elevated temperature, and elevated temperature + enchytraeid worms. The resulting 48 microcosms—sufficient to destructively harvest three replicates of each treatment four different times throughout the course of the 64-day experiment—were arranged in a fully randomized design and maintained at either 12 or 18°C with alternating 12-hour light and dark periods. In addition, throughout the entire course of the study, the microcosms were given distilled water every two days to maintain their original weights.

So what did the researchers find? First, and contrary to their hypothesis, elevated temperature reduced the ability of the enchytraeid worms to enhance the loss of carbon from the microcosms. At the normal ambient temperature, for example, the presence of the worms enhanced dissolved organic carbon (DOC) loss by 16 percent, while at the elevated temperature expected for a doubling of the air's CO_2 content, the worms had no effect at all on DOC. In addition, Cole *et al*. note that "warming may cause drying at the soil surface, forcing enchytraeids to burrow to deeper subsurface horizons." Hence, since the worms are known to have little influence on soil carbon dynamics below a depth of 4 cm (Cole *et al*., 2000), they concluded that this additional consequence of warming would further reduce the ability of enchytraeids to enhance carbon loss from blanket peatlands.

In summarizing their findings, Cole *et al*. say that "the soil biotic response to warming in this study was negative." That is, it was of such a nature that it resulted in a reduced loss of carbon to the atmosphere, which would tend to slow the rate of rise of the air's CO_2 content, just as was suggested by the results of the study of Jongmans *et al*.

Yeates *et al*. (2003) report results from a season-long FACE study of a 30-year-old New Zealand pasture, where three experimental plots had been maintained at the ambient atmospheric CO_2 concentration of 360 ppm and three others at a concentration of 475 ppm (a CO_2 enhancement of only 32 percent) for a period of four to five years. The pasture contained about twenty species of plants, including C_3 and C_4 grasses, legumes and forbs. Nematode, or "roundworm," populations increased significantly in response to the 32 percent increase in the air's CO_2 concentration. Of the various feeding groups studied, Yeates *et al*. report that the relative increase "was lowest in bacterial-feeders (27%), slightly higher in plant (root) feeders (32%), while those with delicate stylets (or narrow lumens; plant-associated, fungal-feeding) increased more (52% and 57%, respectively)." The greatest nematode increases were recorded among omnivores (97 percent) and predators (105 percent). Most dramatic of all, root-feeding populations of the *Longidorus* nematode taxon rose by 330 percent. Also increasing in abundance were earthworms: *Aporrectodea caliginosa* by 25 percent and *Lumbricus rubellus* by 58 percent. Enchytraeids, on the other hand, decreased in abundance, by approximately 30 percent.

With respect to earthworms, Yeates *et al*. note that just as was found in the studies cited in the first part of this review, the introduction of lumbricids has been demonstrated to improve soil conditions in New Zealand pastures (Stockdill, 1982), which benefits pasture plants. Hence, the CO_2-induced increase in earthworm numbers observed in Yeates *et al*.'s study would be expected to do more of the same, while the reduced abundance of enchytraeids they documented in the CO_2-enriched pasture would supposedly lead to less carbon being released to the air from the soil, as per the known ability of enchytraeids to promote carbon loss from British peat lands under current temperatures.

In summary, the lowly earthworm and still lowlier soil nematodes respond to increases in the air's CO_2 content via a number of plant-mediated phenomena in ways that further enhance the positive effects of atmospheric CO_2 enrichment on plant growth and development, while at the same time helping to sequester more carbon more securely in the soil.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/e/earthworms.php.

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7.9. Greening of the Earth

More than two decades ago, Idso (1986) published a small item in *Nature* advancing the idea that the aerial fertilization effect of the CO_2 that is liberated by the burning of coal, gas and oil was destined to dramatically enhance the productivity of earth's vegetation. In a little book he had published four years earlier (Idso, 1982), he had predicted that "CO_2 effects on both the managed and unmanaged biosphere will be overwhelmingly positive." In a monograph based on a lecture he gave nine years later (Idso, 1995), he said "we appear to be experiencing the initial stages of what could truly be called a *rebirth of the biosphere*, the beginnings of a biological rejuvenation that is without precedent in all of human history."

In light of the fact that Idso's worldview is nearly the exact opposite of the apocalyptic vision promulgated by the IPCC, it is instructive to see what real-world observations reveal about the matter. In this section we review studies that show a CO_2-induced greening of Africa, Asia, Europe, North America, the oceans, and the entire globe.

Additional information on this topic, including reviews not discussed here, can be found at http://www.co2science.org/subject/g/subject_g.php under the heading Greening of the Earth.

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7.9.1. Africa

In an article by Fred Pearce that was posted on the website of *New Scientist* magazine on 16 September 2002 titled "Africa's deserts are in 'spectacular' retreat," we were told the story of vegetation reclaiming great tracts of barren land across the entire southern edge of the Sahara. This information likely came as a bit of a surprise to many, since the United Nations Environment Program had reported to the World Summit on Sustainable Development in Johannesburg, South Africa in August of that year that over 45 percent of the continent was experiencing severe desertification. The world of nature, however, told a vastly different story.

Pearce began by stating "the southern Saharan desert is in retreat, making farming viable again in what were some of the most arid parts of Africa," noting that "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."

The good news was not confined to Burkina Faso. "Vegetation," according to Pearce, "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." Besides being widespread in space, the greening was widespread in time, having been happening since at least the mid-1980s.

Quoting Chris Reij of the Free University of Amsterdam, Pearce wrote that "aerial photographs taken in June show 'quite spectacular regeneration of vegetation' in northern Burkina Faso." The data indicated the presence of more trees for firewood and more grassland for livestock. In addition, a survey that Reij was collating showed, according to Pearce, "a 70% increase in yields of local cereals such as sorghum and millet in one province in recent years." Also studying the area was Kjeld Rasmussen of the University of Copenhagen, who reported that since the 1980s there had been a "steady reduction in bare ground" with "vegetation cover, including bushes and trees, on the increase on the dunes."

Pearce also reported on the work of a team of geographers from Britain, Sweden and Denmark that had spent much of the prior summer analyzing archived satellite images of the Sahel. Citing Andrew Warren of University College London as a source of information on this study, he said the results showed "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."

Should these findings take us by surprise? Not in the least, as Nicholson *et al.* (1998) reported in a study of a series of satellite images of the Central and Western Sahel that were taken from 1980 to 1995, they could find no evidence of any overall expansion of deserts and no drop in the rainfall use efficiency of native vegetation. In addition, in a satellite study of the entire Sahel from 1982 to 1990, Prince *et al.* (1998) detected a steady rise in rainfall use efficiency, suggesting that plant productivity and coverage of the desert had increased during this period.

That the greening phenomenon has continued apace is borne out by the study of Eklundh and Olsson (2003), who 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 whenever it passed over the African Sahel for the period 1982-2000. As they describe their findings, "strong positive change in NDVI occurred in about 22% of the area, and weak positive change in 60% of the area," while "weak negative change occurred in 17% of the area, and strong negative change in 0.6% of the area." In addition, they report that "integrated NDVI has increased by about 80% in the areas with strong positive change," while in areas with weak negative change, "integrated NDVI has decreased on average by 13%." The primary story told by these data, therefore, is one of strong positive trends in NDVI for large areas of the African Sahel over the last two decades of the twentieth century. Eklundh and Olsson conclude that the "increased vegetation, as suggested by the observed NDVI trend, could be part of the proposed tropical sink of carbon."

Due to the increase in vegetation over the past quarter-century in the Sahel, the African region was recently featured in a special issue of the *Journal of Arid Environments* titled "The 'Greening' of the Sahel." Therein, Anyamba and Tucker (2005) describe their development of an NDVI history of the region for the period 1981-2003. Comparing this history with the precipitation history of the Sahel developed by Nicholson (2005), they found that "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, they report that "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 over the last few years "is certainly one reason" for the greening phenomenon. However, they find the increase in rainfall "does not fully explain" the increase in greenness.

For one thing, the three Swedish scientists note that "only eight out of 40 rainfall observations showed a statistically significant increase between 1982-1990 and 1991-1999." In addition, they report that "further analysis of this relationship does not indicate an overall relationship between rainfall increase and vegetation trend." So what else could be driving the increase in greenness?

Olsson *et al*. suggest that "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 percent and 35 percent, respectively, since 1980, they could find "no clear relationship" between agricultural productivity and NDVI, which argues against the land management explanation.

A third speculation of Olsson *et al*. is that 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. However, Olsson *et al*. note that "more empirical research is needed to verify this [hypothesis]."

About the only thing left is what Idso (1982, 1986, 1995) has suggested, i.e., that the aerial fertilization effect of the ongoing rise in the air's CO_2 concentration (which greatly enhances vegetative productivity) and its anti-transpiration effect (which enhances plant water-use efficiency and enables plants to grow in areas that were once too dry for them) are the major players in the greening phenomenon. Whatever was the reason for the greening of the Sahel over the past quarter-century, it is clear that in spite of what the IPCC claims were unprecedented increases in anthropogenic CO_2 emissions and global temperatures, the Sahel experienced an increase in vegetative cover that was truly, as Olsson *et al*. write, "remarkable."

