

6. BIOLOGICAL EFFECTS OF CO₂

6.1. Plant Productivity Responses

Perhaps the best known consequence of the rise in atmospheric CO₂ is the stimulation of plant productivity. This growth enhancement occurs because, at a fundamental level, carbon dioxide is the basis of almost all life on Earth, serving as the primary raw material utilized by plants to produce the organic matter out of which they construct their tissues. Consequently, the more CO₂ there is in the air, the better plants grow, which *fact* has been confirmed in literally thousands of laboratory and field studies.

Over the past decade, our organization, the Center for the Study of Carbon Dioxide and Global Change, has amassed the largest database in the world detailing that fact. To date, we have archived *thousands* of results from *hundreds* of peer-reviewed research studies conducted by *hundreds* of researchers. Our archive is available free of charge on the Internet at http://www.co2science.org/data/plant_growth/plantgrowth.php. There, we list the photosynthetic and dry weight responses of plants growing in CO₂-enriched air, arranged by scientific or common plant name. We also provide the full peer-reviewed journal reference and the experimental conditions in which the study was conducted for each individual record.

Because of the enormous amount of data contained in our database, it is impossible for us to present the bulk of that data here. Therefore, we have elected to only provide a brief review of a selected handful of herbaceous and woody plants, which findings, nonetheless, represent typical responses for such plants. For information on a particular plant not included below, please consult our online database.

6.1.1 Herbaceous plants

A 300 ppm increase in the air's CO₂ content typically raises the productivity of most herbaceous plants by about one-third (Cure and Acock, 1986; Mortensen, 1987); and this positive response occurs in plants that utilize all three of the major biochemical pathways (C₃, C₄, CAM) of photosynthesis (Poorter, 1993). Thus, with more CO₂ 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 CO₂ enrichment leads to yield increases of 15% for CAM crops, 49% for C₃ cereals, 20% for C₄ cereals, 24% for fruits and melons, 44% for legumes, 48% for roots and tubers and 37% 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 stated that “it should be considered good fortune that we are living in a world of gradually increasing levels of atmospheric CO₂,” and that “the rising level of atmospheric CO₂ 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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6.1.1.1. Alfalfa

What are some of the ways in which the C₃ legume alfalfa (*Medicago sativa* L.) responds to atmospheric CO₂ enrichment? The papers reviewed below deal with this important forage crop and reveal a variety of positive phenomena.

Morgan *et al.* (2001) grew alfalfa for 20 days post-defoliation in growth chambers maintained at atmospheric CO₂ 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 CO₂ treatment attained total dry weights over the 20-day regrowth period that were 62% 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 CO₂ 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% of field capacity. Under these conditions, the CO₂-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-CO₂ air. In addition, under ambient CO₂ conditions, the water stress treatment increased the mean plant root:shoot ratio by 108%, while in the elevated CO₂ treatment it increased it by 269%. As a result, the nodule biomass on the roots of the CO₂-enriched water-stressed plants was 40 and 100% greater than the nodule biomass on the roots of the well-watered and water-stressed plants, respectively, growing in ambient air. Hence, the CO₂-enriched water-stressed plants acquired 31 and 97% more total plant nitrogen than the well-watered and water-stressed

plants, respectively, growing in ambient air. The bottom line, in terms of productivity, was that the CO₂-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 CO₂.

Luscher *et al.* (2000) grew effectively- and ineffectively-nodulating (good nitrogen-fixing vs. poor nitrogen-fixing) alfalfa plants in large FACE plots for multiple growing seasons at atmospheric CO₂ 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 CO₂ increased the yield of *effectively*-nodulating plants by about 50%, regardless of soil nitrogen supply, while it actually caused a 25% yield *reduction* in *ineffectively*-nodulating plants subjected to low soil nitrogen, yet produced an intermediate yield stimulation of 11% 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 CO₂ 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) CO₂ concentrations for twenty-five days, after which water was withheld for five additional days so they could investigate the interactive effects of elevated CO₂ 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 CO₂ exhibited the best water status during the moisture deficit part of the study, as indicated by leaf water potentials that were approximately 30% higher (less negative) than those observed in plants grown in ambient CO₂. This beneficial adjustment was achieved by partial closure of leaf stomata and by greater production of nonstructural carbohydrates (a CO₂-induced enhancement of 50% 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 CO₂-induced difference in total leaf nonstructural carbohydrates disappeared. This may have resulted from an increased mobilization of nonstructural carbohydrates to roots in the elevated CO₂ 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 CO₂-enriched plants during drought conditions.

The plants grown at elevated CO₂ 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% at 600 ppm CO₂, while it plummeted by approximately 30% at 340 ppm, when water was withheld. Moreover, leaf lipid contents in plants grown with atmospheric CO₂ enrichment were about 22 and 83% higher than those measured in plants grown at ambient CO₂ during periods of ample and insufficient soil moisture supply,

respectively. Furthermore, at elevated CO₂ the average amounts of unsaturation for two of the most important lipids involved in thylakoid membrane composition were approximately 20 and 37% 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 CO₂, 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. These effects are so important, in fact, that some researchers have suggested that adaptive plant responses such as these may allow plants to better cope with *any* altered environmental condition that produces stress.

In view of these many positive effects of atmospheric CO₂ enrichment upon the growth and development of alfalfa plants, one can only hope that the air's CO₂ content continues to rise, as we will need all the help we can get from it to be able to feed the world's still-increasing number of people 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/a/agriculturealfalfa.php>.

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6.1.1.2. Cotton

As the CO₂ 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 CO₂ concentrations boosted photosynthetic rates of cotton by 137 to 190% at growth temperatures ranging from 2°C below ambient to 7°C above ambient.

Elevated CO₂ also enhances total plant biomass and harvestable yield. Reddy *et al.* (1998), for example, reported that plant biomass at 700 ppm CO₂ was enhanced by 31 to 78% at growth temperatures ranging from 20 to 40°C, while boll production was increased by 40%. Similarly, Tischler *et al.* (2000) found that a doubling of the atmospheric CO₂ concentration increased seedling biomass by at least 56%.

These results indicate that elevated CO₂ concentrations tend to ameliorate the negative effects of heat stress on productivity and growth in cotton. In addition, Booker (2000) discovered that elevated CO₂ reduced the deleterious effects of elevated ozone on leaf biomass and starch production.

Atmospheric CO₂ enrichment can also induce changes in cotton leaf chemistry that tend to increase carbon sequestration in plant litter and soils. Booker *et al.* (2000), for example, observed that litter produced from cotton plants grown at 720 ppm CO₂ decomposed at rates that were 10 to 14% slower than those displayed by ambiently-grown plants; and after three years of exposure to air containing 550 ppm CO₂, Leavitt *et al.* (1994) reported that 10% of the organic carbon present in soils beneath CO₂-enriched FACE plots resulted from the extra CO₂ supplied to them.

In summary, as the CO₂ content of the air increases, it would seem to be a good bet that 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 CO₂ 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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6.1.1.3. Maize

Nearly all agricultural species respond to increases in the air's CO₂ content by displaying enhanced rates of photosynthesis and biomass production. In this section, we briefly review some of the impacts of these and other related phenomena as they pertain to corn (*Zea mays* L.) or maize as it is often called.

Maroco *et al.* (1999) grew maize plants for 30 days in plexiglass chambers maintained at either ambient or triple-ambient concentrations of atmospheric CO₂ to determine the effects of elevated CO₂ on the growth of this important agricultural C₄ species. This exercise revealed that elevated CO₂ (1100 ppm) increased maize photosynthetic rates by about 15% relative to those measured in plants grown at 350 ppm CO₂, in spite of the fact that both rubisco and PEP-carboxylase were down-regulated. This increase in carbon fixation likely contributed to the 20% greater biomass accumulation observed in the CO₂-enriched plants. In addition, leaves of CO₂-enriched plants contained approximately 10% fewer stomates per unit leaf area than leaves of control plants; and atmospheric CO₂ enrichment reduced stomatal conductance by as much as 71% in elevated-CO₂-grown plants. As a result of these several different phenomena, the higher atmospheric CO₂ concentration greatly increased the intrinsic water-use efficiency of the CO₂-enriched plants.

In a study designed to examine the effects of elevated CO₂ 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 CO₂ 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 C₄ crop such as corn growing under even the *best* of natural conditions, Leakey *et al.* found that "growth at elevated CO₂ significantly increased leaf photosynthetic CO₂ uptake rate by up to 41%." The greatest whole-day increase was 21% (11 July) followed by 11% (22 July), during a period of low rainfall. Thereafter, however, during a period of greater rainfall, there were no significant differences between the photosynthetic rates of the plants in the two CO₂ treatments, so that over the entire growing season, the CO₂-induced increase in leaf photosynthetic rate averaged 10%.

Additionally, on all but the first day of measurements, stomatal conductance was significantly lower (-23% on average) under elevated CO₂ compared to ambient CO₂, which led to reduced transpiration rates in the CO₂-enriched plants on those days as well; and since "low soil water availability and high evaporative demand can both generate water stress and inhibit leaf net

CO₂ assimilation in C₄ plants," they state that the lower stomatal conductance and transpiration rate they observed under elevated CO₂ "may have counteracted the development of water stress under elevated CO₂ and prevented the inhibition of leaf net CO₂ assimilation observed under ambient CO₂."

The ultimate 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 CO₂ to allow the ameliorating effects of elevated CO₂ to significantly enhance leaf net CO₂ assimilation." Hence, they concluded that "this response of *Z. mays* to elevated CO₂ 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 CO₂ 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 C₄ crops of the semi-arid tropics, including sorghum, sugar cane and millet, plus the C₃ crop rice, particularly throughout much of Africa, where *Striga* is one of the region's most economically important parasitic weeds. Here, too, materials archived on our website describe how atmospheric CO₂ enrichment greatly reduces the damage done by this devastating weed [see, for example, Watling and Press (1997) and Watling and Press (2000)].

Baczek-Kwinta and Koscielniak (2003) studied yet another phenomenon that is impacted by atmospheric CO₂ 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 because of its high yield potential. In such circumstances, however, maize can experience a variety of maladies associated with exposure to periods of low air temperature. Hence, to see if elevated CO₂ 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) CO₂ 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 of all, they report that enrichment of the air with CO₂ successfully inhibited the decrease in the maximal quantum efficiency of photosystem 2, both after chilling and during the one-day

recovery period. And in light of all of these positive effects of elevated CO₂, they concluded that "the increase in atmospheric CO₂ 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 20th 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 CO₂ 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 20th century," which totaled 110% 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%. As a result, it can be appreciated that late 20th-century climate change, which is claimed by climate alarmists to have been *unprecedented over the past two millennia* and is often described by them as *one of the greatest threats ever to be faced by humanity*, has definitely *not* been a problem for corn cultivation in Argentina. In fact, it has actually helped it.

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% 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% for corn, "not including the direct effect of increased atmospheric CO₂ concentrations." Adding expected CO₂ 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%.

In light of their fantastic 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." Consequently, if the GCM-based climate-change predictions prove correct, Canada will be immensely blessed by the incredible boost the changed conditions will bring to the country's agricultural productivity, and especially that of corn.

In summary, it seems fairly clear that as the air's CO₂ content continues to rise, and even if the climate of the world changes in the ways suggested by GCM 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 to top it all off, 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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6.1.1.4. Peanut

Stanciel *et al.* (2000) grew peanuts (*Arachis hypogaea* L.) hydroponically for 110 days in controlled environment chambers maintained at atmospheric CO₂ concentrations of 400, 800 and 1200 ppm, finding that the net photosynthetic rates of plants grown at 800 ppm CO₂ were 29% greater than those of plants grown at 400 ppm CO₂, but that plants grown at 1200 ppm CO₂ displayed photosynthetic rates that were 24% lower than those exhibited by plants grown in 400-ppm CO₂ 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 CO₂. Also, harvest index, which is the ratio of seed dry weight to pod dry weight, was 19 and 31% greater at 800 and 1200 ppm CO₂, respectively, than it was at 400 ppm CO₂. In addition, as the atmospheric CO₂ concentration increased, stomatal conductance decreased, becoming 44 and 50% lower at 800 and 1200 ppm than it was at 400 ppm CO₂. Thus, atmospheric CO₂ 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 CO₂ concentrations of 350 and 700 ppm and daytime-maximum/nighttime-minimum air temperatures of 32/22, 36/26, 40/30 and 44/34°C, 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% in response to the experimental doubling of the air's CO₂ content.

Vegetative biomass, on the other hand, increased by 51% and 54% in the ambient and CO₂-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 CO₂-enriched air, so that the final biomass increase over the entire temperature range investigated was 27% in ambient air and 53% in CO₂-enriched air.

When going from the *lowest* temperature *ambient* CO₂ treatment to the *highest* temperature *elevated* CO₂ treatment, however, there was a whopping 106% increase in vegetative biomass.

In contrast, seed yields in both the ambient and CO₂-enriched air dropped dramatically with each of the three temperature increases studied, declining at the highest temperature regime to but a small percentage of what they were at the lowest temperature regime. Nevertheless, Prasad *et al.* report that "seed yields at 36.4/26.4°C under elevated CO₂ were similar to those obtained at 32/22°C under ambient CO₂," the latter pair of which temperatures they describe as "present-day seasonal temperatures."

In light of these findings, 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 CO₂ 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* [our italics] are *common* [our italics] in *many* [our italics] 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* [our italics] than 32/22°C *from planting to maturity* [our italics]."

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* CO₂ 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?), which in turn suggests that for more realistic values of CO₂-induced global warming, i.e., temperature increases on the order of 0.4°C for a doubling of the air's CO₂ 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 CO₂ 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 CO₂, the Rubisco *photosynthetic efficiency* (the ratio of midday light-saturated carbon exchange rate to Rubisco initial or total activity) of the elevated-CO₂ plants "was 1.3- to 1.9-fold greater than that of the ambient-CO₂ plants at both growth temperatures." He also determined that "leaf soluble sugars and starch of plants grown at elevated CO₂ were 1.3- and 2-fold higher, respectively, than those of plants grown at ambient CO₂." In addition, he discovered that the leaf transpiration of the elevated-CO₂ plants relative to that of the ambient-CO₂ plants was 12% less at near-ambient temperatures and 17% less in the higher temperature regime, while the water

use efficiency of the elevated-CO₂ plants relative to the ambient-CO₂ plants was 56% greater at near-ambient temperatures and 41% greater in the higher temperature environment.

In commenting on his findings, Vu notes that because less Rubisco protein was required by the elevated-CO₂ plants, the subsequent redistribution of excess leaf nitrogen "would increase the efficiency of nitrogen use for peanut under elevated CO₂," just as the optimization of inorganic carbon acquisition and greater accumulation of the primary photosynthetic products in the CO₂-enriched plants "would be beneficial for peanut growth at elevated CO₂." Indeed, in the absence of other stresses, Vu's ultimate conclusion was that "peanut photosynthesis would perform well under rising atmospheric CO₂ 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 CO₂ 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 CO₂ 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 CO₂ on plant growth and development are included in the analyses*. These results support the findings published later in this chapter, which describe the stress-ameliorating effects of atmospheric CO₂ 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 CO₂ content were to materialize, the concurrent rise in the air's CO₂ 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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6.1.1.5. Potato

In the study of Sicher and Bunce (1999), exposure to twice-ambient atmospheric CO₂ concentrations enhanced rates of net photosynthesis in potato plants (*Solanum tuberosum* L.) by 49%; while in the study of Schapendonk *et al.* (2000), a doubling of the air's CO₂ content led to an 80% 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 CO₂ concentrations boosted net photosynthesis by 36% at a VPD of 0.5 kPa (moist air) but by 70% 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 CO₂ 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% and that of the latter by 53%. In addition, although they did not directly report photosynthetic rates, Louche-Tessandier *et al.* (1999) noted that photosynthetic acclimation was reduced in CO₂-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 CO₂ concentrations stimulate photosynthesis in potatoes, it is only to be expected they would also increase potato biomass production. And so they do. Miglietta *et al.* (1998), for example, reported that potatoes grown at 660 ppm CO₂ produced 40% more tuber biomass than control plants grown in ambient air. Such reports are common, in fact, with twice-ambient atmospheric CO₂ concentrations having been reported to produce yield increases of 25% (Lawson *et al.*, 2001), 36% (Chen and Setter, 2003), 37% (Schapendonk *et al.*, 2000), 40% (Olivo *et al.*, 2002), 44% (Sicher and Bunce, 1999), 85% (Olivo *et al.*, 2002) and 100% (Ludewig *et al.*, 1998).