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/africagreen.php.

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7.9.2. Asia

We begin a review of Asia with the modeling work of Liu *et al*. (2004), who derived detailed estimates of the economic impact of predicted climate change on agriculture in China, utilizing county-level agricultural, climate, social, economic and edaphic data for 1275 agriculture-dominated counties for the period 1985-1991, together with the outputs of three general circulation models of the atmosphere that were based on five different scenarios of anthropogenic CO_2-induced climate change that yielded a mean countrywide temperature increase of 3.0°C and a mean precipitation increase of 3.9 percent for the 50-year period ending in AD 2050. In doing so, they determined that "all of China would benefit from climate change in most scenarios." In addition, they state that "the effects of CO_2 fertilization should [also] be included, for some studies indicate that this may produce a significant increase in yield." The significance of these findings is readily grasped when it is realized, in Liu *et al*.'s words, that "China's agriculture has to feed more than one-fifth of the world's population, and, historically, China has been famine prone." They report that "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)."

Moving from agro-ecosystems to natural ones, Su *et al*. (2004) used an ecosystem process model to explore the sensitivity of the net primary productivity (NPP) of an oak forest near Beijing (China) to the global climate changes projected to result from a doubling of the atmosphere's CO_2 concentration from 355 to 710 ppm. The results of this work suggested that the aerial fertilization effect of the specified increase in the air's CO_2 content would raise the forest's NPP by 14.0 percent, that a concomitant temperature increase of 2°C would boost the NPP increase to 15.7 percent, and that adding a 20 percent increase in precipitation would push the NPP increase to 25.7 percent. They calculated that a 20 percent increase in precipitation and a 4°C increase in temperature would also boost the forest's NPP by 25.7 percent.

Grunzweig *et al*. (2003) tell the tale of the Yatir forest, a 2,800-hectare stand of Aleppo and other pine trees, that had been planted some 35 years earlier at the edge of the Negev Desert in Israel. An intriguing aspect of this particular forest, which they characterize as growing in poor soil of only 0.2 to 1.0 meter's depth above chalk and limestone, is that although it is located in an arid part of Asia that receives less annual precipitation than all of the other scores of FluxNet stations in the global network of micrometeorological tower sites that use eddy covariance methods to measure exchanges of CO_2, water vapor and energy between terrestrial ecosystems and the atmosphere (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 that of most temperate forests. Grunzweig *et al*. note that 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. They report that "reducing water loss in arid regions improves soil moisture conditions, decreases water stress and extends water availability," which "can indirectly increase carbon sequestration by influencing plant distribution, survival and expansion into water-limited environments."

That this hypothesis is correct has been demonstrated by Leavitt *et al*. (2003) within the context of the long-term atmospheric CO_2 enrichment experiment of Idso and Kimball (2001) on sour orange trees. It has also been confirmed in nature by Fang (2003), who obtained identical (to the study of Leavitt *et al*.) CO_2-induced WUE responses for 23 groups of naturally occurring trees scattered across western North America over the period 1800-1985, which response, Fang concludes, "would have caused natural trees in arid environments to grow more rapidly, acting as a carbon sink for anthropogenic CO_2," which is exactly what Grunzweig *et al*. found to be happening in the Yatir forest on the edge of the Negev Desert.

Based primarily on satellite-derived Normalized Difference Vegetation Index (NDVI) data, Zhou *et al*. (2001) found that from July 1981 to December 1999, between 40 and 70° N latitude, there was a persistent increase in growing season vegetative productivity in excess of 12 percent over a broad contiguous swath of Asia stretching from Europe through Siberia to the Aldan plateau, where almost 58 percent of the land is forested. And in a companion study, Bogaert *et al*. (2002) determined that this productivity increase occurred at a time when this vast Asian region showed an overall warming trend "with negligible occurrence of cooling."

In another study that included a portion of Europe, 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 within 3196 sample plots comprised of about 50,000 entries, which database, in their words, "contains all available archived and published data." This work revealed that over the period 1961-1998, as they describe it, "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 there was a concomitant increase of ~11 percent in the area of Russian forests. In addition, the team of U.S., Austrian and Russian scientists reported that "within the range of 50-65° of latitude [the range of 90 percent 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 the work of Myneni *et al.* (2001). Therefore, as they continue, "changes in the carbon density of live biomass in Russian forests occur at about the same rate as the increase in the satellite-based estimate in the seasonally accumulated NDVI," which observation strengthens the findings of *all* satellite-based NDVI studies.

Returning to China for several concluding reports, we begin with the work of Brogaard *et al.* (2005), who studied the dry northern and northwestern regions of the country—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," which practices were believed to have been driven by rising living standards, which in combination with a growing population were assumed to have increased the pressure on these marginal lands. In the case of increasing grazing, for example, Brogaard *et al.* note that 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 supposedly "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, in their words, "uses satellite sensor-acquired reflectance in combination with climate data to generate monthly estimates of gross primary production." To their great surprise, this work revealed that "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. In this regard, they mention the possibility of increasing productivity on the agricultural lands of the IMAR, but they note that crops are grown on "only a small proportion of the total land area." Other potential contributing factors they mention are "an increase in precipitation, as well as afforestation projects." Two things they do *not* mention are the aerial fertilization effect and the transpiration-reducing effect of the increase in the air's CO_2 concentration that was experienced over the study period. Applied together, the sum of these positive influences (and possibly others that remain unknown) was demonstrably sufficient to keep plant productivity from declining in the face of greatly increasing animal and human pressures on the lands of the IMAR from 1982 to 1999.

Piao *et al.* (2005a) 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." In doing so, they discovered that "average rainy season NDVI in arid and semiarid regions both increased significantly during the period 1982-1999." Specifically, they found that the NDVI increased for 72.3 percent of total arid regions and for 88.2 percent of total semiarid regions, such that the area of arid regions decreased by 6.9 percent and the area of semiarid regions decreased by 7.9 percent. They also report that 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 that "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 that "variations in the vegetation coverage of these regions partly affect the frequency of sand-dust storm occurrence (Zou and Zhai, 2004)," Piao *et al.* concluded that "increased vegetation coverage in these areas will likely fix soil, enhance its anti-wind-erosion ability, reduce the possibility of released dust, and consequently cause a mitigation of sand-dust storms." They also reported that "recent studies have suggested 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)."

Piao *et al*. (2006) investigated vegetation 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. This work revealed that over the entire study period, NPP rose at a mean annual rate of 0.7 percent. However, Piao *et al*. report that "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 suggest that "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)." In addition, they say that "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 that "satellite-based NDVI data sets for the period of 1982-1999 also indicate consistent trends of NDVI increase," citing multiple references in support of each of these statements. Piao *et al*.'s findings, therefore, add to the growing body of evidence that reveals a significant "greening of the earth" is occurring.

Applying the same techniques, Fang *et al*. (2003) looked at the whole of China, finding that its terrestrial NPP increased by 18.7 percent between 1982 and 1999. Referring to this result as "an unexpected aspect of biosphere dynamics," they say that 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." From 1982 to 1999, the atmosphere's CO_2 concentration rose by approximately 27.4 ppm. The aerial fertilization effect of this CO_2 increase could be expected to have increased the NPP of the conglomerate of forest types found in China by about 7.3 percent. (See the procedures and reasoning described in a *CO_2 Science* editorial, September 18, 2002, http://www.co2science.org/articles/V5/N38/EDIT.php). But this increase is only a part of the total NPP increase we could expect, for Fang *et al*. note that "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 to have occurred in their region of study between 1982 and 1999.

Following this lead, we learn from the study of White *et al*. (1999)—which utilized 88 years of data (1900-1987) that were obtained from 12 different locations within the eastern U.S. deciduous forest that stretches from Charleston, SC (32.8°N latitude) to Burlington, VT (44.5°N latitude)—that a 1°C increase in mean annual air temperature increases the length of the forest's growing season by approximately five days. In addition, White *et al*. determined that a one-day extension in growing season length increased the mean forest NPP of the 12 sites they studied by an average of 1.6 percent. Hence, we could expect an additional NPP increase due to the warming-induced growing season expansion experienced in China from 1982 to 1999 of 1.6 percent/day x 5 days = 8.0 percent, which brings the total CO_2-induced plus warming-induced increase in NPP to 15.3 percent.

Last, we note there is a well-documented positive synergism between increasing air temperature and CO_2 concentration (Idso and Idso, 1994), such that the 1°C increase in temperature experienced in China between 1982 and 1999 could easily boost the initial CO_2-induced 7.3 percent NPP enhancement to the 10.7 percent enhancement that when combined with the 8.0 percent enhancement caused by the warming-induced increase in growing season length would produce the 18.7 percent increase in NPP detected in the satellite data.

In view of these observations, the findings of Fang *et al*. are seen to be right in line with what would be expected to result from the increases in air temperature and atmospheric CO_2 concentration that occurred between 1982 and 1999 in China: a stimulated terrestrial biosphere that is growing ever more productive with each passing year. This is the true observed consequence of rising CO_2 and temperature, and it is about as far removed as one can get from the negative scenarios offered by the IPCC.

Analyzing the same set of data still further, Piao *et al*. (2005b) say their results suggest that "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 found that "during the past 2 decades the amplitude of the seasonal curve of NPP has increased and the annual peak NPP has advanced," which they say "may indirectly explain the enhanced amplitude and advanced timing of the seasonal cycle of atmospheric CO_2 concentration (Keeling *et al*., 1996)," the former of which phenomena they further suggest "was probably due to the rise in atmospheric CO_2 concentration, elevated temperature, and increased atmospheric N and P deposition," while the latter phenomenon they attribute to "advanced spring onset and extended autumn growth owing to climate warming." We are in basic agreement on most of these points, but note that the advanced onset of what may be called biological spring is also fostered by the enhancement of early spring growth that is provided by the ongoing rise in the air's CO_2 concentration.

Citing a total of 20 scientific papers at various places in the following sentence from their research report, Piao *et al*. conclude that "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."

In conclusion, the historical increases in the atmosphere's CO_2 concentration and temperature have fostered a significant greening of the earth, including that observed throughout the length and breadth of Asia. It would appear that the climatic change claimed by the IPCC to have been experienced by the globe over the latter part of the twentieth century either did not occur or was dwarfed by opposing phenomena that significantly benefited China, as its lands grew ever greener during this period and its increased vegetative cover helped to stabilize its soils and throw feared desertification into reverse.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/asiagreen.php.

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7.9.3. Europe

Allen *et al*. (1999) analyzed sediment cores from a lake in southern Italy and from the Mediterranean Sea, developing high-resolution climate and vegetation data sets for this region over the last 102,000 years. These materials indicated that 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, while other proxy indicators revealed that during the more productive woody-plant period of the Holocene, the increased vegetative cover also led to less soil erosion. The results of this study demonstrate that the biosphere can successfully respond to rapid changes in climate. As the 15 researchers involved in the work put it, "the biosphere was a full participant in these rapid fluctuations, contrary to widely held views that vegetation is unable to change with such rapidity." Furthermore, their work revealed that warmer was always better in terms of vegetative productivity.

Osborne *et al*. (2000) used an empirically based mechanistic model of Mediterranean shrub vegetation to address two important questions: (1) Has recent climate change, especially increased drought, negatively impacted Mediterranean shrublands? and (2) Has the historical increase in the air's CO_2 concentration modified this impact? The data-based model they employed suggests that 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 CO_2 concentration experienced over the period was factored into the calculation, however, these negative influences were overpowered, with the net effect that both measures of vegetative prowess increased: net primary productivity by 25 percent and leaf area index by 7 percent. These results, in their words, "indicate that the recent rise in atmospheric CO_2 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."

How can we relate this observation to climate change predictions for the earth as a whole? For a nominal doubling of the air's CO_2 concentration from 300 to 600 ppm, earth's mean surface air temperature is predicted by current climate models to rise by approximately 3°C, which equates to a temperature rise of 0.01°C per ppm CO_2. In the case of the Mediterranean region here described, the temperature rise over the past century was quoted by Osborne *et al.* as being 0.75°C, over which period of time the air's CO_2 concentration rose by approximately 75 ppm, for an analogous climate response of exactly the same value: 0.01°C per ppm CO_2.

With respect to model-predicted changes in earth's precipitation regime, a doubling of the air's CO_2 content is projected to lead to a modest intensification of the planet's hydrologic cycle. In the case of the Mediterranean region over the last century, however, there has been a recent tendency toward drier conditions. Hence, the specific case investigated by Osborne *et al.* represents a much-worse-case scenario than what is predicted by current climate models for the earth as a whole. Nevertheless, the area's vegetation has done even better than it did before the climatic change, thanks to the over-powering beneficial biological effects of the concurrent rise in the air's CO_2 content.

Cheddadi *et al.* (2001) employed a standard biogeochemical model (BIOME3)—which uses monthly temperature and precipitation data, certain soil characteristics, cloudiness, and atmospheric CO_2 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 the air's CO_2 content. Their first step was to validate the model for two test periods: the present and 6000 years before present (BP). Recent instrumental records provided actual atmospheric CO_2, temperature and precipitation data for the present period; while pollen data were used to reconstruct monthly temperature and precipitation values for 6000 years BP, and ice core records were used to determine the atmospheric CO_2 concentration of that earlier epoch. These efforts suggested that winter temperatures 6000 years ago were about 2°C cooler than they are now, that annual rainfall was approximately 200 mm less than today, and that the air's CO_2 concentration averaged 280 ppm, which is considerably less than the value of 345 ppm the researchers used to represent the present, i.e., the mid-point 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 that "BIOME3 can be used to simulate ... the vegetation distribution under ... different climate and [CO_2] conditions than today," where [CO_2] is the abbreviation they use to represent "atmospheric CO_2 concentration."

Cheddadi *et al.*'s next step was to use 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."

More specifically, in the words of the researchers, "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, on the other hand, "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 currently.

What is the basis for these positive developments? Cheddadi *et al.* say "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]." Likewise, they note that "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 that "such mechanisms may help plants to resist long-lasting drought periods that characterize the Mediterranean climate."

Contrary to what is often predicted for much of the world's moisture-challenged lands, therefore, the authors were able to report that "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," where they define a drastic decrease as a decline of 30 percent or more. Equally important in this context is the fact that Hennessy *et al*. (1997) have indicated that a doubling of the air's CO_2 content would in all likelihood lead to a 5 to 10 percent increase in annual precipitation at Mediterranean latitudes, which is also what is predicted for most of the rest of the world. Hence, the results of the present study—where precipitation was held constant—may validly be considered to be a worst-case scenario, with the true vegetative response being even better than the good-news results reported by Cheddadi *et al*., even when utilizing what we believe to be erroneously inflated global warming predictions.

Julien *et al*. (2006) "used land surface temperature (LST) algorithms and NDVI [Normalized Difference Vegetation Index] values to estimate changes in vegetation in the European continent between 1982 and 1999 from the Pathfinder AVHRR [Advanced Very High Resolution Radiometer] Land (PAL) dataset." This program revealed that arid and semi-arid areas (Northern Africa, Southern Spain and the Middle East) have seen their mean LST increase and NDVI decrease, while 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 have experienced either slight increases or decreases in NDVI while LST values have decreased. Considering the results in their totality, the Dutch and Spanish researchers concluded that, 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."

Working in the Komi Republic in the northeast European sector of Russia, Lopatin *et al*. (2006) (1) collected discs and cores from 151 Siberian spruce trees and 110 Scots pines from which they developed ring-width chronologies that revealed yearly changes in forest productivity, (2) developed satellite-based time series of NDVI for the months of June, July, August over the period 1982-2001, (3) correlated their site-specific ring-width-derived productivity histories with same-site NDVI time series, (4) used the resulting relationship to establish six regional forest productivity histories for the period 1982-2001, and (5) 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 indicated that the 1982-2001 trends of integrated NDVI values from June to August were positive, and that the "increase in productivity reflected in [the] NDVI data [was] maximal on the sites with increased temperature and decreased precipitation."

In discussing their findings, the three scientists state that "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 that "in Europe, most forests are managed, except for those in northwestern Russia [the location of their work], where old-growth natural forests are dominant (Aksenov *et al*., 2002)." Consequently, and because of their positive findings, they say we can now conclude that "productivity during recent decades also increased in relatively untouched forests," where non-management-related "climate change with lengthening growing season, increasing CO_2 and nitrogen deposition" are the primary determinants of changes in forest productivity.

In conclusion, this brief review of pertinent studies conducted in Europe strongly contradicts today's obsession with the ongoing rise in the atmosphere's CO_2 content, as well as the many environmental catastrophes it has been predicted to produce. The results of rising CO_2 concentrations and temperatures in the twentieth century were overwhelmingly positive.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/europegreen.php.

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7.9.4. North America

In a paper titled "Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981-1999," Zhou *et al.* (2001) determined that the magnitude of the satellite-derived normalized difference vegetation index (NDVI) rose by 8.44 percent in North America over this period. Noting that 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," they went on to suggest that the increases in plant growth and vitality implied by their NDVI data were primarily driven by concurrent increases in near-surface air temperature, although temperatures may have actually declined throughout the eastern part of the United States over the period of their study.

Zhou *et al.*'s attribution of this "greening" of the continent to increases in near-surface air temperature was challenged by Ahlbeck (2002), who suggested that the observed upward trend in NDVI was primarily driven by the increase in the air's CO_2 concentration, and that fluctuations in temperature were primarily responsible for variations about the more steady upward trend defined by the increase in CO_2. In replying to this challenge, Kaufmann *et al.* (2002) claimed Ahlbeck was wrong and reaffirmed their initial take on the issue. We believe it was Ahlbeck who was "clearly the 'more correct' of the two camps." (See the discussion in *CO_2 Science* at www.co2science.org/articles/V5/N38/EDIT.php.)