A few studies have been conducted at even higher atmospheric CO₂ concentrations. Kauder *et al.* (2000), for example, grew plants for up to seven weeks in controlled environments receiving an extra 600 ppm CO₂, obtaining final tuber yields that were 30% 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 CO₂, Pruski *et al.* (2002) found that the average number of nodes per stem was increased by 64%, the average stem dry weight by 92%, and the average shoot length by 131%.

Atmospheric CO₂ 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 CO₂ concentrations for two consecutive years, finding that the CO₂-enriched plants used 12% less water than the ambient-treatment plants, while they produced 47% more tuber biomass. Hence, the CO₂-enriched plants experienced a 68% increase in *water use efficiency*, 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 CO₂ content increased the instantaneous water-use efficiencies of high-altitude and low-altitude potato species by 90% and 80%, respectively.

In the final phenomenon considered here, we review the findings of three studies that evaluated the ability of atmospheric CO₂ 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 CO₂ concentration for conditions of ambient and high atmospheric O₃ concentrations, as derived from a trans-European set of experiments. At the mean ambient CO₂ concentration of 380 ppm, the high O₃ stress reduced mean tuber yield by approximately 9%. At CO₂ concentrations of 540 and 680 ppm, however, the high O₃ 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 gasses 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 O₃ pollution.

In summary, it is clear that as the CO₂ content of the air increases, potato plants should exhibit increases in photosynthesis, biomass production, water use efficiency and ozone pollution resistance that should significantly enhance the tuber yields of this important agricultural staple.

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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6.1.1.6. 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 ppm CO₂, determining that leaf net photosynthetic rates were significantly higher in the CO₂-enriched chambers than in the ambient-air chambers: 51-75% greater in the *maha* season and 22-33% greater in the *yala* season. Likewise, in the study of Gesch *et al.* (2002), where one-month-old plants were maintained at either 350 ppm CO₂ or switched to a concentration of 700 ppm for ten additional days, the plants switched to CO₂-enriched air immediately displayed large increases in their photosynthetic rates that at the end of the experiment were still 31% 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 CO₂ 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 CO₂ exhibited a 35% 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 CO₂. *And they do.*

In conjunction with the study of DeCosta *et al.* (2003a), DeCosta *et al.* (2003b) found that CO₂-enriched rice plants produced more leaves per hill, more tillers per hill, more total plant biomass, greater root dry weight, more panicles per plant and had harvest indices that were increased by 4% and 2%, respectively, in the *maha* and *yala* seasons, which suite of benefits led to ultimate grain yield increases of 24% and 39% in those two periods. In another study, Kim *et al.* (2003) grew rice crops from the seedling stage to maturity at atmospheric CO₂ concentrations of ambient and ambient plus 200 ppm using FACE technology and three levels of applied nitrogen -- low (LN, 4 g N m⁻²), medium (MN, 8 and 9 g N m⁻²), and high (HN, 15 g N m⁻²) -- for three cropping seasons (1998-2000). They found that "the yield response to elevated CO₂ in crops supplied with MN (+14.6%) or HN (+15.2%) was about twice that of crops supplied with LN (+7.4%)," confirming the importance of N availability to the response of rice to atmospheric CO₂ enrichment that had previously been determined by Kim *et al.* (2001) and Kobaysahi *et al.* (2001).

Various environmental stresses, however, can significantly alter the impact of elevated CO₂ on rice. In the study of Tako *et al.* (2001), for example, rice plants grown at twice-ambient CO₂ concentrations and ambient temperatures displayed no significant increases in biomass production; but when air temperatures were raised by 2°C, the CO₂-enriched plants produced

22% more biomass than the plants grown in non-CO₂-enriched air. In contrast, Ziska *et al.* (1997) reported that CO₂-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 CO₂ boosted their rate of biomass production by 40%. In light of these observations, rice growers should select cultivars that are most responsive to elevated CO₂ concentrations at the air temperatures likely to prevail in their locality in order to maximize their yield production in a future high-CO₂ 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 CO₂ 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 CO₂." They report, for example, that "plants grown under elevated CO₂ were able to maintain midday leaf photosynthesis, and to some extent other photosynthetic-related parameters, longer into the drought period than plants grown at ambient CO₂."

Recovery from the drought-induced water stress was also more rapid in the elevated CO₂ 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 CO₂ [water]-stressed plants to recuperate in midday leaf CER, compared with only 6-8 days for the elevated CO₂ [water]-stressed plants." Similarly, they report that "for the drought imposed during anthesis, midday leaf CER of the elevated CO₂ [water]-stressed plants were fully recovered after 16 days of re-watering, whereas those of the ambient CO₂ [water]-stressed plants were still 21% lagging behind their unstressed controls at that date." Hence, they logically concluded that "rice grown under future rising atmospheric CO₂ 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% of those obtained by uninfected plants. In air of 700 ppm CO₂, however, the infected plants obtained biomass values that were 73% of those obtained by uninfected plants. Thus, atmospheric CO₂ enrichment significantly reduced the negative impact of this parasite on biomass production in rice.

In summary, as the CO₂ 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/agricultureric.php>.

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6.1.1.7. Sorghum

Many laboratory and field experiments have demonstrated a significant positive impact of elevated levels of atmospheric CO₂ on total biomass and grain production in the C₄ crop sorghum (*Sorghum bicolor* (L.) Moench), as may be verified by perusing the results posted within the Plant Growth (Dry Weight) section of our website. Here, we briefly summarize the findings of the subset of those studies.

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 CO₂ 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 CO₂ increased grain yield by only 4% in the plots receiving adequate levels of soil moisture but by fully 16% 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 CO₂ concentrations and ambient concentrations plus 300 ppm. In the first of the two years, the extra CO₂ increased sorghum residue production by 14%, while in the second year it increased crop residue production by 24% and *grain* production by 22%. For a CO₂ increase of 200 ppm comparable to that employed in the study of Ottman *et al.*, these figures translate to crop residue increases of 9% and 16% and a grain increase of 15%.

In a review of primary research papers describing results obtained from large-scale FACE experiments conducted over the prior fifteen years, Ainsworth and Long (2005) determined that, in the mean, sorghum grain yield was increased by approximately 7% in response to a 200-ppm increase in the atmosphere's CO₂ 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 C₃ 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 CO₂. In the absence of parasite infection, the extra 350 ppm of CO₂ boosted plant biomass production by 35%, 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%. When infected with *S. asiatica*, the biomass stimulation provided by the extra CO₂ was about the same; but when infected with *S. hermonthica*, it was almost 80%, which corresponds to a similarly downward adjusted biomass increase of 45%.

In light of these several observations, it would appear that although the CO₂-induced increase in total biomass and grain yield of sorghum is rather modest, ranging from 4 to 16% 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% has been observed) and by parasitic infection (45% has been observed). Consequently, elevated levels of atmospheric CO₂ 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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6.1.1.8. 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." Consequently, it is important to determine how soybeans will likely respond to rising atmospheric CO₂ concentrations with and without concomitant increases in air temperature and under both well-watered and water-stressed conditions. In this section we provide that information in a brief review of the results of several studies that have investigated these aspects of the subject.

Rogers *et al.* (2004) grew soybeans from emergence to grain maturity in ambient and CO₂-enriched air (372 and 552 ppm CO₂, respectively) at the SoyFACE facility of the University of Illinois at Urbana-Champaign, Illinois, USA, while CO₂ 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% in the elevated CO₂ treatment, while mid-day stomatal conductance dropped by 21.9%, in response to the 48% increase in atmospheric CO₂

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% theoretical maximum increase calculated from Rubisco kinetics." Thus, there is an opportunity for soybeans to perhaps become even more responsive to atmospheric CO₂ 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 CO₂ concentrations of ambient and ambient +350 ppm at the Beltsville Agricultural Research Center in Maryland, USA, where net CO₂ 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% greater in the plants growing in the CO₂-enriched air, while nighttime respiration per unit leaf area was not affected by elevated CO₂. However, because the elevated CO₂ increased leaf dry mass per unit area by an average of 23%, respiration *per unit mass* was significantly lower for the leaves of the soybeans growing in the CO₂-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 CO₂ 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 CO₂ concentration back to its pre-dawn maximum value. In an attempt to see if the pre-dawn CO₂ spikes they observed impacted 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 CO₂, a constant 370 ppm CO₂ exposure during the day followed by a constant 500 ppm CO₂ exposure at night, and a CO₂ 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 CO₂ cycle they observed in nature. This program revealed that the 24-hour exposure to 370 ppm CO₂ and the 370-ppm-day/500-ppm-night treatments produced essentially the same results in terms of biomass production after 29 days. However, the CO₂ treatment that mimicked the *observed* atmospheric CO₂ pattern resulted in a plant biomass increase of 20%.

In a study that evaluated a whole range of atmospheric CO₂ 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 CO₂ 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 CO₂ concentrations rose. There was, however, no overall significant effect of treatment CO₂ 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 CO₂ 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 CO₂ provided the raw materials to support greater biomass production at each CO₂ 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 aboveground biomass measured at 330 ppm CO₂, the plants that were grown in sub-ambient CO₂ concentrations of 280, 220 and 160 ppm exhibited 12, 33 and 60% *less* biomass, respectively, while plants grown in atmospheric CO₂ concentrations of 660 and 990 ppm displayed 46 and 66% *more* biomass. Hence, it is likely that soybeans began experiencing increases in total nonstructural carbohydrates and yield as the air's CO₂ concentration began to rise with the onset of the Industrial Revolution; and because nonstructural carbohydrate production rises incrementally with incremental increases in the CO₂ content of the air, soybeans will likely continue to produce ever more total nonstructural carbohydrates that will sustain ever greater yields as the CO₂ content of the air continues to rise in the future.

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 CO₂ concentrations of ambient and ambient plus 300 ppm. Averaged over both years, the elevated CO₂ treatment increased photosynthetic rates in the Ripley and Spencer varieties by 76 and 60%, respectively. However, Spencer showed a greater CO₂-induced increase in vegetative biomass than Ripley (132 vs. 65%). Likewise, elevated CO₂ enhanced seed yield in Spencer by 60% but by only 35% in Ripley, suggesting that cultivar selection for favorable yield responses to atmospheric CO₂ 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 CO₂ 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 CO₂ increased total plant dry mass by approximately 40 and 80% in nodulated soybeans grown at low and high nitrogen supply, respectively, while non-nodulated plants exhibited no CO₂-induced growth response at low nitrogen but an approximate 60% growth enhancement at high nitrogen supply. Hence, it would appear that as the air's CO₂ content continues to rise, non-nodulated soybeans will only display increases in biomass 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 CO₂ concentrations of 400 and 710 ppm, finding that the elevated CO₂ increased

photosynthetic rates in all cultivars by an average of 75%. This photosynthetic enhancement led to CO₂-induced increases in seed yield that averaged 40%, except for one of the ancestral varieties that exhibited an 80% increase in seed yield. Consequently, since the air's CO₂ content is anticipated to continue to rise in the years and decades ahead, plant breeders would be wise to consider utilizing the highly-CO₂-responsive ancestral cultivar identified in this study in future breeding programs.

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 CO₂ concentrations of approximately 360 (ambient) or 720 ppm and soil temperatures of 25 (ambient) or 30°C. He found that elevated CO₂ 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% at 13 days into the experiment to 30% at its conclusion eight days later; yet in spite of this *partial* acclimation, which was far from complete, atmospheric CO₂ enrichment significantly enhanced total plant dry weight at final harvest by 36 and 42% 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 CO₂ 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 CO₂ 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 CO₂ significantly decreased daily and cumulative transpirational water losses compared to plants grown at 360 ppm CO₂, regardless of water treatment. In fact, elevated CO₂ reduced total water loss by 25 and 10% in well-watered and water-stressed plants, respectively. Also, drought stress significantly reduced rates of net photosynthesis among plants of both CO₂ treatments. However, plants grown in elevated CO₂ consistently exhibited higher photosynthetic rates than plants grown at ambient CO₂, regardless of soil water status.

At final harvest, the elevated CO₂ 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%. Also, while root dry weight declined for plants grown under conditions of water stress and ambient CO₂ concentration, no such decline was exhibited by plants subjected to atmospheric CO₂ enrichment and water stress. As the atmospheric CO₂ concentration continues to rise, therefore, soybeans will likely display concurrent increases in photosynthesis and decreases in water loss. Thus, in the future, the water-use efficiency of soybeans will likely be significantly enhanced, allowing plants to better tolerate less frequent rains.

Studying *both* water and high-temperature stress were Ferris *et al.* (1999), who grew soybeans in glasshouses maintained at atmospheric CO₂ 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% of that experienced by the control plants. Averaged across all stress treatments and harvests, this protocol revealed that the high CO₂ treatment increased total plant biomass by 41%. Both high-temperature and water-deficit treatments, singly or in combination, reduced overall biomass by approximately the same degree, regardless of CO₂ treatment. Thus, even when the greatest biomass reductions of 17% occurred in the CO₂-enriched and ambiently grown plants, in response to the combined stresses of high temperature and low soil moisture, plants grown in elevated CO₂ still exhibited an average biomass that was 24% greater than that displayed by plants grown in ambient CO₂.

Averaged across all stress treatments and harvests, elevated CO₂ increased seed yield by 32%. In addition, it tended to ameliorate the negative effects of environmental stresses. CO₂-enriched plants that were water stressed, for example, had an average seed yield that was 34% greater than that displayed by water-stressed controls grown at ambient CO₂, while CO₂-enriched plants exposed to high temperatures produced 38% more seed than their respectively stressed counterparts. In fact, the greatest relative impact of elevated CO₂ on seed yield occurred in response to the combined stresses of high temperature and low soil moisture, with CO₂-enriched plants exhibiting a seed yield that was 50% larger than that of similarly stressed plants grown in ambient CO₂.

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 CO₂ 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 CO₂ 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 CO₂ content, and that they would conduct a set of experiments to find the answer.

The curious scientists grew well-watered and fertilized soybean plants from seed to maturity in pots within two controlled-environment chambers, one maintained at an atmospheric CO₂ concentration of 400 ppm and one at 700 ppm. The chambers were initially kept at a constant air temperature of 25°C. At the onset of seed fill, 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

that 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 CO₂ treatment increased the total isoflavone content of the soybean seeds by 8%. In the second experiment, where air temperature during seed fill was 23°C, the extra CO₂ increased total seed isoflavone content by 104%, while in the third experiment, where air temperature during seed fill was 28°C, the CO₂-induced isoflavone increase was 101%. Finally, when drought-stress was added as a third environmental variable, the extra CO₂ boosted total seed isoflavone content by 186% when seed-fill air temperature was 23°C, while at a seed-fill temperature of 28°C, it increased isoflavone content by 38%.

Under all environmental circumstances studied, enriching the air with an extra 300 ppm of CO₂ 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. Consequently, the direct effects of atmospheric CO₂ enrichment on the health-promoting properties of soybean seeds would appear to be universally beneficial and a boon to the entire human race, especially in light of the fact that Bernacchi *et al.* (2005) characterize the soybean as "the world's most important seed legume."

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 CO₂ *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 CO₂ 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 CO₂." In this regard, however, they note that "Heagle *et al.* (1998) observed a positive significant effect of CO₂ 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 CO₂ effect observed by Heagle *et al.*, bode well for the future production of this important crop and its value to society in a CO₂-enriched and warming world. 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 CO₂ content continues to rise, soybeans will likely respond by displaying significant increases in growth and yield, with possible improvements in seed quality; and 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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6.1.1.9. 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 CO₂ displayed photosynthetic rates that were 77 and 106% greater, respectively, than rates displayed by plants grown in ambient air containing 350 ppm CO₂. Similarly, Bushway and Pritts (2002) reported that strawberry plants grown at atmospheric CO₂ concentrations between 700 and 1000 ppm exhibited

photosynthetic rates that were consistently more than 50% greater than rates displayed by control plants.

Because elevated CO₂ stimulates rates of photosynthesis in strawberry plants, it is only to be expected that it would also increase biomass production in this important agricultural species. And it does. After growing plants in air containing an additional 170 ppm CO₂ above ambient concentrations, Deng and Woodward (1998) reported that total fresh fruit weights were 42 and 17% 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 CO₂ content boosted strawberry fruit yield by 62%.

Thus, as the air's CO₂ content continues to rise, strawberry plants will likely exhibit enhanced rates of photosynthesis and biomass production, which should lead to greater fruit yields in this economically important agricultural 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/agriculturestraw.php>.