About the same time, 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, which was driven by a satellite NDVI record at 8-km spatial resolution. This effort revealed that NPP increases of 30 percent 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 amount is 8.58 percent of the 300 ppm increase often used in experiments on plant growth responses to atmospheric CO_2 enrichment. Consequently, for herbaceous plants that display NPP increases of 30-40 percent in response to a 300-ppm increase in atmospheric CO_2 concentration, the CO_2-induced NPP increase experienced between 1982 and 1998 would be expected to have been 2.6-3.4 percent. Similarly, for woody plants that display NPP increases of 60-80 percent in response to a 300-ppm increase in atmospheric CO_2 (Saxe *et al.*, 1998; Idso and Kimball, 2001), the expected increase in productivity between 1982 and 1998 would have been 5.1-6.9 percent. Since both of these NPP increases are considerably less that the 30 percent or more observed by Hicke *et al.*, additional factors must have helped to stimulate NPP over this period, some of which may have been concomitant increases in precipitation and air temperature, the tendency for warming to lengthen growing seasons and enhance the aerial fertilization effect of rising CO_2 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. Whatever the mix might have been, one thing is clear: Its effect was overwhelmingly positive.

In a study based on a 48-year record derived from an average of 17 measurements per year, Raymond and Cole (2003) demonstrated that the export of alkalinity, in the form of bicarbonate ions, from the Mississippi River to the Gulf of Mexico had increased by approximately 60 percent since 1953. “This increased export,” as they described it, was “in part the result of increased flow resulting from higher rainfall in the Mississippi basin,” which had led to a 40 percent increase in annual Mississippi River discharge to the Gulf of Mexico over the same time period. The remainder, however, had to have been due to increased rates of chemical weathering of soil minerals. What factors might have been responsible for this phenomenon? The two researchers noted that potential mechanisms included “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.” Unfortunately, they forgot to mention the increase in terrestrial plant productivity that is produced by the increase in the aerial fertilization effect provided by the historical rise in the air’s CO_2 content, which also leads to “an increase in plant and microbial production of CO_2 and organic acids in soils.” This phenomenon should have led to an increase in Mississippi River alkalinity equivalent to that which they had observed since 1953.

In a study using data obtained from dominant stands of loblolly pine plantations growing at 94 locations spread across the southeastern United States, Westfall and Amateis (2003) employed mean height measurements made at three-year intervals over a period of 15 years to calculate a site index related to the mean growth rate for each of five three-year periods, which index would be expected to increase monotonically if growth rates were being enhanced above normal by some monotonically increasing factor that promotes growth. This work revealed, in their words, that “mean site index over the 94 plots consistently increased at each remeasurement period,” which would suggest, as they further state, that “loblolly pine plantations are realizing greater than expected growth rates,” and, we would add, that the growth rate increases are growing larger and larger with each succeeding three-year period. As to what could be causing the monotonically increasing growth rates of loblolly pine trees over the entire southeastern United States, Westfall and Amateis named increases in temperature and precipitation in addition to rising atmospheric CO_2 concentrations. However, they report that a review of annual precipitation amounts and mean ground surface temperatures showed no trends in these factors over the period of their study. They also suggested that 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 tended to favor the ever-increasing aerial fertilization effect of atmospheric CO_2 enrichment as being responsible for the accelerating pine tree growth rates.

Returning to satellite studies, Lim *et al*. (2004) correlated the monthly rate of relative change in NDVI, which they derived from advanced very high resolution radiometer data, with the rate of change in atmospheric CO_2 concentration during the natural vegetation growing season within three different 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) over the period 1982-1992, after which they explored the temporal progression of annual minimum NDVI over the period 1982-2001 throughout the eastern humid temperate zone of North America. The result of these operations was that 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 CO_2 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 CO_2.” In addition, they determined that the yearly “minimum vegetation greenness increased over the period 1982-2001 for all the regions of the eastern humid temperate zone in North America.” As for the cause of this phenomenon, Lim *et al*. say that rising CO_2 could “increase minimum greenness by stimulating photosynthesis at the beginning of the growing season,” citing the work of Idso *et al*. (2000).

In a somewhat similar study, but one that focused more intensely on climate change, 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 (Tmax) and minimum temperature (Tmin) over an 11-year period (1990-2000) for six biomes in the conterminous United States (Evergreen Needleleaf Forest, Deciduous Broadleaf Forest, Mixed Forest, Open Shrubland, Woody Savanna and Grassland), focusing on within- and across-biome variance in long-term average gNDVI and emphasizing the degree to which this variance is explained by spatial gradients in long-term average seasonal climate. The results of these protocols indicated that the greatest positive climate-change impacts on biome productivity were caused by increases in spring, winter and fall precipitation, as well as increases in fall and spring temperature, especially Tmin, which has historically increased at roughly twice the rate of Tmax in the United States. Hence, "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 nonforested ecoregions in the conterminous US, with associated implications for carbon budgets and woody proliferation."

Goetz *et al*. (2005) transformed satellite-derived NDVI data obtained across boreal North America (Canada and Alaska) for the period 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. Over the course of the study, this work revealed that area-wide tundra experienced a significant increase in Pg in response to a similar increase in air temperature; and Goetz *et al*. say "this observation is supported by a wide and increasing range of local field measurements characterizing elevated net CO_2 uptake (Oechel *et al*., 2000), 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)." In the case of interior forest, on the other hand, there was 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 latter seemingly aberrant observation is in harmony with the fact that at low temperatures the growth-promoting effects of increasing atmospheric CO_2 levels are often very small or even non-existent (Idso and Idso, 1994), which is what appears to have been the case with North American boreal forests over the same time period. As a result, Canada's and Alaska's tundra ecosystems exhibited increasing productivity over the past couple of decades, while their boreal forests did not.

Also working in Alaska, Tape *et al*. (2006) analyzed repeat photography data from a photo study of the Colville River conducted between 1945 and 1953, as well as 202 new photos of the same sites that were obtained between 1999 and 2002, to determine the nature of shrub expansion in that region over the past half-century. This approach revealed, in their words, that "large shrubs have increased in size and abundance over the past 50 years, colonizing areas where previously there were no large shrubs." In addition, they say their review of plot and remote sensing studies confirms that "shrubs in Alaska have expanded their range and grown in size" and that "a population of smaller, intertussock shrubs not generally sampled by the repeat photography, is also expanding and growing." Taken together, they conclude that "these three lines of evidence allow us to infer a general increase in tundra shrubs across northern Alaska." Tape *et al*. attribute this to large-scale pan-Arctic warming. From analyses of logistic growth curves, they estimate that the expansion began about 1900, "well before the current warming in Alaska (which started about 1970)." Hence, they conclude that "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 we would add that the 80-ppm increase in the atmosphere's CO_2 concentration since 1900 likely played a role in the shrub expansion as well. If continued, the researchers say the transition "will alter the fundamental architecture and function of this ecosystem with important ramifications," the great bulk of which, in our opinion, will be positive.

Working at eight different sites within the Pacific Northwest of the United States, Soule and Knapp (2006) studied ponderosa pine trees 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." In addition, 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 say that all sites were located in areas "where ozone concentrations and nitrogen deposition are typically low."

At all eight of the sites that met all of these criteria, Soule and Knapp obtained core samples from about 40 mature trees that included "the potentially oldest trees on each site," so that their results would indicate, as they put it, "the response of mature, naturally occurring ponderosa pine trees that germinated before anthropogenically elevated CO_2 levels, but where growth, particularly post-1950, has occurred under increasing and substantially higher atmospheric CO_2 concentrations." Utilizing meteorological evaluations of the Palmer Drought Severity Index, they thus compared ponderosa pine radial growth rates during matched wet and dry years pre- and post-1950. Overall, the two researchers found a post-1950 radial growth enhancement that was "more pronounced during drought years compared with wet years, and the greatest response occurred at the most stressed site." As for the magnitude of the response, they determined that "the relative change in growth [was] upward at seven of our [eight] sites, ranging from 11 to 133%." With respect to the significance of their observations, Soule and Knapp say their results show that "radial growth has increased in the post-1950s period ... while climatic conditions have generally been unchanged," which further suggests that "nonclimatic driving forces are operative." In addition, 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 free-air CO_2 enrichment (FACE) studies (Ainsworth and Long, 2005)." They conclude their findings "suggest that elevated levels of atmospheric CO_2 are acting as a driving force for increased radial growth of ponderosa pine, but that the overall influence of this effect may be enhanced, reduced or obviated by site-specific conditions."

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 where younger trees slightly removed from the islands escaped the ravages of the flames. There, "within each of a total of 24 burned islands," in the words of the three researchers, "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 both the old and young trees would have been approximately the same age: 1900-1929 for the old trees and 1970-1999 for the young trees. During the first of these periods, the atmosphere's CO_2 concentration averaged 299 ppm; during the second it averaged 346 ppm. Also, the mean rate-of-rise of the atmosphere's CO_2 concentration was 0.37 ppm/year for first period and 1.43 ppm/year for the second.