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6.1.1.10. Sunflower

As the CO₂ content of the air increases, sunflower plants (*Helianthus annuus* L.) will likely display enhanced rates of photosynthetic carbon uptake. In the study of Sims *et al.* (1999), for example, exposure to twice-ambient atmospheric CO₂ concentrations enhanced rates of net photosynthesis in individual upper-canopy sunflower leaves by approximately 50%. Similarly, Luo *et al.* (2000) reported that sunflowers grown at 750 ppm CO₂ displayed canopy carbon uptake rates that were fully 53% greater than those exhibited by plants grown at 400 ppm CO₂.

Because elevated levels of atmospheric CO₂ stimulate rates of photosynthesis in sunflower plants, they should also increase biomass production in this important agricultural species. The study of Zerihun *et al.* (2000) suggests this inference is correct, as they reported that twice-ambient CO₂ concentrations increased whole plant biomass in sunflowers by 44, 13 and 115% when the plants were simultaneously exposed to low, medium and high levels of soil nitrogen.

In summary, it is clear that as the CO₂ content of the air increases, sunflower plants should exhibit enhanced rates of photosynthesis and biomass production, which should consequently lead to greater seed yields in this important agricultural 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/agriculturesun.php>.

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6.1.1.11. Tomato

In the study of Ziska *et al.* (2001), tomato plants (*Lycopersicon esculentum* Mill.) grown at a nocturnal atmospheric CO₂ concentration of 500 ppm displayed total plant biomass values that were 10% greater than those exhibited by control plants growing in air containing 370 ppm CO₂. This result was likely the consequence of the elevated CO₂ reducing the rate of nocturnal respiration in the plants, which would have allowed them to utilize the retained carbon to produce more biomass.

This CO₂-induced benefit, as well as a host of other positive effects of atmospheric CO₂ 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%. However, in fungal-infected plants grown at twice-ambient atmospheric CO₂ concentrations, the elevated CO₂ 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 CO₂ concentration increased the average value of the root-zone salinity threshold in tomato plants by about 60%. In addition, they reported that the water-use efficiency of the CO₂-enriched plants was about twice that of the ambiently-grown plants.

As the CO₂ 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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6.1.1.12. 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 CO₂ concentrations of ambient and ambient plus 350 ppm CO₂ for two years, determining that the elevated CO₂ increased both final grain yield and total aboveground biomass by 19%. In another study, Masle (2000) grew two varieties of wheat for close to a month in greenhouses maintained at atmospheric CO₂ concentrations of 350 and 900 ppm, finding that the CO₂-enriched plants exhibited biomass increases of 52 to 93%, depending upon variety and vernalization treatment.

Based on a plethora of experimental observations of this nature, many scientists 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 21st century, finding that a doubling of the air's CO₂ concentration would likely enhance wheat yields there between 12 and 49% *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 CO₂ concentration with concomitant climate changes derived from five different general circulation models of the atmosphere, they obtained simulated yield increases of 30 to 55%, 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 ten 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 CO₂ increase that drove the predicted changes in climate not been included in the model. When they did include the increase in the air's CO₂ 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% increase in greenhouse gases per year and a doubled climate variability; hence, they would have to be considered highly unlikely to ever occur.

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% 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."

The final paper to deal with this subject that we have reviewed to this point in time is that of Van Ittersum *et al.* (2003), who 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 CO₂ 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 CO₂ content, finding that wheat grain yield increased linearly at a rate of 10-16% for each 100-ppm increase in atmospheric CO₂ concentration, with only a slight concomitant increase in deep drainage (a big win-tiny loss outcome). For a likely future CO₂ increase of 200 ppm, for example, increases in grain yield varied between 3 and 17% for low nitrogen fertilizer application rates and between 21 and 34% 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 CO₂ increase on wheat grain yield were enhanced an extra 3-8% 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%. 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%. Consequently, it was determined that the CO₂-induced increase in temperature predicted by the world's climate alarmists could well increase the net profitability of Western Australian wheat farmers by anywhere from 25-55%, while at the same time mitigating what van Ittersum *et al.* refer to as "one of Australia's most severe land degradation problems."

In light of these several observations, it should be clear to most everyone that in a wide variety of circumstances, atmospheric CO₂ 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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6.1.2. Woody plants

The growth response of woody plants to atmospheric CO₂ enrichment has also been extensively studied. Ceulemans and Mousseau (1994), for example, tabulated the results of 95 separate experimental investigations related to this topic; while 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% for an approximate

doubling of the air's CO₂ 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 CO₂ 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 CO₂ enrichment of the air to be manifest. In the world's longest such experiment, for example, Kimball *et al.* (2007) observed a 70% sustained increase in biomass production over the entire last decade of a 17-year long study in response to a 75% increase in the air's CO₂ 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 several additional studies that have examined the growth response of woody plants to atmospheric CO₂ enrichment, which again, represent only a small fraction of the studies that are archived on our website in our Plant Growth Data section (see http://www.co2science.org/data/plant_growth/plantgrowth.php).

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6.1.2.1. Aspen-Poplar

Several studies have documented the effects of elevated levels of atmospheric CO₂ 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 CO₂ concentrations of 650 ppm exhibited photosynthetic rates that were approximately 10% greater than those displayed by seedlings maintained at ambient CO₂ concentrations; while in the longer five-month study of Kubiske *et al.* (1998), atmospheric CO₂ 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 CO₂-induced photosynthetic increases in two male and two female aspen clones; and when six aspen genotypes were grown in open-top chambers for 2.5 years at atmospheric CO₂ concentrations of 350 and 700 ppm, Curtis *et al.* (2000) reported that the elevated CO₂ concentrations increased rates of net photosynthesis by 128 and 31% at high and low soil nitrogen contents, respectively. In addition, in a study that only looked at air temperature effects that was conducted at ambient CO₂ 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%.

In a FACE study, where O₃-sensitive and O₃-tolerant clones were grown for six months in field plots receiving 360 and 560 ppm CO₂ in combination with ambient and enriched (1.5 times ambient) O₃ levels, Noormets *et al.* (2001) reported that CO₂-induced increases in photosynthetic rates were at least *maintained*, and sometimes even *increased*, when clones were simultaneously exposed to elevated O₃. After an entire year of treatment exposure, in fact, Karnosky *et al.* (1999) noted that the powerful ameliorating effect of elevated CO₂ on ozone-induced damage was still operating strongly in this system; for O₃-induced foliar damages in O₃-sensitive and O₃-tolerant clones were reduced from 55 and 17%, respectively, at ambient CO₂, to 38 and 3%, respectively, at elevated CO₂.

With respect to biomass production, Pregitzer *et al.* (2000) reported that 2.5 years of exposure to twice-ambient concentrations of atmospheric CO₂ increased fine-root biomass in six aspen genotypes by an average of 65 and 17% on nitrogen-rich and nitrogen-poor soils, respectively. Using this same experimental system, Zak *et al.* (2000) determined that elevated CO₂ enhanced total seedling biomass by 38% at high soil nitrogen and by 16% 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% CO₂-induced increases in total seedling biomass at high and low soil nitrogen levels, respectively.

Thus, as the air's CO₂ content continues to increase, aspen seedlings will likely display enhanced rates of photosynthesis and biomass production, regardless of genotype, gender, O₃-sensitivity, 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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6.1.2.2. 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 CO₂ concentrations of

either 370 or 570 ppm. Over the first year of their study, the saplings growing on calcareous soil in CO₂-enriched air exhibited a 9% increase in stem diameter; and they speculated that this initial small difference may ultimately "cumulate to higher 'final' tree biomass through compounding interest."

And they were right! At the end of *three* years of differential CO₂ exposure, the trees in the CO₂-enriched chambers were experiencing net ecosystem carbon exchange rates that were 58% greater than the rates of the trees in the ambient CO₂ chambers, regardless of soil type; while the stem dry mass of the CO₂-enriched trees was increased by about 13% 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 CO₂ concentrations of 350 and 700 ppm, finding that the doubling of the air's CO₂ content increased seedling carbon uptake by 63%. They also noted that the majority of the assimilated carbon was allocated to the early development of leaves, which would clearly 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 CO₂ concentrations displayed large reductions in photosynthetic rates when simultaneously exposed to twice-ambient levels of ozone. However, at twice-ambient CO₂ concentrations, twice-ambient ozone concentrations had no negative effects on the trees' photosynthetic rates. Thus, atmospheric CO₂ 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 CO₂ 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 CO₂-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 CO₂-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 ¹²C and ¹³C 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% over that time period, no doubt in response to the concomitant rise in the air's CO₂ concentration over the last 100 years.

In conclusion, as the CO₂ 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 CO₂ 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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6.1.2.3. Birch

In the relatively short-term study of Wayne *et al.* (1998), yellow birch seedlings (*Betula pendula*) grown for two months at atmospheric CO₂ concentrations of 800 ppm exhibited photosynthetic rates that were about 50% greater than those displayed by control seedlings fumigated with air containing 400 ppm CO₂. Similarly, in the three-month study of Tjoelker *et al.* (1998a), paper birch seedlings grown at 580 ppm CO₂ displayed photosynthetic rates that were approximately 30% greater than those exhibited by seedlings exposed to 370 ppm CO₂. Likewise, Kellomaki and Wang (2001) reported that birch seedlings exposed to an atmospheric CO₂ concentration of 700 ppm for five months displayed photosynthetic rates that were about 25% greater than seedlings grown at 350 ppm CO₂. 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 CO₂ displayed photosynthetic rates that were fully 110% greater than rates displayed by their ambiently-grown counterparts. Thus, short-

term photosynthetic enhancements resulting from atmospheric CO₂ enrichment appear to persist for several years or longer.

Because elevated CO₂ enhances photosynthetic rates in birch trees, it likely will also lead to increased biomass production in these important deciduous trees, as it indeed has in several experiments. In the three-month study of Tjoelker *et al.* (1998b), for example, a 57% increase in the air's CO₂ content increased the biomass of paper birch seedlings by 50%. When similar seedlings were grown at 700 ppm CO₂ for four months, Catovsky and Bazzaz (1999) reported that elevated CO₂ increased total seedling biomass by 27 and 130% 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 over 50%. In the longer two-year study of Berntson and Bazzaz (1998), twice-ambient levels of CO₂ increased the biomass of a mixed yellow and white birch mesocosm by 31%; and in another two-year study, Wayne *et al.* (1998) reported that yellow birch seedlings grown at 800 ppm CO₂ produced 60 and 227% more biomass than seedlings grown at 400 ppm CO₂ at ambient and elevated air temperatures, respectively. Finally, after exposing silver birch seedlings to twice-ambient CO₂ concentrations for four years, Wang *et al.* (1998) noted that CO₂-enriched seedlings produced 60% more biomass than ambiently-grown seedlings. Hence, atmospheric CO₂ enrichment clearly enhances birch biomass in both short- and medium-term experiments.

In some studies, elevated CO₂ 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 CO₂ for three months experienced 10-25% reductions in stomatal conductance, which contributed to 40-80% increases in water-use efficiency. Similar CO₂-induced reductions in stomatal conductance (21%) were reported in silver birch seedlings grown for four years at 700 ppm CO₂ by Rey and Jarvis (1998).

The results of these several studies suggest that the ongoing rise in the air's CO₂ 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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6.1.2.4. Citrus Trees

How does atmospheric CO₂ 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 CO₂ displayed rates of photosynthesis that were more than 300% greater than those measured on control cuttings grown at 300 ppm CO₂. In addition, elevated CO₂ 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 CO₂ concentrations increased photosynthetic rates in mycorrhizal- and non-mycorrhizal-treated sour orange seedlings by 118 and 18%, respectively.

Such CO₂-induced increases in photosynthesis should ultimately lead to enhanced biomass production; and so they do. Idso and Kimball (2001), for example, have documented how a 75% increase in the air's CO₂ content has boosted the long-term production of aboveground wood and fruit biomass in sour orange trees by 80% in a study that has been ongoing since November of 1987. Furthermore, Idso *et al.* (2002) have additionally demonstrated that the

300-ppm increase in the air's CO₂ content has increased the fresh weight of individual oranges by an average of 4% and the vitamin C content of their juice by an average of 5%.

In summary, these peer-reviewed studies suggest that as the air's CO₂ 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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6.1.2.5. Eucalyptus

In the eight-month study of Roden *et al.* (1999), *Eucalyptus pauciflora* seedlings growing at 700 ppm CO₂ displayed seasonal rates of net photosynthesis that were approximately 30% 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 CO₂ exhibited photosynthetic rates that were 120% higher than those observed in control plants growing at 380 ppm CO₂. Moreover, after a one-month period of water stress,

photosynthetic rates of CO₂-enriched seedlings were still 12% greater than rates displayed by ambiently-grown water-stressed seedlings.

Because elevated CO₂ 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 CO₂ displayed 134 and 98% more biomass than seedlings growing at 400 ppm CO₂ at low and high soil nitrogen concentrations, respectively. Similarly, *Eucalyptus pauciflora* seedlings growing at twice-ambient CO₂ concentrations for eight months produced 53% more biomass than control seedlings (Roden *et al.*, 1999).

In summary, as the CO₂ 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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6.1.2.6. Fruit-Bearing

Several studies have recently documented the effects of elevated atmospheric CO₂ concentrations on photosynthesis in various fruiting trees. In an eight-day experiment, Pan *et al.* (1998) found that twice-ambient CO₂ concentrations increased rates of net photosynthesis in one-year-old apple seedlings by 90%. In a longer three-month study, Keutgen and Chen (2001) noted that cuttings of *Citrus madurensis* exposed to 600 ppm CO₂ displayed rates of photosynthesis that were more than 300% greater than rates observed in control cuttings exposed to 300 ppm CO₂. Likewise, in the review paper of Schaffer *et al.* (1997), it was noted that atmospheric CO₂ 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 CO₂ exhibited photosynthetic rates that were 44% greater than

those displayed by seedlings grown in ambient air, independent of a concomitant soil moisture treatment.

Because elevated CO₂ enhances the photosynthetic rates of fruiting trees, it should also lead to increased biomass production in them. And it does. In the two-year study of Centritto *et al.* (1999b), for example, well-watered and water-stressed seedlings growing at twice-ambient CO₂ concentrations displayed basal trunk areas that were 47 and 51% larger than their respective ambient controls. Similarly, in a study spanning *more than thirteen years*, Idso and Kimball (2001) demonstrated that the aboveground wood biomass of mature sour orange trees growing in air enriched with an additional 300 ppm of CO₂ was 80% greater than that attained by control trees growing in ambient air.

As the CO₂ 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, they were stimulated to essentially the same degree as aboveground wood biomass, i.e., by 80% in response to a 75% increase in the air's CO₂ 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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atmospheric carbon dioxide and root restriction. *Journal of the American Society of Horticultural Science* **122**: 849-855.

6.1.2.7. Nitrogen-Fixing

In the six-week study of Schortemeyer *et al.* (1999), seedlings of *Acacia melanoxylon* grown at twice-ambient atmospheric CO₂ concentrations displayed photosynthetic rates that were 22% greater than those of ambiently-grown seedlings. In addition, the CO₂-enriched seedlings exhibited biomass values that were twice as large as those displayed by control seedlings grown in air of 350 ppm CO₂. Likewise, Polley *et al.* (1999) reported that a doubling of the atmospheric CO₂ concentration for three months increased honey mesquite (*Prosopis glandulosa*) seedling root and shoot biomass by 37 and 46%, respectively.

Several studies have investigated the effects of elevated CO₂ on black locust (*Robinia pseudoacacia*) seedlings. Uselman *et al.* (2000), grew seedlings for three months at 700 ppm CO₂ and reported that this treatment increased the root exudation of organic carbon compounds by 20%, while Uselman *et al.* (1999) reported no CO₂-induced increases in the root exudation of organic nitrogen compounds. Nonetheless, elevated CO₂ enhanced total seedling biomass by 14% (Uselman *et al.*, 2000).

In the study of Olesniewicz and Thomas (1999), black locust seedlings grown at twice-ambient CO₂ concentrations for two months exhibited a 69% 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 CO₂-enriched plants by 212 and 90% in non-inoculated and inoculated seedlings, respectively. Ultimately, elevated CO₂ enhanced total plant biomass by 180 and 51% in non-inoculated and inoculated seedlings, respectively.

Thus, it would appear that as the CO₂ 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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6.1.2.8. Oak

In this next section, we review several published responses of oak (genus *Quercus*) trees to atmospheric CO₂ enrichment.

In the two-month study of Anderson and Tomlinson (1998), northern red oak seedlings exposed to 700 ppm CO₂ displayed photosynthetic rates that were 34 and 69% 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 CO₂ concentrations exhibited rates of photosynthesis at the onset of senescence that were 97% greater than those displayed by ambiently-growing seedlings.

Because elevated CO₂ enhances photosynthetic rates in oak trees, it should also lead to increased biomass production in them; and indeed it does. In the year-long study of Staudt *et al.* (2001), for example, *Quercus ilex* seedlings grown at 700 ppm CO₂ displayed trunk and branch biomasses that were 90% greater than those measured on seedlings growing at 350 ppm CO₂. Also, in the eight-month inter-generational study performed by Polle *et al.* (2001), seedlings produced from acorns collected from ambient and CO₂-enriched mother trees and germinated in air of either ambient or twice-ambient atmospheric CO₂ concentration displayed whole-plant biomass values that were 158 and 246% 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 CO₂ concentrations, finding that elevated CO₂ enhanced seedling biomass by 92 and 128% under well-watered and water-stressed conditions, respectively; and in a similar study conducted by Tomlinson and Anderson (1998), water-stressed seedlings growing at 700 ppm CO₂ displayed biomass values that were similar to those exhibited by well-watered plants growing in ambient air. Thus, atmospheric CO₂ enrichment continues to benefit oak trees even under water-stressed conditions.

Additional studies have demonstrated that oak seedlings also respond positively to atmospheric CO₂ 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 CO₂ concentration enhanced seedling biomass by 140 and 30% 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 CO₂ displayed biomass increases that were 110 and 140% 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 CO₂ 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 CO₂ 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 CO₂ enrichment causing the trees to experience less oxidative stress and, therefore, that they had less need for antioxidative enzymes.

In some studies, elevated CO₂ has also 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 CO₂-emitting spring exhibited less water loss and more favorable turgor pressures than trees growing further away from the springs. In fact, the resulting improvement in water-use efficiency was so significant that Tognetti *et al.* (1998b) stated that "such marked increases in water-use efficiency under elevated CO₂ might be of great importance in Mediterranean environments in the perspective of global climate change."

In summary, it is clear that as the CO₂ 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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6.1.2.9. Pine

6.1.2.9.1. LOBLOLLY

Tissue *et al.* (1997) grew loblolly pine tree seedlings (*Pinus taeda* L.) for a period of four years in open-top chambers maintained at atmospheric CO₂ concentrations of either 350 or 650 ppm in a study of the long-term effects of elevated CO₂ on the growth of this abundant pine species. This experiment indicated there was a mean biomass accumulation in the seedlings grown in CO₂-enriched air that was 90% greater than that attained by the seedlings grown in ambient air.

Johnson *et al.* (1998) reviewed eleven 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 CO₂ 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 CO₂ enrichment were negligible. For

moderate soil nitrogen deficiencies, however, a doubling of the air's CO₂ content sometimes boosted growth by as much as 1,000%. 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ enrichment in this *Duke Forest Face Study*, the growth rate of the CO₂-enriched trees was about 24% greater than that of the trees exposed to ambient CO₂, in spite of the likelihood of soil nutrient limitations and a severe summer drought (rainfall in August 1997 was about 90% 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 CO₂ had increased the average yearly dry matter production of the CO₂-enriched trees by 32%, 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% 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 CO₂ 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 CO₂ had increased the average standing crop of fine roots by 23%.

Returning to other types of studies, Gavazzi *et al.* (2000) grew one-year-old loblolly pine seedlings for about four months in pots placed within growth chambers maintained at atmospheric CO₂ concentrations of either 360 or 660 ppm and adequate or inadequate levels of soil moisture, while the pots were seeded with a variety of C₃ and C₄ 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 CO₂ increased total seedling biomass by 22% in both water treatments. In the elevated CO₂ and water-stressed treatment, however, they also found that seedling root-to-shoot ratios were about 80% greater than they were in the elevated CO₂ and well-watered treatment, due to a 63% 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 CO₂ did *not* increase weed biomass; in fact, it *reduced* it by approximately 22%. Consequently, in assessing the effects of elevated CO₂ on competition between loblolly pine seedlings and weeds, the seedlings were definitely the winners, with the researchers concluding that the CO₂-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 CO₂ 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 CO₂ enrichment* 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."

Could it be that the results of these comprehensive studies are manifestations of the *greening of the earth* phenomenon, which has been postulated by Idso (1982, 1986, 1995) to result from the historical increase in the air's CO₂ content? The many observations filed under the several sub-sections of the Greening of the Earth heading later in this chapter suggest that such may well be the case. Such is also suggested by the results of the studies reported here, which indicate that as the CO₂ 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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6.1.2.9.2. PONDEROSA

Walker *et al.* (1998b) grew Ponderosa pine seedlings (*Pinus ponderosa* Dougl. ex P. Laws & C. Laws) for an entire year in *controlled environment chambers* with atmospheric CO₂ 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 CO₂ enrichment and soil nutrition on seedling growth and fungal colonization of the seedlings' roots. After twelve 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 CO₂ enrichment. Averaged over all nitrogen and phosphate treatments, total root dry weights at 525 and 700 ppm CO₂ were 92

and 49% greater, respectively, than those observed at ambient CO₂, while shoot dry weights were 83 and 26% greater. Consequently, seedlings grown at 525 and 700 ppm CO₂ had total dry weights that were 86 and 35% greater, respectively, than those measured at ambient CO₂. In addition, elevated CO₂ increased the total number of ectomycorrhizal fungi on roots by 170% at 525 ppm CO₂ and 85% at 700 ppm CO₂ relative to the number observed at ambient CO₂.

Walker *et al.* (1998a) grew Ponderosa pine seedlings for *two* growing seasons *out-of-doors in open-top chambers* having atmospheric CO₂ concentrations of 350, 525 and 700 ppm on soils of low, medium and high nitrogen content to determine the interactive effects of these variables on juvenile tree growth. The elevated CO₂ concentrations had little effect on most growth parameters after the first growing season, with the one exception of belowground biomass, which increased with both CO₂ and soil nitrogen. After two growing seasons, however, elevated CO₂ significantly increased all growth parameters, including tree height, stem diameter, shoot weight, stem volume and root volume, with the greatest responses typically occurring at the highest CO₂ concentration in the highest soil nitrogen treatment. Root volume at 700 ppm CO₂ and high soil nitrogen, for example, exceeded that of all other treatments by at least 45%, as did shoot volume by 42%. Similarly, at high CO₂ and soil nitrogen coarse root and shoot weights exceeded those at ambient CO₂ and high nitrogen by 80 and 88%, respectively.

Johnson *et al.* (1998) reviewed eleven 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 CO₂ 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 CO₂ enrichment were negligible. For moderate soil nitrogen deficiencies, however, a doubling of the air's CO₂ content sometimes boosted growth by as much as 1,000%. In addition, atmospheric CO₂ enrichment mitigated the negative growth response of ponderosa pine to extremely high soil nitrogen in two separate studies.

Maherali and DeLucia (2000) grew Ponderosa pine seedlings for six months in controlled environment chambers maintained at atmospheric CO₂ concentrations ranging from 350 to 1100 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 CO₂ had no significant effect on stomatal conductance, seedlings grown in the high temperature treatment exhibited a 15% 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% in the low temperature treatment and 62% in the high temperature treatment when the atmospheric CO₂ concentration was raised from 350 to 1100 ppm.

Tingey *et al.* (2005) studied the effects of atmospheric CO₂ 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 CO₂ 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 CO₂ while intensity increased only 20% or less," noting that similar *extensity* results had been obtained over shorter periods of 4 months to 2 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 of all, Soule and Knapp (2006) studied Ponderosa pine trees growing naturally at eight different 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 CO₂ 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 CO₂ levels, but where growth, particularly post-1950, has occurred under increasing and substantially higher atmospheric CO₂ concentrations." Utilizing meteorological evaluations of the Palmer Drought Severity Index, they 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 CO₂ are acting as a driving force for increased radial growth of ponderosa pine, but that the overall influence of this effect may be enhanced, reduced or obviated by site-specific conditions."

Summarizing their findings -- which illustrate what one would expect from the results of the growth chamber and field studies described above -- Soule and Knapp recount how they had "hypothesized that ponderosa pine...would respond to gradual increases in atmospheric CO₂ over the past 50 years, and that these effects would be most apparent during drought stress and on environmentally harsh sites," and they 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 CO₂-driven growth-enhancement effect exists for ponderosa pine growing under specific natural conditions within the [USA's] interior Pacific Northwest," providing yet another important real-world example of the ongoing CO₂-induced *greening of the earth*.

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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6.1.2.9.3. SCOTS

Rouhier and Read (1998) grew Scots pine seedlings (*Pinus sylvestris* L.) for four months in growth cabinets maintained at atmospheric CO₂ 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 CO₂ on mycorrhizal fungi and their interactive effects on seedling growth. These procedures resulted in the doubled atmospheric CO₂ content increasing seedling dry mass by an average of 45% regardless of fungal inoculation. In addition, the extra CO₂ increased the number of hyphal tips associated with seedling roots by about 62% for both fungal species. Hyphal growth was also accelerated by elevated CO₂; and after 55 days of treatment, the mycorrhizal network produced by one of the fungal symbionts occupied 444% more area than its counterpart exposed to ambient CO₂.

These results suggest that as the air's CO₂ 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 CO₂ concentrations for six months, while they studied the effects of elevated CO₂ on root growth and respiration. In doing so, they learned that the elevated CO₂ treatment significantly increased total root length by 122% and dry mass by 135% relative to the roots of seedlings grown in ambient-CO₂ air. In addition, although starch

accumulation in the CO₂-enriched roots was nearly 90% greater than that observed in the roots produced in the ambient-CO₂ treatment, the carbon-to-nitrogen ratio of the CO₂-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 CO₂ enrichment with the huge root systems they typically produce in CO₂-enriched air.

Kainulainen *et al.* (1998) constructed open-top chambers around Scots pine trees that were about twenty years old and fumigated them with combinations of ambient or CO₂-enriched air (645 ppm) and ambient or twice-ambient (20 to 40 ppb) ozone-enriched air for three growing seasons to study the interactive effects of these gases on starch and secondary metabolite production. In doing so, they determined that elevated CO₂ and O₃ (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 CO₂ alone significantly enhanced starch production in current-year needles, although neither extra CO₂, extra O₃, 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 CO₂ 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 CO₂-enriched air reduced cumulative sap flow by 14% at ambient air temperatures, but that sap flow was unaffected by atmospheric CO₂ concentration in the trees growing at the elevated air temperatures. These findings suggest that cumulative water-use by Scotts pine trees in a CO₂-enriched world of the future will likely be less than or equal to -- but no more than -- what it is today.

Seven years later, however, 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 CO₂ 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 CO₂ 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 CO₂ was similar to that of elevated temperature alone, indicating a dominant role for temperature and a lack of interaction between elevated CO₂ and temperature." These observations suggest that as the air's CO₂ 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. As demonstrated in various places throughout our website, however, there is good reason to believe we will not see *CO₂-induced* global temperature increases of the magnitude employed in this study during what yet remains of the current interglacial.

Also working with closed-top chambers that were constructed around 20-year-old Scots pines and fumigated with air containing 350 and 700 ppm CO₂ 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 CO₂ 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 CO₂-enriched trees growing at ambient air temperatures was 57% greater than that displayed by control trees growing at ambient CO₂ and ambient air temperatures, while the trees exposed to elevated CO₂ and elevated air temperature exhibited cumulative stem-diameter growth that was 67% greater than that displayed by trees exposed to ambient-CO₂ air and ambient air temperatures. Consequently, as the air's CO₂ 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 CO₂ 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 CO₂ during growth did *not* affect subsequent rates of needle decomposition, nor did elevated O₃ 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 CO₂ 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%, respectively. However, when the air's CO₂ concentration was simultaneously increased from 350 to 700 ppm, the corresponding mean NPP increases rose to 41 and 55%. Last of all, when the air's CO₂ content was doubled at the prevailing ambient temperature, the mean value of the NPP rose by 27%. Consequently, as the air's CO₂ 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 CO₂ 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 CO₂-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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6.1.2.10. Spruce

In this next section, we review some recently published responses of spruce trees (genus *Picea*) to atmospheric CO₂ enrichment.

Several studies have recently documented the effects of elevated CO₂ on photosynthesis in various varieties of spruce. In the relatively short-term study of Tjoelker *et al.* (1998a), black spruce seedlings grown for three months at atmospheric CO₂ concentrations of 580 ppm exhibited photosynthetic rates that were about 28% greater than those displayed by control seedlings fumigated with air containing 370 ppm CO₂. Similarly, Egli *et al.* (1998) reported that Norway spruce seedlings grown at 570 ppm CO₂ displayed photosynthetic rates that were 35% 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 CO₂ enhanced rates of photosynthesis in current-year needles by 50% in Norway spruce (Roberntz and Stockfors, 1998) and 100% in Sitka spruce (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 CO₂ exhibited photosynthetic rates that were 19 and 33% greater than those observed in control trees growing in ambient air and receiving low and high amounts of nitrogen fertilization, respectively.

Because elevated CO₂ enhances photosynthetic rates in spruce species, this phenomenon should lead to increased biomass production in these important coniferous trees; and so it does. In the short-term three-month study of Tjoelker *et al.* (1998b), for example, black spruce seedlings receiving an extra 210 ppm CO₂ displayed final dry weights that were about 20% greater than those of seedlings growing at ambient CO₂. Similarly, after growing Sitka spruce for three years in open-top chambers, Centritto *et al.* (1999) reported that a doubling of the atmospheric CO₂ concentration enhanced sapling dry mass by 42%.

In summary, it is clear that as the CO₂ 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/treespruce.php>.

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6.1.2.11. Tropical

Several studies have recently documented the effects of elevated atmospheric CO₂ 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 CO₂ concentration of 860 ppm exhibited photosynthetic rates that were consistently 50-100% greater than those displayed by control seedlings fumigated with air containing 390 ppm CO₂. Similarly, Lovelock *et al.* (1999b) reported that a 10-month 390-ppm increase in the air's CO₂ content boosted rates of net photosynthesis in 30-m tall *Luehea seemannii* trees by 30%. Likewise, in the review paper of Schaffer *et al.* (1999), it was noted that atmospheric CO₂ 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 1700-m² synthetic rainforest mesocosm displayed a 79% enhancement in net ecosystem carbon exchange rate in response to a 72% increase in the air's CO₂ content.

Because elevated CO₂ enhances photosynthetic rates in tropical and sub-tropical trees, it should also lead to increased carbohydrate and biomass production in these species. And it does! At a tropical forest research site in Panama, for example, twice-ambient CO₂ concentrations enhanced foliar sugar concentrations by up to 30% (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 CO₂ (700 ppm) enhanced dry weights of an "uncut" Brazilian savannah tree species (*Keilmeyera coriacea*) by about 50%, while it enhanced the dry weight of the same "cut" species by nearly 300%. Although not specifically

quantified, Schaffer *et al.* (1997) noted that twice-ambient CO₂ 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 CO₂ concentration increased seedling dry weight in *Schima superba* by 14 and 49% when grown at ambient and elevated (5°C above ambient) air temperatures, respectively.

Thus, it is clear that as the air's CO₂ 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 CO₂ 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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6.1.2.12. Wood Density

Numerous experiments have demonstrated that trees grown in air enriched with CO₂ nearly always sequester more biomass in their trunks and branches than do trees grown in ambient air. Several studies have also looked at the effects of elevated CO₂ on the *density* of that sequestered biomass, some of which are summarized here.

Rogers *et al.* (1983) observed no difference in the wood density of loblolly pine (*Pinus taeda*) trees grown at 340 and 718 ppm CO₂ for ten weeks; but they found a 33% CO₂-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 CO₂, finding no effect of atmospheric CO₂ enrichment on the stem density of sweetgum, but a mean increase of 9% in the stem density of loblolly pine.