The results of this exercise revealed that the slope of the linear regression describing the rate-of-growth of the ring-width residuals for the later period (when the air's CO_2 concentration was 15 percent greater and its rate-of-rise 285 percent greater) was more than twice that of the linear regression describing the rate-of-growth of the ring-width residuals during the earlier period. As the researchers describe it, these results show that "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," and they say that "these results are consistent with expectations for CO_2-fertilization effects." In fact, they say "the response of the studied young trees can be taken as strong circumstantial evidence for the atmospheric CO_2-fertilization effect."

Another thing Wang *et al.* learned was that "postdrought growth response was much stronger for young trees (1970-1999) compared with old trees at the same development stage (1900-1929)," and they add that "higher atmospheric CO_2 concentration in the period from 1970-1999 may have helped white spruce recover from severe drought." In a similar vein, they also determined that young trees showed a weaker relationship to precipitation than did old trees, noting that "more CO_2 would lead to greater water-use efficiency, which may be dampening the precipitation signal in young trees."

In summary, Wang *et al.*'s unique study provides an exciting real-world example of the benefits the historical increase in the air's CO_2 content has likely conferred on nearly all of earth's plants, and especially its long-lived woody species. Together with the results of the other North American studies we have reviewed, this body of research paints a picture of a significant greening of North America in the twentieth century.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/namergreen.php.

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7.9.5. Oceans

Rising air temperatures and atmospheric CO_2 concentrations in the twentieth century also have affected the productivity of earth's seas. We begin with a study that takes a much longer view of the subject.

Elderfield and Rickaby (2000) note that the typically low atmospheric CO_2 concentrations of glacial periods have generally been attributed to an increased oceanic uptake of CO_2, "particularly in the southern oceans." However, the assumption that intensified phytoplanktonic photosynthesis may have stimulated CO_2 uptake rates during glacial periods has always seemed at odds with the observational fact that rates of photosynthesis are generally much reduced in environments of significantly lower-than-current atmospheric CO_2 concentrations, such as typically prevail during glacial periods.

The two scientists provide a new interpretation of Cd/Ca systematics in sea water that helps to resolve this puzzle, as it allows them to more accurately estimate surface water phosphate conditions during glacial times and thereby determine the implications for concomitant atmospheric CO_2 concentrations. What they found, in their words, is that "results from the Last Glacial Maximum [LGM] show similar phosphate utilization in the subantarctic to that of today, but much smaller utilization in the polar Southern Ocean," which implies, according to Delaney (2000), that Antarctic productivity was lower at that time than it is now, but that *sub*antarctic productivity was about the same as it has been in modern times, due perhaps to greater concentrations of bio-available iron compensating for the lower atmospheric CO_2 concentrations of the LGM.

So what caused the much smaller utilization of phosphate in the polar Southern Ocean during the LGM? Noting that the area of sea-ice cover in the Southern Ocean during glacial periods may have been as much as double that of modern times, Elderfield and Rickaby suggest that "by restricting communication between the ocean and atmosphere, sea ice expansion also provides a mechanism for reduced CO_2 release by the Southern Ocean and lower glacial atmospheric CO_2." Hence, it is possible that phytoplanktonic productivity in the glacial Southern Ocean may have been no higher than it is at the present time, notwithstanding the greater supply of bio-available iron typical of glacial epochs.

In the case of the interglacial period in which we currently live, Dupouy *et al.* (2000) say it has long been believed that N_2 fixation in the world's oceans is unduly low, in consequence of the present low supply of wind-blown iron compared to that of glacial periods, and that this state of affairs leads to low phytoplanktonic productivity, even in the presence of higher atmospheric CO_2 concentrations. The evidence they acquired, however, suggests that marine N_2 fixation may be much greater than what has generally been thought to be the case. In particular, they note that several *Trichodesmium* species of N_2-fixing cyanobacteria have "a nearly ubiquitous distribution in the euphotic zone of tropical and subtropical seas and could play a major role in bringing new N to these oligotrophic systems." And this feat, in their words, "could play a significant role in enhancing new production."

The importance of these findings is perhaps best appreciated in light of the findings of Pahlow and Riebesell (2000), who in studying data obtained from 1173 stations in the Atlantic and Pacific Oceans, covering the years 1947 to 1994, detected changes in Northern Hemispheric deep-ocean Redfield ratios that are indicative of increasing nitrogen availability there, which increase was concomitant with an increase in export production that has resulted in ever-increasing oceanic carbon sequestration. These investigators further suggest that the growing supply of nitrogen has its origin in anthropogenic activities that release nitrous oxides to the air. In addition, the increased carbon export may be partly a consequence of the historical increase in the air's CO_2 concentration, which has been demonstrated to have the ability to enhance phytoplanktonic productivity (see Section 6.1.3.4. in this document), analogous to the way in which elevated concentrations of atmospheric CO_2 enhance the productivity of terrestrial plants, including their ability to fix nitrogen.

Further elucidating the productivity-enhancing power of the ongoing rise in the air's CO_2 content is the study of Pasquer *et al*. (2005), who employed a complex model of growth regulation of diatoms, pico/nano phytoplankton, coccolithophorids and *Phaeocystis* spp. by light, temperature and nutrients (based on a comprehensive analysis of literature reviews focusing on these taxonomic groups) to calculate changes in the ocean uptake of carbon in response to a sustained increase in atmospheric CO_2 concentration of 1.2 ppm per year for three marine ecosystems where biogeochemical time-series of the data required for model initialization and comparison of results were readily available. These systems were (1) the ice-free Southern Ocean Time Series station KERFIX (50°40'S, 68°E) for the period 1993-1994 (diatom-dominated), (2) the sea-ice associated Ross Sea domain (76°S, 180°W) of the Antarctic Environment and Southern Ocean Process Study AESOPS in 1996-1997 (*Phaeocystis*-dominated), and (3) the North Atlantic Bloom Experiment NABE (60°N, 20°W) in 1991 (coccolithophorids). Their results, in their words, "show that at all tested latitudes the prescribed increase of atmospheric CO_2 enhances the carbon uptake by the ocean." Indeed, we calculate from their graphical presentations that (1) at the NABE site a sustained atmospheric CO_2 increase of 1.2 ppm per year over a period of eleven years increases the air-sea CO_2 flux in the last year of that period by approximately 17 percent, (2) at the AESOPS site the same protocol applied over a period of six years increases the air-sea CO_2 flux by about 45 percent, and (3) at the KERFIX site it increases the air-sea CO_2 flux after nine years by about 78 percent. Although the results of this interesting study based on the complex SWAMCO model of Lancelot *et al*. (2000), as modified by Hannon *et al*. (2001), seem overly large, they highlight the likelihood that the ongoing rise in the air's CO_2 content may be having a significant positive impact on ocean productivity and the magnitude of the ocean carbon sink.

But what about increasing temperatures? Sarmiento *et al*. (2004) conducted a massive computational study that employed six coupled climate model simulations to determine the biological response of the global ocean to the climate warming they simulated from the beginning of the Industrial Revolution to the year 2050. Based on vertical velocity, maximum winter mixed-layer depth and sea-ice cover, they defined six biomes and calculated how their surface geographies would change in response to their calculated changes in global climate. Next, they used satellite ocean color and climatological observations to develop an empirical model for predicting surface chlorophyll concentrations from the final physical properties of the world's oceans as derived from their global warming simulations, after which they used three primary production algorithms to estimate the response of oceanic primary production to climate warming based on their calculated chlorophyll concentrations. When all was said and done, the thirteen scientists from Australia, France, Germany, Russia, the United Kingdom and the United States arrived at a global warming-induced *increase* in global ocean primary production that ranged from 0.7 to 8.1 percent.

So what do real-world measurements of oceanic productivity reveal? Goes *et al*. (2005) analyzed seven years (1997-2004) of satellite-derived ocean color data pertaining to the Arabian Sea, as well as associated sea surface temperatures (SSTs) and winds. They report that for the region located between 52 to 57°E and 5 to 10°N, "the most conspicuous observation was the consistent year-by-year increase in phytoplankton biomass over the 7-year period." This phenomenon was so dramatic that by the summer of 2003, in their words, "chlorophyll *a* concentrations were >350% higher than those observed in the summer of 1997." They also report that the increase in chlorophyll *a* was "accompanied by an intensification of sea surface winds, in particular of the zonal (east-to-west) component," noting that these "summer monsoon winds are a coupled atmosphere-land-ocean phenomenon, whose strength is significantly correlated with tropical SSTs and Eurasian snow cover anomalies on a year-to-year basis." More specifically, they say that "reduced snow cover over Eurasia strengthens the spring and summer land-sea thermal contrast and is considered to be responsible for the stronger southwest monsoon winds." In addition, they state that "the influence of southwest monsoon winds on phytoplankton in the Arabian Sea is not through their impact on coastal upwelling alone but also via the ability of zonal winds to laterally advect newly upwelled nutrient-rich waters to regions away from the upwelling zone." They conclude that "escalation in the intensity of summer monsoon winds, accompanied by enhanced upwelling and an increase of more than 350 percent in average summertime phytoplankton biomass along the coast and over 300 percent offshore, raises the possibility that the current warming trend of the Eurasian landmass is making the Arabian Sea more productive."