Conroy *et al.* (1990) grew seedlings of two *Pinus radiata* families at 340 and 660 ppm CO₂ for 114 weeks, finding CO₂-induced trunk density increases for the two families of 5.4 and 5.6% when soil phosphorus was less than adequate and increases of 5.6 and 1.2% when it was 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 CO₂ concentrations of 280, 420 and 560 ppm at three different rates of wet nitrogen deposition. On average, they found that wood density was 12% greater in the trees grown at the two higher CO₂ 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 CO₂ for three years, during which time the wood density of the trees increased by approximately 7%. Tognetti *et al.* (1998) studied two species of oak tree - one deciduous (*Quercus pubescens*) and one evergreen (*Quercus ilex*) - growing in the vicinity of CO₂ springs in central Italy that raised the CO₂ concentration of the surrounding air by approximately 385 ppm. This increase in the air's CO₂ content increased the wood density of the deciduous oaks by 4.2% and that of the evergreen oaks by 6.4%.

Telewski *et al.* (1999) grew loblolly pine trees for four years at ambient and ambient plus 300 ppm CO₂. In their study, wood density determined directly from mass and volume measurements was increased by 15% by the extra CO₂; while average ring density determined by X-ray densitometry was increased by 4.5%.

Beismann *et al.* (2002) grew different genotypes of spruce and beech (*Fagus sylvatica*) seedlings for four years in open-top chambers maintained at atmospheric CO₂ concentrations of 370 and 590 ppm in combination with low and high levels of wet nitrogen application on both rich calcareous and poor acidic soils to study the effects of these factors on seedling toughness (fracture characteristics) and rigidity (bending characteristics such as modulus of elasticity). They found that some genotypes of each species were sensitive to elevated CO₂, 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 CO₂ enrichment increased wood toughness in spruce seedlings grown on acidic soils by 12 and 18% at low and high levels of nitrogen deposition, respectively. In addition, atmospheric CO₂ enrichment increased this same wood property in spruce seedlings grown on calcareous soils by about 17 and 14% with low and high levels of nitrogen deposition, respectively. In contrast, elevated CO₂ had no significant effects on the mechanical wood properties of beech seedlings, regardless of soil type.

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 CO₂ concentration of approximately 580 ppm and maintained the air in half of each of the two CO₂ treatments at 2°C above ambient. In the ambient temperature treatment the 60% increase in the air's CO₂ concentration significantly increased latewood density by 27% and maximum wood density by 11%, while in the elevated-temperature treatment it significantly increased latewood density by 25% and maximum wood density by 15%. These changes led to mean overall CO₂-induced wood density increases of 2.8% in the ambient-temperature treatment and 5.6% in the elevated-temperature treatment.

In light of these several observations, it is clear that different species of trees sometimes respond differently to atmospheric CO₂ enrichment, and that they respond with still greater variety under different sets of environmental conditions. In general, however, atmospheric CO₂ enrichment tends to increase wood density in both seedlings and mature trees 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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6.1.2.13. Forests

Forests contain perennial trees that remove CO₂ from the atmosphere during photosynthesis and store it's 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 CO₂ content affect forest productivity and carbon sequestration, which has a great impact on the rate of rise of the air's CO₂ 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 CO₂ 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% 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 an 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% 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%. In addition, he determined that a proportional increase in anthropogenic nitrogen deposition likely increased forest net primary productivity by 25%. And when he combined the two effects, the net primary productivity stimulation rose to 40%, 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.

Back 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 pine trees were 65% greater than rates observed in control trees exposed to ambient air. These greater rates of carbon fixation contributed to the 24% greater growth rates observed in the CO_2 -enriched pine trees in the first year of this long-term study (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% 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%, 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% 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 ten-year-old sweetgum plantation in Tennessee, USA, to study the effects of elevated CO_2 on the growth and

productivity of this forest community. After two years of treatment, Norby *et al.* (2001) reported that the modest 35% increase in the air's CO₂ content boosted tree biomass production by an average of 24%. In addition, Wullschlegler and Norby (2001) noted that CO₂-enriched trees displayed rates of transpirational water loss that were approximately 10% lower than those exhibited by control trees grown in ambient air. Consequently, elevated CO₂ enhanced seasonal water use efficiencies of these mature sweetgum trees by 28 to 35%.

On a smaller scale, Pritchard *et al.* (2001) constructed idealized ecosystems (containing five different species) representative of regenerating longleaf pine (*Pinus palustris* Mill.) communities of the southeastern USA, fumigating them for 18 months with air containing 365 and 720 ppm CO₂ to study the effects of elevated CO₂ on this forest community. They reported that elevated CO₂ increased the above- and belowground biomass of the dominant longleaf pine individuals by 20 and 62%, respectively. At the ecosystem level, elevated CO₂ stimulated total aboveground biomass production by an average of 35%. Similar results for regenerating temperate forest communities have been reported by Berntson and Bazzaz (1998), who documented a 31% increase in Transition Hardwood-White Pine-Hemlock forest mesocosm biomass in response to two years of fumigation with twice-ambient concentrations of atmospheric CO₂.

It is thus clear that as the air's CO₂ 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 CO₂-induced increases in growth and range expansion should ultimately result in large increases in global carbon sequestration within forests, and may actually reduce the rate of rise of the air's CO₂ concentration.

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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6.1.3. Aquatic plants

As demonstrated above, it is universally acknowledged that atmospheric CO₂ 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.

6.1.3.1. Freshwater Algae

How do freshwater algae respond to increases in the air's CO₂ 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 CO₂ 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 CO₂. When the cells were harvested (in the exponential growth phase) at the conclusion of this period, the biomass (cell density) of the twice-ambient CO₂ treatment was found to be 10.9% and 8.3% greater than that of the ambient-air treatment in the low- and high-light regimes, respectively, although only the high-light result was statistically significant. The two scientists thus concluded from these observations that a "doubled atmospheric CO₂ concentration would affect the growth of *C. pyrenoidosa* when it grows under bright solar radiation, and such an effect would increase by a great extent when the cell density becomes high." Their data also suggest that 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 CO₂ concentration of the air and three enriched to ten times the ambient CO₂ concentration), Andersen and Andersen (2006) measured the CO₂-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 CO₂-enriched cylinders was increased by 220% in early July, by 90% in mid-August, and by a whopping 3,750% 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 CO₂," 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 CO₂," 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 CO₂ 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 CO₂ concentrations of 350 and 700 ppm that they maintained at two air-water exchange rates characterized by CO₂ 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 CO₂ elevation should become proportional to the increased atmospheric CO₂," which suggests that algal productivity "would double at the predicted increase of atmospheric CO₂ 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 CO₂ 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 CO₂ 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 CO₂," 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 CO₂. This protocol revealed that exposure to the latter high CO₂ 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 CO₂-induced increase in biomass was approximately 300%, while under high light conditions it was approximately 600%.

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 CO₂ 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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6.1.3.2. Freshwater Macrophytes

In this section we discuss the findings of papers that investigate the influence of CO₂ 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 spiralis*) 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 CO₂ concentrations. With the harvesting of plants at the end of the study, this protocol revealed that the CO₂-induced growth enhancement of the plants was *linear* (in contrast to the gradually-declining CO₂-induced growth enhancements typically exhibited by most terrestrial plants as the air's CO₂ content climbs ever higher), and that the linear relationship extended to the highest atmospheric CO₂ concentration studied: 2100 ppm. In addition, he found that the CO₂-induced growth increase experienced by the plants in the higher of the two water temperature treatments (a 128% increase in going from an atmospheric CO₂ concentration of 365 ppm to one of 2100 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; for 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 CO₂ content of the air above the water within which they grew, and that [it] did so from the value of the [then] current global mean (365 ppm) to a concentration fully *ten times larger* [our italics]."

In another study of a closely allied species, Yan *et al.* (2006) collected turions of *Vallisneria spirulosa* from Liangzi Lake, Hubei Province, China, and planted them in tanks containing 15-cm-deep layers of fertile lake sediments, topped with 40 cm of lake water, that were placed in two glasshouses - one maintained at the ambient atmospheric CO₂ concentration of 390 ppm and the other maintained at an elevated concentration of 1000 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 CO₂ was 2.3 times that of plants grown in ambient CO₂, with biomass of leaves, roots and rhizomes increasing by 106%, 183% and 67%, respectively." 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 CO₂ were 1.7-4.3 and 1.9-3.4 times those in ambient CO₂."

Over 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 CO₂ that produced a 10-fold increase in the air's CO₂ concentration. This ultra-CO₂-enrichment led to a 30% increase in plant biomass, as well as "higher O₂ release to the sediment which is important for the cycling and retention of nutrients in sediments of oligotrophic softwater lakes." And when the ultra-CO₂-enrichment was maintained for an entire growing season (May-November), Andersen and Andersen (2006) report that the ten-fold increase in aquatic CO₂ concentration enhanced the biomass production of *Littorella uniflora* by a much larger 78%.

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 CO₂ was continuously circulated. This work revealed that in addition to the leaves of the plants being larger in the CO₂-enriched treatment, there were 75% 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-CO₂ tanks also produced twice

as many flowers as the plants growing in ambient air; and the flowers that blossomed in the CO₂-enriched air were more substantial than those that bloomed in the air of ambient CO₂ concentration: they had more petals, the petals were longer, and they had a greater percent dry matter content, such that each flower consequently weighed about 50% more than each flower in the ambient-air treatment. In addition, the stems that supported the flowers were slightly longer in the CO₂-enriched tanks; and the percent dry matter contents of both the flower and leaf stems were greater, so that the total dry matter in the flower and leaf stems in the CO₂-enriched tanks exceeded that of the flower and leaf stems in the ambient-air tanks by approximately 60%.

Just above the surface of the soil that covered the bottoms of the tanks, there were also noticeable differences. Plants in the CO₂-enriched tanks had more and bigger basal rosette leaves, which were attached to longer stems of greater percent dry matter content, which led to the total biomass of these portions of the plants being 2.9 times greater than the total biomass of the corresponding portions of the plants in the ambient-air tanks. In addition, plants in the CO₂-enriched tanks had more than twice as many unopened basal rosette leaves.

The greatest differences of all, however, were 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 CO₂-enriched tanks than it was in the ambient-air tanks; while the number of major roots produced there was found to be 3.2 times greater. And as with all other plant parts, the percent dry matter contents of the new roots and rhizomes were also greater in the CO₂-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 CO₂-enriched tanks than it was in the ambient-air tanks; while the total dry matter production of all plant parts - those in the submerged soil, those in the free water, and those in the air above - was 3.7 times greater in the high-CO₂ enclosures.

Over the second growing season, the growth enhancement in the high-CO₂ tanks was somewhat less; but the plants in those tanks were so far ahead of the plants in the ambient-air tanks that in their first five months of growth, they produced what it took the plants in the ambient-air tanks fully 21 months to produce.

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 CO₂ 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 CO₂ concentration of the air above the tanks led to only a 19% increase in the biomass production of the plants floating in the cooler water, but that it led to a 66% 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 CO₂ 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 that the photosynthetic and growth rates of the plants growing in ambient air "first decreased, then stagnated, and finally became negative when mean air temperature rose above 30°C." In the high CO₂ treatment, 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 of all, in a study of an *emergent* freshwater macrophyte, Ojala *et al.* (2002) grew water horsetail (*Equisetum fluviatile*) plants at ambient and double-ambient atmospheric CO₂ concentrations and ambient and ambient + 3°C air temperatures for three years, although the plants were only subjected to the double-ambient CO₂ condition for approximately five months of each year. This work revealed that the increase in air temperature boosted maximum shoot biomass by 60%, but that the elevated CO₂ had no effect on this aspect of plant growth. However, elevated CO₂ and temperature - both singly and in combination - positively impacted *root* growth, which was enhanced by 10, 15 and 25% by elevated air temperature, CO₂, and the two factors together, respectively.

In light of the several experimental findings discussed above, we conclude that the ongoing rise in the air's CO₂ 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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6.1.3.3. Marine Macroalgae

How do marine macroalgae respond to increases in the air's CO₂ content? The results of the studies discussed below provide a glimpse of what the future may hold in this regard, as the atmosphere's CO₂ 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 CO₂, air enriched with an extra 650 ppm CO₂, and air enriched with an extra 1250 ppm CO₂ for a period of 19 days. Compared to the control treatments, the relative growth enhancements in the + 650-ppm and +1250-ppm CO₂ treatments were 20% and 60%, respectively, for *G. chilensis*, and 130% and 190%, 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 CO₂-limited, especially when the population density is high and water movement is slow." Hence, as the air's CO₂ 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 CO₂ and O₂ concentrations. In doing so, they found that oxygen concentrations ranging from 10 to 200% of ambient had no significant effect on either the seaweed's daily net carbon gain or its total wet biomass production rate. In contrast, CO₂ concentrations ranging from 67 to 500% of ambient had highly significant effects on these parameters. At twice the ambient CO₂ concentration, for example, daily net carbon gain and total wet biomass production rates were 52 and 314% greater than they were at ambient CO₂.

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%, its mean rate of nitrate uptake during the study's 12-hour light periods by some 200%, and its nitrate reductase activity by approximately 20% over a wide range of substrate nitrate concentrations.

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." As a result, 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, there is reason to believe that just as with freshwater macrophytes, the ongoing rise in the air's CO_2 content should help marine macroalgae to become ever 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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6.1.3.4. Marine Microalgae

How do marine microalgae respond to increases in the air's CO₂ content? Based on the late 20th-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 CO₂; and the more recent work of other researchers seems to suggest the same.

In a study of the unicellular marine diatom *Skeletonema costatum*, 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 $\mu\text{mol m}^{-2} \text{s}^{-1}$, while continuously aerating the culture solutions with air of either 350 or 1000 ppm CO₂ 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 CO₂, 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 CO₂, respectively," and that "the contents of cellular chlorophyll *a* were higher for the alga grown at 1000 ppm CO₂ than that at 350 ppm CO₂." 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 CO₂, 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 CO₂ 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 CO₂ 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% 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 CO₂-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 CO₂ 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 mM) and low (0.5 mM) nitrate concentrations, while continuously aerating half of the cultures with ambient air of approximately 350 ppm CO₂ and the other half with air of approximately 10,000 ppm CO₂. In doing so, they discovered that atmospheric CO₂ 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, on the other hand, the extra CO₂ increased photosynthesis by 114%. In the case of biomass production, the results were even more extreme: in the low-N treatment elevated CO₂ 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 CO₂ in aquatic systems, i.e. whether an increase in atmospheric CO₂ 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 CO₂ greatly stimulated photosynthesis and biomass production, once the logarithmic growth phase had run its course and equilibrium growth was attained, approximately 70% of the carbon assimilated by the chlorophyte was released to the water, while in the low-CO₂ treatment only 35% 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 CO₂ enrichment and sufficient N availability is that the internal C:N balance of the phytoplankton is maintained within a rather tight range. Even more exciting is the fact that 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 CO₂ 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 CO₂ 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 CO₂ 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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6.2. Water Use Efficiency

Another major consequence of atmospheric CO₂ enrichment is that plants exposed to elevated levels of atmospheric CO₂ 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 CO₂ concentrations. In addition, they tend to produce less of these pores per unit area of leaf surface at higher levels of atmospheric CO₂. Both of these changes tend to reduce most plants' rates of water loss by transpiration; and the amount of carbon they gain per unit of water lost – or water-use efficiency – therefore typically rises, greatly increasing their ability to withstand drought. And with fewer and smaller stomatal openings, plants exposed to elevated levels of atmospheric CO₂ are also less susceptible to damage by noxious air pollutants – including ozone and oxides of nitrogen and sulfur – that gain entry into plants via these portals. 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.

6.2.1. Agricultural Species

In the study of Serraj *et al.* (1999), soybeans grown at 700 ppm CO₂ displayed 10 to 25% reductions in total water loss while simultaneously exhibiting increases in dry weight of as much as 33%. Thus, elevated CO₂ significantly increased the water-use efficiencies of the

studied plants. Likewise, Garcia *et al.* (1998) determined that spring wheat grown at 550 ppm CO₂ exhibited a water-use efficiency that was about one-third greater than that exhibited by plants grown at 370 ppm CO₂. Similarly, Hakala *et al.* (1999) reported that twice-ambient CO₂ concentrations increased the water-use efficiency of spring wheat by 70 to 100%, depending on experimental air temperature. In addition, Hunsaker *et al.* (2000) reported CO₂-induced increases in water-use efficiency for field-grown wheat that were 20 and 10% higher than those displayed by ambiently-grown wheat subjected to high and low soil nitrogen regimes, respectively. Also, pea plants grown for two months in growth chambers receiving atmospheric CO₂ concentrations of 700 ppm displayed an average water-use efficiency that was 27% greater than that exhibited by ambiently-grown control plants (Gavito *et al.*, 2000).

In some cases, the water-use efficiency increases caused by atmospheric CO₂ enrichment are spectacularly high. De Luis *et al.* (1999), for example, demonstrated that alfalfa plants subjected to atmospheric CO₂ 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 CO₂ under water-stressed and well-watered conditions, respectively. Also, when grown at an atmospheric CO₂ concentration of 700 ppm, a 2.7-fold increase in water-use efficiency was reported by Malmstrom and Field (1997) for oats infected with the barley yellow dwarf virus.

In addition to enhancing the water-use efficiencies of agricultural C₃ crops, as reported in the preceding paragraphs, elevated CO₂ also enhances the water-use efficiencies of crops possessing alternate carbon fixation pathways. Maroco *et al.* (1999), for example, demonstrated that maize - a C₄ crop - grown for 30 days at an atmospheric CO₂ concentration of 1100 ppm exhibited an intrinsic water-use efficiency that was 225% higher than that of plants grown at 350 ppm CO₂. In addition, Conley *et al.* (2001) reported that a 200-ppm increase in the air's CO₂ content boosted the water-use efficiency of field-grown sorghum by 9 and 19% under well-watered and water-stressed conditions, respectively. Also, Zhu *et al.* (1999) reported that pineapple - a CAM plant - grown at 700 ppm CO₂ exhibited water-use efficiencies that were always significantly greater than those displayed by control plants grown at 350 ppm CO₂ over a range of growth temperatures.

It is clear from the studies above that as the CO₂ content of the air continues to rise, nearly all of earth's agricultural species will respond favorably by exhibiting increases in water-use efficiency. It is thus 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. Therefore, one can expect global agricultural productivity to rise in tandem with future increases in the atmosphere's CO₂ concentration.

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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6.2.2. 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 CO₂ concentrations of 440 and 600 ppm, exhibited cumulative water-use efficiencies that were 17 and 28% greater, respectively, than control communities grown at 280 ppm CO₂. Similarly, Szente *et al.* (1998) reported a doubling of the atmospheric CO₂ concentration increased the water-use efficiency

two C₃ grasses and two broad-leaved species common to the loess grasslands of Budapest by 72 and 266%, respectively. In addition, Leymarie *et al.* (1999) calculated that twice-ambient CO₂ concentrations increased the water-use efficiency of the herbaceous weedy species *Arabidopsis thaliana* by 41 and 120% under well-watered and water-stressed conditions, respectively. Other CO₂-induced increases in C₃ plant water-use efficiency have been documented by Clark *et al.* (1999) for several New Zealand pasture species and Roumet *et al.* (2000) for various Mediterranean herbs.

Elevated CO₂ has also been shown to substantially increase the water-use efficiency of C₄ grassland species. Adams *et al.* (2000), for example, reported that twice-ambient CO₂ concentrations enhanced the daily water-use efficiency of a C₄ tallgrass prairie in Kansas, USA, dominated by *Andropogon gerardii*. LeCain and Morgan (1998) also documented enhanced water-use efficiencies for six different C₄ grasses grown with twice-ambient CO₂ concentrations. Likewise, Seneweera *et al.* (1998) reported that a 650-ppm increase in the air's CO₂ content dramatically increased the water-use efficiency of the perennial C₄ grass *Panicum coloratum*.

As the air's CO₂ content continues to rise, nearly all of earth's grassland species - including both C₃ and C₄ plants - will likely experience increases in water-use efficiency. Concomitantly, the productivity of the world's grasslands should also increase, even if available moisture decreases in certain areas. Moreover, such CO₂-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. Thus, this phenomenon will likely contribute to a greater "greening of the globe."

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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6.2.3. Woody Species

The effect of elevated atmospheric CO₂ 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; Wullschlegler 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 CO₂ for three months, displayed water-use efficiencies that were 40 to 80% larger than those exhibited by their respective controls grown at 370 ppm CO₂.

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 CO₂ displayed water-use efficiencies that were 50% 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 CO₂ had water-use efficiencies that were 52 and 94% 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 CO₂ concentrations for decades, due to their proximity to CO₂-emitting springs and vents in the earth, allowing scientists to assess the long-term effects of this phenomenon. In Venezuela, for example, the water-use efficiency of a common tree exposed to a lifetime atmospheric CO₂ concentration of approximately 1,000 ppm rose 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 CO₂ concentration around 465 ppm exhibited water-use efficiencies that were 100% greater than control trees growing at a lifetime CO₂ 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 CO₂ concentration ranging from 500 to 1000 ppm displayed "such marked increases in water-use efficiency under elevated CO₂," 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 CO₂ concentrations on water-use efficiency are likely to persist and increase with increasing atmospheric CO₂ concentrations.

In some cases, scientists have looked to the past and determined the positive impact the historic rise in the air's CO₂ 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%. Similarly, Feng (1999) used tree-ring chronologies derived from a number of trees in western North America to calculate a 10 to 25% increase in tree water-use efficiency from 1750 to 1970, during which time the atmospheric CO₂ concentration rose by approximately 16%. 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 CO₂ 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 CO₂ for three years, finding that elevated atmospheric CO₂ 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 CO₂ 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 CO₂ 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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6.3. Amelioration of Environmental Stresses

Atmospheric CO₂ enrichment has also been shown to help ameliorate the detrimental effects of several environmental stresses on plant growth and development, including high soil salinity, high air temperature, low light intensity and low levels of soil fertility. Elevated levels of CO₂ have additionally been demonstrated to reduce the severity of low temperature stress, oxidative stress, and the stress of herbivory. In fact, the percentage growth enhancement produced by an increase in the air's CO₂ concentration is generally even greater under stressful and resource-limited conditions than it is when growing conditions are ideal. In this section we examine several such benefits that the rise in atmospheric CO₂ portends for the biosphere.

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 CO₂ with Other Variables.

6.3.1. Disease

As the air's CO₂ content continues to rise, nearly all of earth's plants should continue to exhibit increasing rates of photosynthesis and, as a result, increased biomass production. But what about plants that are suffering from various pathogenic diseases? Will they be able to reap the benefits of the many positive effects of atmospheric CO₂ enrichment?

We begin our exploration of this important subject with some introductory comments of Chakraborty and Datta (2003), who note there are a number of CO₂-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 CO₂," among which 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." In what follows, we summarize the findings of some additional studies we have reviewed on our website that have dealt with these and other related phenomena.

Malmstrom and Field (1997) grew individual oat plants for two months in pots placed within phytocells maintained at atmospheric CO₂ 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 CO₂ stimulated rates of net photosynthesis in all plants, regardless of pathogen infection. However, the greatest percentage increase occurred in diseased individuals (48% vs. 34%). Moreover, atmospheric CO₂ enrichment decreased stomatal conductance by 50% in infected plants but by only 34% in healthy ones, which led to a CO₂-induced doubling of the instantaneous water-use efficiency of the healthy plants, but an

increase of fully 2.7-fold in the diseased plants. Last of all, after 60 days of growth under these conditions, they determined that the extra CO₂ increased total plant biomass by 36% in infected plants, but by only 12% in healthy plants. In addition, while elevated CO₂ had little effect on root growth in the healthy plants, it increased root biomass in the infected plants by up to 60%. Consequently, it can be appreciated that as the CO₂ 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 CO₂ enrichment "may reduce losses of infected plants to drought" and "may enable diseased plants to compete better with healthy neighbors."

Tiedemann and Firsching (2000) grew spring wheat plants from germination to maturity in controlled-environment chambers maintained at ambient (377 ppm) and elevated (612 ppm) concentrations of atmospheric CO₂ and at ambient (20 ppb) and elevated (61 ppb) concentrations of ozone (and combinations thereof), the latter 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 CO₂ increased the photosynthetic rates of the diseased plants by 20 and 42% at the ambient and elevated ozone concentrations, respectively. It also enhanced the yield of the infected plants, increasing it by 57%, 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 CO₂ concentrations of 350 and 700 ppm. In addition, at week five of the study, half of all plants growing in each CO₂ 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% at both atmospheric CO₂ concentrations. However, the elevated CO₂ had increased the total biomass of the healthy and diseased plants by the same amount (+30%), with the result that the *infected* tomato plants grown at 700 ppm CO₂ had biomass values that were essentially identical to those of the *healthy* tomato plants grown at 350 ppm CO₂. Thus, the extra CO₂ *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 CO₂. By these means they determined that the aggressiveness of the pathogen was reduced at the twice-ambient level of atmospheric CO₂, 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 CO₂ the overall level of aggressiveness of the two [pathogen] isolates was significantly reduced on both cultivars."

Simultaneously, however, pathogen *fecundity* was found to *increase* at twice-ambient CO₂. Of this finding, Chakraborty and Datta report that their results "concur with the handful of studies that have demonstrated increased pathogen fecundity at elevated CO₂ (Hibberd *et al.*, 1996a; Klironomos *et al.*, 1997; Chakraborty *et al.*, 2000)." How this happened in the situation they investigated, according to Chakraborty and Datta, is that the overall increase in fecundity at high CO₂ "is a reflection of the altered canopy environment," wherein "the 30% larger *S. scabra* plants at high CO₂ (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 CO₂, it is difficult to know the ultimate outcome of atmospheric CO₂ 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 CO₂ 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 CO₂ 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 CO₂. In these circumstances, the whole-plant biomass of paper birch was increased by 55% in the CO₂-enriched portions of the glasshouse, while that of sugar maple was increased by 30%. Also, concentrations of condensed tannins were increased by 27% in the paper birch (but not the sugar maple) saplings grown in the CO₂-enriched air; and 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 CO₂-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 CO₂ 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 CO₂-enrichment on two of the world's most extensively grown cool-season forage crops (*Lolium perenne* and *Trifolium repens*) at the Swiss FACE facility near Zurich, they determined that "at elevated CO₂ 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 CO₂-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 CO₂ 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.

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 CO₂, reflecting the development of a level of resistance in susceptible cv. Fitzroy at high CO₂." In fact, with respect to the plants inoculated at twelve 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 CO₂."

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 CO₂, 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 CO₂." Consequently, as the air's CO₂ content continues to rise, it would appear that the Fitzroy cultivar of the pasture legume *Stylosanthes scabra* will indeed acquire a greater intrinsic resistance to the devastating anthracnose disease.

McElrone *et al.* (2005) "assessed how elevated CO₂ affects a foliar fungal pathogen, *Phyllosticta minima*, of *Acer rubrum* [red maple] growing in the understory at the Duke Forest free-air CO₂ enrichment experiment in Durham, North Carolina, USA ... in the 6th, 7th, and 8th years of the CO₂ exposure." Surveys conducted in those years, 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 CO₂ "also significantly reduced disease severity in infected plants in all years (e.g. mean lesion area reduced 35%, 50%, and 10% in 2002, 2003, and 2004, respectively)."

What underlying mechanism or mechanisms produced these beneficent consequences? Thinking it could have been a direct deleterious effect of elevated CO₂ on the fungal pathogen, McElrone *et al.* performed some side experiments in controlled environment chambers. However, they found that the elevated CO₂ 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 CO₂ enrichment, but that "stomatal conductance was reduced by 21-36% under elevated CO₂, providing smaller openings for infecting germ tubes." In addition, they concluded that reduced disease severity under elevated CO₂ was also likely due to altered leaf chemistry, as elevated CO₂ increased total leaf phenolic concentrations by 15% and tannin concentrations by 14%.

Because the phenomena they found to be important in reducing the amount and severity of fungal pathogen infection (leaf spot disease) of red maple have been demonstrated to be operative in most other plants as well, McElrone *et al.* say these CO₂-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." And because of their insightful work, that future is looking particularly bright in terms of the never-ending struggle between earth's plants and the pathogens that prey upon them. Although elevated CO₂ helps *both* sides of the conflict, it helps plants *more* and in *more ways*.

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 1000 ppm CO₂ for a period of eight weeks, where they were irrigated daily with a complete nutrient solution containing either 5 or 8 mM NH₄NO₃. 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 constituents identified and quantified.

This work revealed, in the researchers words, that "plants grown at elevated CO₂ and 5 mM NH₄NO₃ showed a marked and significant decrease in content of nicotine in leaves as well as in roots," while at 8 mM NH₄NO₃ the same was found to be true of upper leaves but not of lower leaves and roots. With respect to the PVY part of the study, they further report that the "plants grown at high CO₂ 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

5-liter pots placed within open-top chambers maintained at atmospheric CO₂ 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 antimicrobial compounds, produced in soybeans) in response to the application of β-glucan elicitor (derived from mycelial walls of *Phytophthora sojae*) to carefully created and replicated wounds in the surfaces of several soybean cotyledons. In doing so, they found that the IAC-14 cultivar did *not* exhibit a CO₂-induced change in glyceollin production in response to elicitation - as Braga *et al.* had hypothesized would be the case, since this cultivar is susceptible to stem canker disease -- but they found that the IAC-18 cultivar (which has the potential to resist the disease to varying degrees) experienced a 100% CO₂-induced increase in the amount of glyceollins produced after elicitation, a response the researchers described as *remarkable*. As for its significance, Braga *et al.* say the CO₂-induced response they observed "may increase the potential of the soybean defense since infection at early stages of plant development, followed by a long incubation period before symptoms appear, is characteristic of the stem canker disease cycle caused by Dpm [*Diaporthe phaseolorum* (Cooke & Ellis) Sacc. f. sp. *meridionalis* Morgan-Jones]." Hence, they say the response they observed "indicates that raised CO₂ levels forecasted for next decades may have a real impact on the defensive chemistry of the cultivars."

Last of all, 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 CO₂ concentration on leaf photosynthetic rates of stiff goldenrod (*Solidago rigida*) growing in monoculture for two full seasons, together with its concomitant effects on the incidence and severity of leaf spot disease. Although they found that elevated CO₂ 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 CO₂." More specifically, they found that "disease incidence was on average *more than twice as high* [our italics] under ambient as under elevated CO₂," and that "disease severity (proportion of leaf area with lesions) was on average 67% lower under elevated CO₂ compared to ambient conditions."

In discussing their results, Strengbom and Reich say the "indirect effects from elevated CO₂, i.e., lower disease incidence, had a stronger effect on realized photosynthetic rate than the direct effect of higher CO₂," which as noted above was negligible in their study. Hence, they conclude "it may be necessary to consider potential changes in susceptibility to foliar diseases to correctly estimate the effects on plant photosynthetic rates of elevated CO₂." In addition, they note that the plants grown in CO₂-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 CO₂ (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 CO₂ 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 CO₂ concentrations.

In summation, the vast bulk of the available data clearly suggests that atmospheric CO₂ enrichment asserts its greatest positive influence on *infected* as opposed to *healthy* plants. Moreover, it would appear that elevated CO₂ has the ability to significantly ameliorate the deleterious effects of various stresses imposed upon plants by numerous pathogenic invaders. Consequently, as the atmosphere's CO₂ 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 humanity'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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6.3.2. 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 CO₂ content may impact this phenomenon, for better or for worse. Consequently, 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.

6.3.2.1. 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 CO₂ 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-CO₂-grown foliage did not affect larval growth rates, development or final pupal weights; neither was moth survivorship significantly altered. Hence, the authors concluded that their study "provides no evidence that increasing atmospheric CO₂ concentrations will affect the potential for outbreak of *Operophtera brumata* on this host." What it did show, however, was a significant CO₂-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 CO₂ concentrations of 350 and 700 ppm with bird cherry-oat aphids (*Rhopalosiphum padi*). After nine weeks, the plants growing in the CO₂-enriched air had experienced a 37% increase in productivity and were covered with far fewer aphids than the plants growing in ambient air. The result, therefore, was a win for the favored plants and a loss for the destructive insects.

Goverde *et al.* (1999) collected four genotypes of *Lotus corniculatus* near Paris and grew them in controlled environment chambers kept at atmospheric CO₂ concentrations of 350 and 700 ppm. Larvae of the Common Blue Butterfly (*Polyommatus icarus*) that were allowed to feed upon the foliage produced in the CO₂-enriched air ate more, grew larger and experienced shorter development times than larvae feeding on the foliage produced in the ambient-air treatment, suggesting that this butterfly species will likely become ever more robust and plentiful as the air's CO₂ content continues to rise.

Brooks and Whittaker (1999) removed grassland monoliths containing eggs of the xylem-feeding spittlebug *Neophilaenus lineatus* from the UK's Great Dun Fell in Cumbria and placed them in glasshouses maintained at atmospheric CO₂ concentrations of 350 and 600 ppm for two years. Survival of the spittlebug's nymphal states was reduced by 24% in both of the generations produced in their experiment, suggesting that this particular insect will likely cause less tissue damage to the plants of this species-poor grassland in a CO₂-enriched world of the future.