To the north and west on the other side of Eurasia, Marasovic *et al*. (2005) analyzed monthly observations of basic hydrographic, chemical and biological parameters, including primary production, that had been made since the 1960s at two oceanographic stations, one near the coast (Kastela Bay) and one in the open sea. They found that mean annual primary production in Kastela Bay averaged about 430 mg C m^{-2} d^{-1} over the period 1962-72, exceeded 600 mg C m^{-2} d^{-1} over the period 1972-82, and rose to over 700 mg C m^{-2} d^{-1} over the period 1982-96, accompanied by a similar upward trend in percent oxygen saturation of the surface water. The initial value of primary production in the open sea was much less (approximately 150 mg C m^{-2} d^{-1}), but it began to follow the upward trend of the Kastela Bay data after about one decade. Marasovic *et al*. thus concluded that "even though all the relevant data indicate that the changes in Kastela Bay are closely related to an increase of anthropogenic nutrient loading, similar changes in the open sea suggest that primary production in the Bay might, at least partly, be due to global climatic changes," which, in their words, are "occurring in the Mediterranean and Adriatic Sea open waters" and may be directly related to "global warming of air and ocean," since "higher temperature positively affects photosynthetic processes."

Raitsos *et al*. (2005) investigated the relationship between Sea-viewing Wide Field-of-view Sensor (SeaWiFS) chlorophyll-*a* measurements in the Central Northeast Atlantic and North Sea (1997-2002) and simultaneous measurements of the Phytoplankton Color Index (PCI) collected by the Continuous Plankton Recorder survey, which is an upper-layer plankton monitoring program that has operated in the North Sea and North Atlantic Ocean since 1931. By developing a relationship between the two data bases over their five years of overlap, they were able to produce a Chl-*a* history for the Central Northeast Atlantic and North Sea for the period 1948-2002. Of this record they say that "an increasing trend is apparent in mean Chl-*a* for the area of study over the period 1948-2002." They also say "there is clear evidence for a stepwise increase after the mid-1980s, with a minimum of 1.3mg m^{-3} in 1950 and a peak annual mean of 2.1 mg m^{-3} in 1989 (62% increase)." Alternatively, it is possible that the data represent a more steady long-term upward trend upon which is superimposed a decadal-scale oscillation. In a final comment on their findings, they note that "changes through time in the PCI are significantly correlated with both sea surface temperature and Northern Hemisphere temperature," citing Beaugrand and Reid (2003).

In a contemporaneous study, Antoine *et al.* (2005) applied revised data-processing algorithms to two ocean-sensing satellites, the Coastal Zone Color Scanner (CZCS) and SeaWiFS, over the periods 1979-1986 and 1998-2002, respectively, to provide an analysis of the decadal changes in global oceanic phytoplankton biomass. Results of the analysis showed "an overall increase of the world ocean average chlorophyll concentration by about 22%" over the two decades under study.

Dropping down to the Southern Ocean, Hirawake *et al.* (2005) analyzed chlorophyll *a* data obtained from Japanese Antarctic Research Expedition cruises made by the Fuji and Shirase ice-breakers between Tokyo and Antarctica from 15 November to 28 December of nearly every year between 1965 and 2002 in a study of interannual variations of phytoplankton biomass, calculating results for the equatorial region between 10°N and 10°S, the Subtropical Front (STF) region between 35°S and 45°S, and the Polar Front (PF) region between 45°S and 55°S. They report that an increase in chl *a* was "recognized in the waters around the STF and the PF, especially after 1980 around the PF in particular," and that "in the period between 1994 and 1998, the chl *a* in the three regions exhibited rapid gain simultaneously." They also say "there were significant correlations between chl *a* and year through all of the period of observation around the STF and PF, and the rates of increase are 0.005 and 0.012 mg chl *a* m^{-3} y^{-1}, respectively." In addition, they report that the satellite data of Gregg and Conkright (2002) "almost coincide with our results." In commenting on these findings, the Japanese scientists say that "simply considering the significant increase in the chl *a* in the Southern Ocean, a rise in the primary production as a result of the phytoplankton increase in this area is also expected."

Also working in the Southern Hemisphere, Sepulveda *et al.* (2005) presented "the first reconstruction of changes in surface primary production during the last century from the Puyuhuapi fjord in southern Chile, using a variety of parameters (diatoms, biogenic silica, total organic carbon, chlorins, and proteins) as productivity proxies." Noting that the fjord is located in "a still-pristine area," they say it is "suitable to study changes in past export production originating from changes in both the paleo-Patagonian ice caps and the globally important Southern Ocean."

The analysis revealed that the productivity of the Puyuhuapi fjord "was characterized by a constant increase from the late 19th century to the early 1980s, then decreased until the late 1990s, and then rose again to present-day values." For the first of these periods (1890-1980), they additionally report that "all proxies were highly correlated ($r > 0.8$, $p < 0.05$)," and that "all proxies reveal an increase in accumulation rates." From 1980 to the present, however, the pattern differed among the various proxies; and the researchers say that "considering that the top 5 cm of the sediment column (~10 years) are diagenetically active, and that bioturbation by benthic organisms may have modified and mixed the sedimentary signal, paleo-interpretation of the period 1980-2001 must be taken with caution." Consequently, there is substantial solid evidence that, for the first 90 years of the 111-year record, surface primary production in the Puyuhuapi fjord rose dramatically, while with lesser confidence it appears to have leveled out over the past two decades. In spite of claims that the "unprecedented" increases in mean global air temperature and CO_2 concentration experienced since the inception of the Industrial Revolution have been bad for the biosphere, Sepulveda *et al.* presented yet another case of an ecosystem apparently thriving in such conditions.

Still, claims of impending ocean productivity declines have not ceased, and some commentators single out the study of Behrenfeld *et al.* (2006) in support of their claims. Working with NASA's Sea-viewing Wide Field-of-view Sensor (Sea WiFS), the team of 10 U.S. scientists calculated monthly changes in net primary production (NPP) from similar changes in upper-ocean chlorophyll concentrations detected from space over the past decade. (See Figure 7.9.5.) They report that this period was dominated by an initial NPP increase of 1,930 teragrams of carbon per year (Tg C yr^{-1}), which they attributed to the significant cooling of "the 1997 to 1999 El Niño to La Niña transition," and they note that this increase was "followed by a prolonged decrease averaging 190 Tg C yr^{-1}," which they attributed to subsequent warming.

The means by which changing temperatures were claimed by the researchers to have driven the two sequential linear-fit trends in NPP is based on their presumption that a warming climate increases the density contrast between warmer surface waters and cooler underlying nutrient-rich waters, so that the enhanced stratification that occurs with warming "suppresses nutrient exchange through vertical mixing," which decreases NPP by reducing the supply of nutrients to the surface waters where photosynthesizing phytoplankton predominantly live. By contrast, the ten scientists suggest that "surface cooling favors elevated vertical exchange," which increases NPP by enhancing the supply of nutrients to the ocean's surface waters, which are more frequented by phytoplankton than are under-lying waters, due to light requirements for photosynthesis.

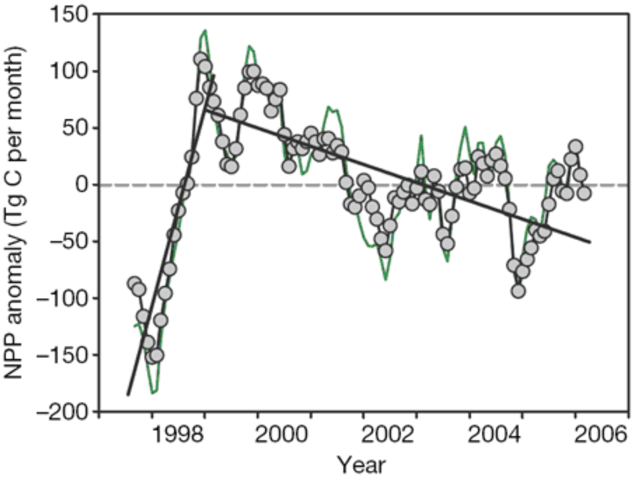

Figure 7.9.5. Monthly anomalies of global NPP (green line) plus similar results for the permanently stratified ocean regions of the world (grey circles and black line), adapted from Behrenfeld *et al.* (2006).