Joutei *et al.* (2000) grew bean (*Phaseolus vulgaris*) plants in controlled environments kept at atmospheric CO₂ concentrations of 350 and 700 ppm, to which they introduced the destructive agricultural mite *Tetranychus urticae*, observing that female mites produced 34% and 49% less offspring in the CO₂-enriched chambers in their first and second generations, respectively. This CO₂-induced reduction in the reproductive success of this invasive insect, *which negatively affects more than 150 crop species worldwide*, bodes well for mankind's ability to grow the food we will need to feed our growing numbers in the years ahead.

In a somewhat different experiment, Peters *et al.* (2000) fed foliage derived from FACE plots of calcareous grasslands of Switzerland (maintained at 350 and 650 ppm CO₂) to terrestrial slugs, finding they exhibited no preference with respect to the CO₂ treatment from which the foliage was derived. Also, in a study that targeted no specific insect pest, Castells *et al.* (2002) found

that a doubling of the air's CO₂ content enhanced the total phenolic concentrations of two Mediterranean perennial grasses (*Dactylis glomerata* and *Bromus erectus*) by 15% and 87%, respectively, which compounds tend to enhance plant defensive and resistance mechanisms to attacks by both herbivores and pathogens.

Finally, within a still more different context, 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 CO₂ environment than in ambient air, which is a big plus for modern agriculture. In addition, Coviella *et al.* (2000) determined that "elevated CO₂ appears to eliminate differences between transgenic [Bt-containing] and nontransgenic plants for some key insect developmental/fitness variables including length of the larval stage and pupal weight," which could prove to be a big plus for nature in the event of inadvertent Bt gene transference to wild relatives of transgenic crop lines.

In summary, the majority of evidence that has been accumulated to date suggests that rising atmospheric CO₂ 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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6.3.2.2. Woody Plants

6.3.2.2.1. MAPLE

Working with *Acer rubrum* saplings beginning their fourth year of growth in open-top chambers maintained at four different atmospheric CO₂/temperature conditions - (1) ambient temperature, ambient CO₂, (2) ambient temperature, elevated CO₂ (ambient + 300 ppm), (3) elevated temperature (ambient + 3.5°C), ambient CO₂, and (4) elevated temperature, elevated CO₂ - 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 CO₂-enriched foliage ate a comparably poorer food source than those feeding on ambient CO₂-grown plants, irrespective of temperature," and that there was a minor reduction in leaf water content due to CO₂ enrichment. Nevertheless, they found the "CO₂-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* [our italics] on gypsy moth performance." They also found that "irrespective of CO₂ 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, which would appear to confer an *advantage* upon this particular herbivore in this particular situation.

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 CO₂ will increase herbivory (Bezemer and Jones, 1998; Cannon, 1998; Coviella and Trumble, 1999; Hunter, 2001; Lincoln *et al.*, 1993; Whittaker, 1999). However, because there are so many feedbacks and complex interactions among the numerous components of real-world ecosystems, they 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) CO₂ conditions." This forest is dominated by loblolly pine trees that account for fully 92% of the ecosystem's total woody biomass. In addition, it contains 48 species of other woody plants (trees, shrubs and vines) that have naturally established themselves in the forest's understory. 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*.

So what did they find? As Hamilton *et al.* describe it, "we found that elevated CO₂ 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 CO₂ reduced overall herbivory by more than 40%," 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 CO₂ 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 CO₂, 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 CO₂ (Stilling *et al.*, 2003)."

Consequently, and in spite of all of the predictions of increased destruction of natural ecosystems by insects and other herbivorous arthropods in a CO₂-enriched world of the future, just the *opposite* 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 CO₂ 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% per leaf under ambient CO₂ and 3.3% per leaf under elevated CO₂." Greatest effects were observed in 2001, when they report that "across 12 species the average

damage per leaf under ambient CO₂ was 3.1% compared with 1.7% for plants under elevated CO₂," which was "indicative of a 46% decrease in the total area and total mass of leaf tissue damaged by chewing insects in the elevated CO₂ plots."

What was responsible for these welcome results? Knepp *et al.* say that "given the consistent reduction in herbivory under high CO₂ across species in 2001, it appears that some universal feature of chemistry or structure that affected leaf suitability was altered by the treatment." Another possibility they discuss is that "forest herbivory may decrease under elevated CO₂ 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 CO₂ prolongs the time that insect herbivores are susceptible to natural enemies, which may be abundant in open-top chambers and FACE experiments but absent from greenhouse experiments." In addition, they suggest that "decreased foliar quality and increased per capita consumption under elevated CO₂ may increase exposure to toxins and insect mortality," also noting that "CO₂-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-CO₂ world of the future? In their concluding paragraph, Knepp *et al.* say that "in contrast to the view that herbivore damage will increase under elevated CO₂ as a result of compensatory feeding on lower quality foliage, our results and those of Stiling *et al.* (2002) and Hamilton *et al.* (2004) in open experimental systems suggest that damage to trees may decrease."

But what if herbivore-induced damage happens to *increase* - for some strange reason in some situations - in a future CO₂-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 CO₂ concentrations of either 356 or 645 ppm for 70 days to determine the effects of elevated CO₂ on photosynthesis and growth. In addition, on the 49th day of differential CO₂ exposure, 50% of the saplings' leaf area was removed from half of the trees in order to study the impact of concomitant *simulated herbivory*. This protocol revealed that the 70-day CO₂ enrichment treatment increased the total dry weight of the non-defoliated seedlings by about 10%. When the trees were stressed by simulated herbivory, however, the CO₂-enriched maples produced 28% more dry weight over the final phase of the study than the maples in the ambient-air treatment did. This result thus led Kruger *et al.* to conclude that in a high-CO₂ world of the future "sugar maple might be more capable of tolerating severe defoliation events which in the past have been implicated in widespread maple declines."

All in all, therefore, it would appear that earth's maple trees - and probably many, if not most, other trees - may fare much better in the future with respect to the periodic assaults of leaf-damaging herbivores, as the air's CO₂ 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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6.3.2.2.2. OAK

Dury *et al.* (1998) grew four-year-old *Quercus robur* seedlings in pots in greenhouses maintained at ambient and twice-ambient atmospheric CO₂ concentrations in combination with ambient and elevated (ambient plus 3°C) air temperatures for approximately one year to study the interactive effects of elevated CO₂ and temperature on leaf nutritional quality. 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 CO₂ caused a temporary increase in leaf phenolic concentrations and a decrease in leaf nitrogen content.

In one of the first attempts to move outside the laboratory/greenhouse and study the effects of atmospheric CO₂ enrichment on trophic food webs in a natural ecosystem, Stiling *et al.* (1999) enclosed portions of a native scrub-oak community in Florida (USA) within 3.6-m-diameter open-top chambers and fumigated them with air having CO₂ concentrations of either 350 or 700 ppm for approximately one year, in order to see if elevated CO₂ 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% less on the foliage of trees growing in CO₂-enriched air than on the foliage of trees growing in ambient air. In addition, atmospheric CO₂ enrichment consistently reduced the absolute numbers of the study's six leaf miner species. At the same time, however, the elevated CO₂ treatment increased the leaf area consumed by the *less abundant* herbivore miners by approximately 40% relative to the areas mined by the *more abundant* herbivores present on the foliage exposed to ambient air; but in spite of this increase in feeding, the leaf miners in the CO₂-enriched chambers experienced significantly greater mortality than those in the ambient-air chambers. Although CO₂-induced reductions in leaf nitrogen content played a minor role in this phenomenon, the greatest factor contributing to increased herbivore mortality was *a four-fold increase in parasitization by various wasps*, which could more readily detect the more-exposed leaf miners on the CO₂-enriched foliage.

If extended to agricultural ecosystems, these findings suggest that crops may experience less damage from such herbivores in a high-CO₂ world of the future, thus increasing potential harvest and economic gains. In addition, with reduced numbers of leaf miners in CO₂-enriched air, farmers could reduce their dependency upon chemical pesticides to control them, thus reducing the negative impacts of these agricultural chemicals on the environment.

In another study conducted on five scrub-oak forest species at the same experimental facility, Stiling *et al.* (2002b) investigated the effects of an approximate doubling of the air's CO₂ concentration on a number of characteristics of several insect herbivores. As before, they found 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 CO₂ than in ambient CO₂, for all five plant species," *and* they found that "the response to elevated CO₂ 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 CO₂ than in ambient CO₂." These effects were so powerful, in fact, that in addition to the *relative* densities of insect herbivores being reduced in the CO₂-enriched chambers, and "even though there were more leaves of most plant species in the elevated CO₂ chambers," the *total* densities of leaf miners in the high-CO₂ chambers were also lower for all plant species. Consequently, it would appear that in a high-CO₂ 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 CO₂ could boost plant growth *beyond what might be expected based on pure plant responses to elevated CO₂* [our italics]," which is a truly exciting observation.

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% 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 sixteen open-top chambers (half exposed to ambient air and half exposed to air containing an extra 350 ppm of CO₂) 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 CO₂." Specifically, they found that leafminer abundance was 44% lower ($P = 0.096$) in the CO₂-enriched chambers compared to the ambient-air chambers, and that the abundance of leaves suffering chewing damage was 37% lower ($P = 0.072$) in the CO₂-enriched air. The implications of these findings are rather obvious: myrtle oak trees growing in their natural habitat will likely suffer far less damage from both leaf miners and leaf chewers as the air's CO₂ 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 CO₂ was begun in May of 1996, Hall *et al.* (2005b) studied the four species that dominate the community and are present in every experimental chamber: the three oaks (*Quercus myrtifolia*, *Q. chapmanii* and *Q. geminata*) plus the nitrogen-fixing legume *Galactia elliotii*. At three-month intervals from May 2001 to May 2003, undamaged leaves were removed from each of these species in all chambers and analyzed for various chemical constituents, 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 CO₂-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 CO₂-enriched leaves, with across-species mean increases of 6.8% for condensed tannins, 6.1% for hydrolyzable tannins, 5.1% for total phenolics and 4.3% for lignin. In addition, there were large and often significant CO₂-induced decreases in all leaf damage categories among all species: chewing (-48%, $P < 0.001$), mines (-37%, $P = 0.001$), eye spot gall (-45%, $P < 0.001$), leaf tier (-52%, $P = 0.012$), leaf mite (-23%, $P = 0.477$) and leaf gall (-16%, $P = 0.480$). Hall *et al.* thus concluded that the changes they observed in leaf chemical constituents and herbivore damage "suggest that damage to plants may decline as atmospheric CO₂ levels continue to rise."

In the final study to come out of the Florida scrub-oak ecosystem that we have reviewed, Hall *et al.* (2005a) studied the effects of an extra 350 ppm of CO₂ on litter quality, herbivore activity and their interactions. Over the three years of this experiment (2000, 2001, 2002), they determined that "changes in litter chemistry from year to year were far larger than effects of CO₂ or insect damage, suggesting that these may have only minor effects on litter decomposition." The one exception to this finding, in their words, was that "condensed tannin concentrations increased under elevated CO₂ regardless of species, herbivore damage, or growing season," rising by 11% in 2000, 18% in 2001 and 41% in 2002 as a result of atmospheric CO₂ enrichment, as best we can determine from their bar graphs. Also, the five researchers report that "lepidopteran larvae can exhibit slower growth rates when feeding on elevated CO₂ plants (Fajer *et al.*, 1991) and become more susceptible to pathogens, parasitoids, and predators (Lindroth, 1996; Stiling *et al.*, 1999)," noting further that at their field site, "which hosts the longest continuous study of the effects of elevated CO₂ on insects, herbivore populations decline[d] markedly under elevated CO₂ (Stiling *et al.*, 1999, 2002, 2003; Hall *et al.*, 2005)."

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 CO₂ 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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6.3.2.2.3. OTHER

Stiling *et al.* (1999) enclosed portions of a Florida scrub-oak community in open-top chambers and maintained them at atmospheric CO₂ 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 CO₂-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 CO₂-enriched foliage. Consequently, leaf miners in the elevated CO₂ 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 over 98% 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 CO₂ than in ambient CO₂, for all five plant species." In addition, they report that "more host-plant induced mortality was found for all miners on all plants in elevated CO₂ than in ambient CO₂." These effects were so powerful, in fact, that in addition to the *relative* densities of insect herbivores being reduced in the CO₂-enriched chambers, and "even though there were more leaves of most plant species in the elevated CO₂ chambers," the *total* densities of leaf miners in the high-CO₂ chambers were also lower for all plant species.

In another study of oak trees, Dury *et al.* (1998) grew four-year-old *Quercus robur* saplings in pots placed within greenhouses maintained at ambient and twice-ambient atmospheric CO₂ concentrations in combination with ambient and elevated (ambient plus 3°C) air temperatures. Although no herbivores were included in the experiment, the authors determined that elevated CO₂ would "not [be] expected to affect nutritional quality of foliage for spring-feeding larvae." The increase in temperature, however, increased leaf toughness and led them to conclude that insects feeding on such foliage would experience prolonged larval development and reduced growth.

In another study that did not involve herbivores, Gleadow *et al.* (1998) grew eucalyptus seedlings in glasshouses maintained at 400 and 800 ppm CO₂ for a period of six months, observing biomass increases of 98% and 134% in high and low nitrogen treatments, respectively. They also studied a sugar-based compound called *prunasin*, which produces cyanide in response to tissue damage caused by foraging herbivores. Although elevated CO₂ caused no significant change in leaf prunasin content, it was determined that the proportion of nitrogen allocated to prunasin increased by approximately 20% in the CO₂-enriched saplings, suggestive of a *potential* for increased prunasin production had the saplings been under attack by herbivores.

In a study of *simulated* herbivory, Kruger *et al.* (1998) grew seedlings of one-year-old maple (*Acer saccharum*) and two-year-old aspen (*Populus tremuloides*) in glasshouses with atmospheric CO₂ concentrations of 356 and 645 ppm for 70 days. At the 49-day point of the experiment, half of the leaf area on half of the trees in each treatment was removed. This defoliation caused the final dry weights of both species to decline in the ambient-air glasshouse. In the CO₂-enriched glasshouse, on the other hand, the defoliated maple trees ended up weighing just as much as the non-defoliated maple trees; while the defoliated aspen trees ended up weighing a little less, but not significantly less, than their non-defoliated counterparts. Hence, atmospheric CO₂ enrichment helped both species to better recover from the debilitating effect of leaf removal, which suggests that these trees may be better able to deal with the physical damage that might be inflicted upon them by herbivores in a future world of higher atmospheric CO₂ concentration.

In another study of mechanical defoliation, Lovelock *et al.* (1999) grew seedlings of the tropical tree *Copaifera aromatica* for 50 days in pots placed within open-top chambers maintained at atmospheric CO₂ concentrations of 390 and 860 ppm. At the 14-day point of the experiment, half of the seedlings in each treatment had about 40% of their total leaf area removed. In this case, none of the defoliated trees of either CO₂ treatment fully recovered from this

manipulation; but at the end of the experiment, the total plant biomass of the defoliated trees in the CO₂-enriched treatment was 15% greater than that of the defoliated trees in the ambient-CO₂ treatment, again attesting to the benefits of atmospheric CO₂ enrichment in helping trees to deal with herbivory.

Docherty *et al.* (1997) grew beech and sycamore saplings in glasshouses maintained at atmospheric CO₂ concentrations of 350 and 600 ppm, while groups of three sap-feeding aphid species and two sap-feeding leafhopper species were allowed to feed on them. Overall, elevated CO₂ had few significant effects on the performance of the insects, although there was a non-significant tendency for elevated CO₂ to reduce the individual weights and populations sizes of the aphids.

Finally, Hattenschwiler and Schafellner (1999) grew seven-year-old spruce (*Picea abies*) trees at atmospheric CO₂ concentrations of 280, 420 and 560 ppm and various nitrogen deposition treatments for three years, allowing nun moth larvae to feed on current-year needles for a period of 12 days. Larvae placed upon the CO₂-enriched foliage consumed less needle biomass than larvae placed upon the ambiently-grown foliage, regardless of nitrogen treatment. In fact, this effect was so pronounced that the larvae feeding on needles produced by the CO₂-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 CO₂. Since the nun moth is a deadly defoliator that resides in most parts of Europe and East Asia between 40 and 60°N latitude and is commonly regarded as the coniferous counterpart of its close relative the gypsy moth, which feeds primarily on deciduous trees, the results of this study thus suggest that the ongoing rise in the air's CO₂ 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 herbivorous insects as the air's CO₂ 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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6.3.3. Insects

As the atmosphere's CO₂ 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.