It is informative to note, however, that from approximately the middle of 2001 to the end of the data series in early 2006 (which interval accounts for more than half of the data record), there has been, if anything, a slight increase in global NPP. (See again Figure 7.9.5.) Does this observation mean there has been little to no net global warming since mid-2001? Or does it mean the global ocean's mean surface temperature actually cooled a bit over the last five years? Neither alternative is what one would expect if global warming were a real problem. On the other hand, the relationship between global warming and oceanic productivity may not be nearly as strong as what Behrenfeld *et al.* have suggested; and they themselves say "modeling studies suggest that shifts in ecosystem structure from climate variations may be as [important as] or more important than the alterations in bulk integrated properties reported here," noting that some "susceptible ecosystem characteristics" that might be so shifted include "taxonomic composition, physiological status, and light absorption by colored dissolved organic material." It is possible that given enough time, the types of phenomena Behrenfeld *et al.* describe as possibly resulting in important "shifts in ecosystem structure" could compensate for or even overwhelm what might initially appear to be negative warming-induced consequences.

Another reason for not concluding too much from the oceanic NPP data set of Behrenfeld *et al.* is that it may be of too short a duration to reveal what might be occurring on a much longer timescale throughout the world's oceans, or that its position in time may be such that it does not allow the detection of greater short-term changes of the opposite sign that may have occurred a few years earlier or that might occur in the near future.

Consider, for example, the fact that the central regions of the world's major oceans were long thought to be essentially vast biological deserts (Ryther, 1969), but that several studies of primary photosynthetic production conducted in those regions over the 1980s (Shulenberger and Reid, 1981; Jenkins, 1982; Jenkins and Goldman, 1985; Reid and Shulenberger, 1986; Marra and Heinemann, 1987; Laws *et al.*, 1987; Venrick *et al.*, 1987; Packard *et al.*, 1988) yielded results that suggested marine productivity at that time was twice or more as great as it likely was for a long time prior to 1969, causing many of that day to speculate that "the ocean's deserts are blooming" (Kerr, 1986).

Of even greater interest, perhaps, is the fact that over this particular period of time (1970-1988), the data repository of Jones *et al.* (1999) indicates the earth experienced a (linear-regression-derived) global warming of 0.333°C, while the data base of the Global Historical Climatology Network indicates the planet experienced a similarly calculated global warming of 0.397°C. The mean of these two values (0.365°C) is nearly twice as great as the warming that occurred over the post-1999 period studied by Behrenfeld *et al.*; yet this earlier much larger warming (which according to the ten researchers' way of thinking should have produced a major decline in ocean productivity) was concomitant with a huge increase in ocean productivity. Consequently, it would appear that just the opposite of what Behrenfeld *et al.* suggest about global warming and ocean productivity is likely to be the more correct of the two opposing cause-and-effect relationships.

Moving closer to the present, Levitan *et al.* (2007) published a study of major significance that addresses the future of oceanic productivity under rising atmospheric CO_2 concentrations. In their paper the authors note that "among the principal players contributing to global aquatic primary production, the nitrogen (N)-fixing organisms (diazotrophs) are important providers of new N to the oligotrophic areas of the oceans," and they cite several studies which demonstrate that "cyanobacterial (phototrophic) diazotrophs in particular fuel primary production and phytoplankton blooms which sustain oceanic food-webs and major economies and impact global carbon (C) and N cycling." These facts compelled them to examine how the ongoing rise in the air's CO_2 content might impact these relationships. They began by exploring the response of the cyanobacterial diazotroph *Trichodesmium* to changes in the atmosphere's CO_2 concentration, choosing this particular diazotroph because it dominates the world's tropical and sub-tropical oceans in this regard, contributing over 50 percent of total marine N fixation.

The eight Israeli and Czech researchers grew *Trichodesmium* IMS101 stock cultures in YBCII medium (Chen *et al.*, 1996) at 25°C and a 12-hour:12-hour light/dark cycle (with the light portion of the cycle in the range of 80-100 μmol photons m^{-2} s^{-1}) in equilibrium with air of three different CO_2 concentrations (250, 400 and 900 ppm, representing low, ambient and high concentrations, respectively), which was accomplished by continuously bubbling air of the three CO_2 concentrations through the appropriate culture vessels throughout various experimental runs, each of which lasted a little over three weeks, during which time they periodically monitored a number of diazotrophic physiological processes and properties.

So what did the scientists learn? Levitan *et al.* report that *Trichodesmium* in the high CO_2 treatment "displayed enhanced N fixation, longer trichomes, higher growth rates and biomass yields." In fact, they write that in the high CO_2 treatment there was "a three- to four-fold increase in N fixation and a doubling of growth rates and biomass," and that the cultures in the low CO_2 treatment reached a stationary growth phase after only five days, "while both ambient and high CO_2 cultures exhibited exponential growth until day 15 before declining."

In discussing possible explanations for what they observed, the researchers suggest that "enhanced N fixation and growth in the high CO_2 cultures occurs due to reallocation of energy and resources from carbon concentrating mechanisms required under low and ambient CO_2." Consequently, they conclude, in their words, that "in oceanic regions, where light and nutrients such as P and Fe are not limiting, we expect the projected concentrations of CO_2 to increase N fixation and growth of *Trichodesmium*," and that "other diazotrophs may be similarly affected, thereby enhancing inputs of new N and increasing primary productivity in the oceans." And to emphasize these points, they write in the concluding sentence of their paper that "*Trichodesmium's* dramatic response to elevated CO_2 may consolidate its dominance in subtropical and tropical regions and its role in C and N cycling, fueling subsequent primary production, phytoplankton blooms, and sustaining oceanic food-webs."

Arrigo *et al*. (2008) introduce their work by writing that "between the late 1970s and the early part of the 21st century, the extent of Arctic Ocean sea ice cover has declined during all months of the year, with the largest declines reported in the boreal summer months, particularly in September (8.6 ± 2.9% per decade)," citing the work of Serreze *et al*. (2007). In an effort to "quantify the change in marine primary productivity in Arctic waters resulting from recent losses of sea ice cover," the authors "implemented a primary productivity algorithm that accounts for variability in sea ice extent, sea surface temperature, sea level winds, downwelling spectral irradiance, and surface chlorophyll *a* concentrations," and that "was parameterized and validated specifically for use in the Arctic (Pabi *et al*., 2008) and utilizes forcing variables derived either from satellite data or NCEP reanalysis fields."

Arrigo *et al*. determined that "annual primary production in the Arctic increased yearly by an average of 27.5 Tg C per year since 2003 and by 35 Tg C per year between 2006 and 2007," 30 percent of which total increase was attributable to decreased minimum summer ice extent and 70 percent of which was due to a longer phytoplankton growing season. Arrigo *et al*. thus conclude that if the trends they discovered continue, "additional loss of ice during Arctic spring could boost productivity >3-fold above 1998-2002 levels." Hence, they additionally state that if the 26 percent increase in annual net CO_2 fixation in the Arctic Ocean between 2003 and 2007 is maintained, "this would represent a weak negative feedback on climate change."

On the other side of the globe and working in the Southern Ocean, Smith and Comiso (2008) employed phytoplankton pigment assessments, surface temperature estimates, modeled irradiance, and observed sea ice concentrations—all of which parameters were derived from satellite data—and incorporated them into a vertically integrated production model to estimate primary productivity trends according to the technique of Behrenfeld *et al*. (2002). Of this effort, the two authors say that "the resultant assessment of Southern Ocean productivity is the most exhaustive ever compiled and provides an improvement in the quantitative role of carbon fixation in Antarctic waters." So what did they find? During the nine years (1997-2006) analyzed in the study, "productivity in the entire Southern Ocean showed a substantial and significant increase," which increase can be calculated from the graphical representation of their results as ~17 percent per decade. In commenting on their findings, the two researchers note that "the highly significant increase in the productivity of the entire Southern Ocean over the past decade implies that long-term changes in Antarctic food webs and biogeochemical cycles are presently occurring," which changes we might add are positive.

In light of these several real-world observations, we find no indications of a widespread decline in oceanic productivity over the twentieth century in response to increases in air temperature and CO_2 concentration. In fact, we see evidence that just the opposite is occurring, that environmental changes are occurring that are proving to be beneficial.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/o/oceanproductivity.php.

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7.9.6. Global

How have earth's terrestrial plants responded—on average and in their entirety—to the atmospheric temperature and CO_2 increases of the past quarter-century? In this subsection we report the results of studies that have looked at either the world as a whole or groups of more than two continents at the same time.

In one of the earlier studies of the subject, Joos and Bruno (1998) used ice core and direct observations of atmospheric CO_2 and ^{13}C to reconstruct the histories of terrestrial and oceanic uptake of anthropogenic carbon over the past two centuries. This project revealed, in their words, that "the biosphere acted on average as a source [of CO_2] during the last century and the first decades of this century ... Then, the biosphere turned into a [CO_2] sink," which implies a significant increase in global vegetative productivity over the last half of the twentieth century.

More recently, Cao *et al.* (2004) derived net primary production (NPP) values at 8-km and 10-day resolutions for the period 1981-2000 using variables based almost entirely on satellite observations, as described in the Global Production Efficiency Model (GLO-PEM), which consists, in their words, "of linked components that describe the processes of canopy radiation absorption, utilization, autotrophic respiration, and the regulation of these processes by environmental factors (Prince and Goward, 1995; Goetz *et al.*, 2000)." They learned that over the last two decades of the twentieth century, when temperatures were rising, "there was an increasing trend toward enhanced terrestrial NPP," which they say was "caused mainly by increases in atmospheric carbon dioxide and precipitation."

A year later, Cao *et al.* (2005) used the CEVSA (Carbon Exchanges in the Vegetation-Soil-Atmosphere system) model (Cao and Woodward, 1998; Cao *et al.*, 2002), forced by observed variations in climate and atmospheric CO_2, 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 from 1981-2000 with the GLO-PEM model that uses data almost entirely from remote sensing, including both the normalized difference vegetation index (NDVI) and meteorological variables (Prince and Goward, 1995; Cao *et al.*, 2004). This protocol revealed, in Cao *et al.*'s words, that "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." *However*, they found that "combined changes in temperature and precipitation increased global NEP significantly," and that "increases in atmospheric CO_2 produced further increases in NPP and NEP." They also discovered that "the CO_2 fertilization effect [was] particularly strong in the tropics, compensating for the negative effect of warming on NPP." Enlarging on this point, they write that "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." The end result of the application of these models and measurements was their finding that 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 that "the NEP that was induced by CO_2 fertilization and climatic variation accounted for 30 percent of the total terrestrial carbon sink implied by the atmospheric carbon budget (Schimel *et al.*, 2001), and the fraction changed from 13 percent in the 1980s to 49 percent in the 1990s," which indicates the growing importance of the CO_2 fertilization effect. Also, they say "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," which suggests that as long as the air's CO_2 content continues its upward course, so too will its stimulation of the terrestrial biosphere likely continue its upward course.

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 they found 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 was found to correlate strongly with greening trends in Europe, eastern Eurasia and tropical Africa. Precipitation, on the other hand, was *not* found to be a significant driver of increases in greenness, except for isolated and spatially fragmented regions. Some decreases in greenness were also observed, mainly in the Southern Hemisphere in southern Africa, southern South America and central Australia, which trends were associated with concomitant increases in temperature and decreases in precipitation. There were also large regions of the globe that showed no trend in greenness over the 17-year period, as well as large areas that underwent strong greening that showed no association with trends of either temperature or precipitation. These greening trends, as they concluded, must have been the result of other factors, such as "CO_2 fertilization, reforestation, forest regrowth, woody plant proliferation and trends in agricultural practices," about which others will have more to say as we continue.

Working with satellite observations of vegetative activity over the period 1982 to 1999, Nemani *et al.* (2003) discovered that the productivity of earth's terrestrial vegetation rose significantly over this period. More specifically, they determined that terrestrial net primary production (NPP) increased by 6.17 percent, or 3.42 PgC, over the 18 years between 1982 and 1999. What is more, they observed net positive responses over all latitude bands studied: 4.2 percent (47.5-22.5°S), 7.4 percent (22.5°S-22.5°N), 3.7 percent (22.5-47.5°N), and 6.6 percent (47.5-90.0°N).

The eight researchers 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 everywhere.

With respect to the latter factor, Nemani *et al.* say "an increase in NPP of only 0.2% per 1-ppm increase in CO_2 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 that terrestrial NPP increased by more than 1 percent per year in Amazonia alone, noting that "this result cannot be explained solely by CO_2 fertilization."

We tend to agree with Nemani *et al.* on this point, but also note that the aerial fertilization effect of atmospheric CO_2 enrichment is most pronounced at higher temperatures, rising from next to nothing at a mean temperature of 10°C to a 0.33 percent NPP increase per 1-ppm increase in CO_2 at a mean temperature of 36°C for a mixture of plants comprised predominantly of herbaceous species (Idso and Idso, 1994). For woody plants, we could possibly expect this number to 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 percent to 1 percent NPP increase per 1-ppm increase in atmospheric CO_2, which would represent the lion's share of the growth stimulation observed by Nemani *et al.* in tropical Amazonia.

The message of Nemani *et al.*'s study is that satellite-derived observations indicate the planet's terrestrial vegetation significantly increased its productivity over the last two decades of the twentieth century, in the face of a host of both real and imagined environmental stresses, chief among the latter of which was what the IPCC claims to be unprecedented CO_2-induced global warming.

Perhaps the most striking evidence for the significant twentieth century growth enhancement of earth's forests by the historical increase in the air's CO_2 concentration was provided by the study of Phillips and Gentry (1994). Noting that 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 that global forest productivity was increasing *in situ*. In doing so, they found that the turnover rates of these highly productive forests had indeed been rising ever higher since at least 1960, with an apparent pan-tropical acceleration since 1980. In discussing what might be causing this phenomenon, they stated that "the accelerating increase in turnover coincides with an accelerating buildup of CO_2," and as Pimm and Sugden (1994) stated in a companion article, it was "the consistency and simultaneity of the changes on several continents that lead 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 group of eleven researchers headed by Phillips (Phillips *et al*., 1998), working with data on tree basal area (a surrogate for tropical forest biomass) for the period 1958-1996, which they obtained from several hundred plots of mature tropical trees scattered about the world, found that average forest biomass for the tropics as a whole had increased substantially. In fact, they calculated that the increase amounted to approximately 40 percent of the missing terrestrial carbon sink of the entire globe. They suggested that "intact forests may be helping to buffer the rate of increase in atmospheric CO_2, thereby reducing the impacts of global climate change," as Idso (1991a,b) had earlier suggested, and they identified the aerial fertilization effect of the ongoing rise in the air's CO_2 content as one of the factors responsible for this phenomenon. Other contemporary studies also supported their findings (Grace *et al*., 1995; Malhi *et al*., 1998), verifying the fact that neotropical forests were indeed accumulating ever more carbon. Phillips *et al*. (2002) continued to state that this phenomenon was occurring "possibly in response to the increasing atmospheric concentrations of carbon dioxide (Prentice *et al*., 2001; Malhi and Grace, 2000)."

As time progressed, however, it became less popular (i.e., more "politically incorrect") to report positive biological consequences of the ongoing rise in the air's CO_2 concentration. The conclusions of Phillips and others began to be repeatedly challenged (Sheil, 1995; Sheil and May, 1996; Condit, 1997; Clark, 2002; Clark *et al*., 2003). In response to those challenges, *CO_2 Science* published an editorial rebuttal (see http://www.co2science.org/articles/V6/N25/EDIT.php), after which Phillips, joined by 17 other researchers (Lewis *et al*., 2005b), 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 concerns of the critics of Phillips *et al*.'s work was that their meta-analyses included sites with a wide range of tree census intervals (2-38 years), which they claimed could be confounding or "perhaps even driving conclusions from comparative studies," as Lewis *et al*. (2005b) describe it. However, in Lewis *et al*.'s detailed study of this potential problem, which they concluded was indeed real, they found that re-analysis of Phillips *et al*.'s published results "shows that the pan-tropical increase in stem turnover rates over the late twentieth century cannot be attributed to combining data with differing census intervals." Or as they state more obtusely in another place, "the conclusion that turnover rates have increased in tropical forests over the late twentieth 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*. (2005b) additionally noted that "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, as they continued, "recent analyses from Amazonia have shown that growth, recruitment and mortality rates have simultaneously increased within the same plots over the 1980s and 1990s, as has net above-ground biomass, both in areas largely unaffected, and in those strongly affected, by ENSO events (Baker *et al*., 2004; Lewis *et al*., 2004a; Phillips *et al*., 2004)."

In a satellite study of the world's tropical forests, 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)." This work revealed that solar radiation variability was the primary factor responsible for interannual variations in GPP, followed by temperature and precipitation variability, while in terms of GPP trends, Ichii *et al*. report that "recent changes in atmospheric CO_2 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 0.67 PgC $year^{-1}$ $decade^{-1}$, while in Africa and Asia it was about 0.3 PgC $year^{-1}$ $decade^{-1}$. Likewise, they report that "CO_2 fertilization effects strongly increased recent NPP trends in regional totals."

In a review of these several global forest studies, as well as 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 twentieth century." In doing so, they found that "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 that "less than 7% of forests are in strongly water-limited systems."

Last, Young and Harris (2005) analyzed, 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. In doing so, they employed two different datasets derived from the sensor: the Pathfinder AVHRR Land (PAL) data set and the Global Inventory Modeling and Mapping Studies (GIMMS) dataset. Based on their analysis of the PAL data, the two researchers determined that "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." With respect to the GIMMS dataset, they report that "even more areas were found to be persistently increasing (greater than 20%) and persistently decreasing (more than 3%)." All in all, they report that "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—which is the ultimate food source for nearly all of the biosphere—the researchers mention global warming (perhaps it's not so bad after all), as well as "associated precipitation change and increases in atmospheric carbon dioxide," citing Myneni *et al*. (1997) and Ichii *et al*. (2002). In addition, they say that "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)).

In conclusion, the results of these many studies demonstrate there has been an increase in plant growth rates throughout the world since the inception of the Industrial Revolution, and that this phenomenon has been gradually accelerating over the years, in concert with the historical increases in the air's CO_2 content and its temperature.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/g/greeningearth.php.

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