6.3.3.1. Aphids

Docherty *et al.* (1997) grew beech and sycamore saplings in glasshouses maintained at atmospheric CO₂ concentrations of 350 and 600 ppm, while groups of three sap-feeding aphid species were allowed to feed on the saplings. Overall, the elevated CO₂ had few significant effects on aphid feeding and performance. There was, however, a non-significant tendency for elevated CO₂ to reduce the individual weights and population sizes of the aphids, suggesting that future increases in the air's CO₂ content *might* reduce aphid feeding pressures on beech and sycamore saplings, and possibly other plants as well.

Whittaker (1999) reviewed the scientific literature dealing with population responses of herbivorous insects to atmospheric CO₂ 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 CO₂ exposure were those classified as phloem feeders, specifically, aphids. Although this finding

appeared to tip the scales in favor of 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 CO₂ concentrations of 350 and 700 ppm before inoculating them with aphids (*Rhopalosiphum padi*). After nine additional weeks of differential CO₂ exposure, the plants were harvested and their associated aphids counted. Although elevated CO₂ increased plant dry matter production by 37%, this phenomenon did *not* result in similar increases in aphid colonization. In fact, the plants grown in air of elevated CO₂ concentration contained *far* fewer aphids than the plants grown in ambient air.

Percy *et al.* (2002) grew the most widely distributed tree species in all of North America - trembling aspen - in twelve 30-m-diameter FACE rings in air maintained at (1) ambient CO₂ and O₃ concentrations, (2) ambient O₃ and elevated CO₂ (560 ppm during daylight hours), (3) ambient CO₂ and elevated O₃ (46.4-55.5 ppb during daylight hours), and (4) elevated CO₂ and O₃ 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 CO₂ did not affect aphid abundance; but it increased the densities of natural enemies of the aphids, which over the long term would tend to reduce aphid numbers. Also, by itself, elevated O₃ did not affect aphid abundance, but it had a strong negative effect on natural enemies of aphids, which over the long term would tend to increase aphid numbers. When both trace gases were applied together, however, elevated CO₂ *completely counteracted* the reduction in the abundance of natural enemies of aphids caused by elevated O₃. Hence, elevated CO₂ tended to reduce the negative impact of aphids on trembling aspen in this comprehensive study.

At about the same time, Holopainen (2002) reviewed the scientific literature dealing with this phenomenon, i.e., the joint effects of elevated concentrations of atmospheric O₃ and CO₂ on aphid-plant interactions. After compiling the results of 26 pertinent studies, it was found that atmospheric CO₂ enrichment increased aphid performance in six studies, decreased it in six studies, and had no significant impact on it in the remaining 14 studies, while similar results were found for aphid-plant interactions in the presence of elevated O₃ concentrations.

Newman (2003) reviewed what was known, and *not* known, about aphid responses to concurrent increases in atmospheric CO₂ and air temperature, while also investigating the subject via the aphid population model of Newman *et al.* (2003). This literature review and model analysis lead him to conclude that when the air's CO₂ concentration and temperature are both elevated, "aphid population dynamics will be more similar to current ambient conditions than expected from the results of experiments studying either factor alone." And if that sounds ambiguous, *it is*. We can only draw the general conclusion, according to Newman, that "insect responses to CO₂ 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 impacts of high temperature, period of exposure, and developmental stage on the survival of the aphid *Metopolophium dirhodum*, which they say "is the most abundant of the three cereal aphid species in Germany and central European countries." This protocol revealed, 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% 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% reduction of population size)." Consequently, 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 CO₂ and O₃ 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 CO₂ (+200 ppm) and O₃ (1.5 x ambient) on the performance of *Ceppegillettea betulaefoliae* aphids feeding on paper birch trees in what they call "the first investigation of the long-term effects of elevated CO₂ and O₃ atmospheres on natural insect herbivore populations." At the individual scale, they report that "elevated CO₂ and O₃ 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 O₃ had a strong positive effect," but that "elevated CO₂ 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 CO₂ or O₃ are also complex." In particular, they note that "tree-feeding aphids show few significant responses to elevated CO₂ (Docherty *et al.*, 1997), while crop-feeding species may respond positively (Awmack *et al.*, 1997; Bezemer *et al.*, 1998; Hughes and Bazzaz, 2001; Zhang *et al.*, 2001; Stacey and Fellowes, 2002), negatively (Newman *et al.*, 1999) or not at all (Hughes and Bazzaz, 2001), and the same species may show different responses on different host plant species (Awmack *et al.*, 1997; Bezemer *et al.*, 1999)." In summarizing their observations, they thus stated that "aphid individual performance did not predict population responses to CO₂ and O₃," and they concluded that "elevated CO₂ and O₃ atmospheres are unlikely to affect *C. betulaefoliae* populations in the presence of natural enemy communities."

In a study of a different aphid (*Chaitophorus stevensis*) conducted at the same FACE site, Mondor *et al.* (2004) focused on 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 CO₂, 38 ppb O₃), elevated CO₂ (537 ppm), elevated O₃ (51 ppb), and elevated CO₂ and O₃ (537 ppm CO₂, 51 ppb O₃). Within each treatment, several aspen leaves containing a single aphid colony of 25 ± 2 individuals were treated in one of two 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% of adults dispersed from the leaf under elevated CO₂, while 100% dispersed under elevated O₃," indicating that the effects of elevated CO₂ and elevated O₃ 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 CO₂ (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 CO₂ levels (Stiling *et al.*, 1999; Percy *et al.*, 2002), but are negatively affected by elevated O₃ (Gate *et al.*, 1995; Percy *et al.*, 2002)."

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 CO₂ concentrations of 370, 550 and 750 ppm. Approximately two months after seeding, 20 apterous adult aphids (*Sitobion avenae*) from an adjacent field were placed 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; and for the next two weeks the number of offspring laid on those plants were recorded and removed daily to measure reproductive activity. Last of all, 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 CO₂ treatment were 32% more numerous than those in ambient air, while aphids in the 750-ppm treatment were 50% more numerous. Alate aphids also produced more offspring on host plants grown in elevated CO₂: 13% more in

the 550-ppm treatment and 19% more in the 750-ppm treatment. As for the wheat plants, Chen *et al.* report that "elevated CO₂ generally enhanced plant height, aboveground biomass, ear length, and number of and dry weight of grains per ear, consistent with most other studies." With respect to aboveground biomass, for example, the 550-ppm treatment displayed an increase of 36%, while the 750-ppm treatment displayed an increase of 50%, 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 CO₂ on the plant traits." Hence, they concluded that "the increased productivity occurring in plants exposed to higher levels of CO₂ more than compensate for the increased capacity of the aphids to cause damage." In this experiment, therefore, we have a situation where both the plant and the insect that feeds on it were simultaneously benefited by the applied increases in atmospheric CO₂ concentration. In other words, the CO₂-induced responses resulted in a win-win situation with no loser, as both plant and insect profited.

Last of all, 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 CO₂ 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 CO₂ levels," (2) "more dry matter and fat content and less soluble protein were found in *A. gossypii* in elevated CO₂," (3) "cotton aphid fecundity significantly increased ... through successive generations reared on plants grown under elevated CO₂," (4) "significantly higher mean relative growth rates were observed in lady beetle larvae under elevated CO₂," 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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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6.3.3.2. 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 CO₂ concentrations of 350 and 600 ppm for 20 months, with and without soil nitrogen fertilization, while 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 CO₂-enriched foliage was not significantly different from that of larvae placed on foliage produced in ambient air, regardless of nitrogen treatment. In addition, feeding upon CO₂-enriched foliage did not affect larval growth rate, development or final pupal weight. Consequently, Kerslake *et al.* state that their study "provides no evidence that increasing atmospheric CO₂ concentrations will affect the potential for outbreak of *Operophtera brumata* on this host."

Hattenschwiler and Schafellner (1999) grew seven-year-old spruce trees at atmospheric CO₂ concentrations of 280, 420 and 560 ppm and 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 twelve 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 CO₂ significantly enhanced needle starch, tannin and phenolic concentrations, while significantly decreasing needle water and nitrogen contents. Thus, atmospheric CO₂ enrichment reduced overall needle quality from the perspective of this foliage-consuming moth, as nitrogen content is the primary factor associated with leaf quality. Increasing nitrogen deposition, on the other hand, tended to enhance needle quality, for it lowered starch, tannin and phenolic concentrations while boosting needle nitrogen content. Nevertheless, the positive influence of nitrogen deposition on needle quality was not large enough to completely offset the quality reduction caused by elevated CO₂.

In light of these observations, it was no surprise that larvae placed on CO₂-enriched foliage consumed less needle biomass than larvae placed on low-CO₂-grown foliage, regardless of nitrogen treatment, and that the larvae feeding on CO₂-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 CO₂. As a result, Hattenschwiler and Schafellner state that "altered needle quality in response to elevated CO₂ will impair the growth and development of *Lymantria monacha* larvae," which should lead to reductions in the degree of spruce tree destruction caused by this voracious defoliator.

Stiling *et al.* (2002) studied the effects of an approximate doubling of the air's CO₂ concentration on a number of characteristics of several insect herbivores feeding on plants native to a scrub-oak forest ecosystem at the Kennedy Space Center, Florida, USA, in eight ambient and eight CO₂-enriched open-top chambers. In describing their findings, 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 CO₂ than in ambient CO₂," and that "the response to elevated CO₂ was the same across all plant species." Also, they report that "more host-plant induced mortality was found for all miners on all plants in elevated CO₂ than in ambient CO₂." These effects were so powerful, in fact, that in addition to the *relative* densities of insect herbivores being reduced in the CO₂-enriched chambers, and "even though there were more leaves of most plant species in the elevated CO₂ chambers," the *total* densities of leaf miners in the high-CO₂ chambers were also lower for all plant species. Hence, it would appear that in a higher CO₂ world of the future, earth's natural ecosystems may well be able to better withstand the onslaughts of various insect pests, including moths, that have plagued them in years and ages past. An interesting implication of this finding, as Stiling *et al.* note, is that "reductions in herbivore loads in elevated CO₂ could boost plant growth *beyond what might be expected based on pure plant responses to elevated CO₂* [our italics]," which is a truly exciting observation.

Williams *et al.* (2003) bagged first instar gypsy moth larvae on branches of red maple saplings that were entering their fourth year of growth within open-top chambers that were maintained

at four sets of CO₂/temperature conditions: (1) ambient temperature, ambient CO₂, (2) ambient temperature, elevated CO₂ (ambient + 300 ppm), (3) elevated temperature (ambient + 3.5°C), ambient CO₂, and (4) elevated temperature, elevated CO₂. Under these conditions they measured several parameters that were required to test their hypothesis that a CO₂-enriched atmosphere would lead to reductions in foliar nitrogen concentrations and increases in defensive phenolics that would in turn lead to increases in insect mortality. The results they obtained indicated, in their words, "that larvae feeding on CO₂-enriched foliage ate a comparably poorer food source than those feeding on ambient CO₂-grown plants, irrespective of temperature." Nevertheless, they determined that "CO₂-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, which is good.

Because increases in the air's CO₂ concentration typically lead to greater decreases in the concentrations of nitrogen in the foliage of C₃ as opposed to C₄ grasses, Barbehenn *et al.* (2004) say "it has been predicted that insect herbivores will increase their feeding damage on C₃ plants to a greater extent than on C₄ plants (Lincoln *et al.*, 1984, 1986; Lambers, 1993). To test this hypothesis, they thus grew *Lolium multiflorum* (Italian ryegrass, a common C₃ pasture grass) and *Bouteloua curtipendula* (sideoats gramma, a native C₄ rangeland grass) in chambers maintained at either the ambient atmospheric CO₂ concentration of 370 ppm or the doubled CO₂ concentration of 740 ppm for two months, after which newly-molted sixth-instar larvae of *Pseudaletia unipuncta* (a grass-specialist noctuid) and *Spodoptera frugiperda* (a generalist noctuid) were allowed to feed upon the grasses' foliage.

As expected, Barbehenn *et al.* found that foliage protein concentration decreased by 20% in the C₃ grass, but by only 1% in the C₄ grass, when they were grown in CO₂-enriched air; and 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 C₃ 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] C₃ grass," and they note that "this result does not support the hypothesis that C₃ plants will be subject to greater rates of herbivory relative to C₄ plants in future [high-CO₂] atmospheric conditions (Lincoln *et al.*, 1984)." In addition, and "despite significant changes in the nutritional quality of *L. multiflorum* under elevated CO₂," they note 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 CO₂ 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 C₃ plants grown under elevated CO₂."

In light of these observations, and contrary to early simplistic thought on the matter, Barbehenn *et al.* suggest "there will not be a single pattern that characterizes all grass feeders" with respect to their feeding preferences and developmental responses in a world where certain C₃ plants may experience foliar protein concentrations 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 impacted by the ongoing rise in the air's CO₂ content.

A case in point is the study of Chen *et al.* (2005), who grew well watered and fertilized cotton plants of two varieties (one expressing *Bacillus thuringiensis* toxin genes and one a non-transgenic cultivar from the same recurrent parent) in pots placed within open-top chambers maintained at either 376 or 754 ppm CO₂ in Sanhe County, Hebei Province, China, from planting in mid-May to harvest in October, 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 CO₂ treatment increased immature boll concentrations of condensed tannins by approximately 22% and 26% in transgenic and non-transgenic 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-CO₂ treatment, the negative cotton bollworm responses were expressed most strongly of all.

Last of all, we report the findings of Rossi *et al.* (2004), who, in a follow-up study to that of Stiling *et al.* that was conducted in the same experimental facilities, 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 sixteen 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 CO₂." Leafminer abundance was 44% lower ($P = 0.096$) in the CO₂-enriched chambers compared to the ambient-air chambers, while the abundance of leaves suffering chewing damage was 37% lower ($P = 0.072$) in the CO₂-enriched air.

In conclusion, and considering the results of all of the studies reviewed in this summary, it would appear that the ongoing rise in the air's CO₂ content will *not* result in greater damage to earth's vegetation by the larvae of the many moths that inhabit the planet. If anything, it could well *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/moths.php>.

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6.3.3.3. Other Insects

We have treated the subject on what effect the air's rising CO₂ content might have on the delicate balance that exists between various plants and the insects that feed on them in some detail with respect to aphids and moths in the previous two subsections of this report. Here, we review the results of studies that have reported on 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 CO₂ concentrations of 350 and 600 ppm. As far as they could determine, there were no significant effects of the extra CO₂ on either the feeding or performance characteristics of either leafhopper species.

In a literature review of more than 30 studies published two years later, Whittaker (1999) found that chewing insects (leaf chewers and leaf miners) showed either no change or actual *reductions* in abundance in response to atmospheric CO₂ enrichment, noting, however, that population reductions in this feeding guild were often accompanied by increased herbivory in response to CO₂-induced reductions in leaf nitrogen content.

Contemporaneously, Stiling *et al.* (1999) reported the results of what may possibly have been the first attempt to study the effects of elevated CO₂ on trophic webs in a natural ecosystem, specifically, a nutrient-poor scrub-oak community in Florida, USA, where sixteen open-top chambers of 3.6-m diameter were fumigated with air of either 350 or 700 ppm CO₂ for approximately one year. At the end of this period, total leaf miner densities were 38% less on the CO₂-enriched foliage than on the foliage of the ambiently-grown plants. Moreover, atmospheric CO₂ enrichment consistently reduced the numbers of all six species of leaf miners studied. In a compensatory development, however, exposure to elevated CO₂ increased the amount of leaf area consumed by the less abundant leaf miners by approximately 40%. Nevertheless, leaf miners in the CO₂-enriched chambers experienced significantly greater mortality than those in the control chambers. Although CO₂-induced reductions in leaf nitrogen content were determined to have played a minor role in the mortality increase, the greatest factor contributing to this phenomenon was a four-fold increase in parasitization by various wasps that could more readily detect the more-exposed leaf miners on the CO₂-enriched foliage.

Three years later, Stiling *et al.* (2002) reported even more dramatic effects of the elevated CO₂ of this experiment on leaf chewers. The relative levels of damage by these insects (primarily larval lepidopterans and grasshoppers) were significantly lower in the elevated CO₂ chambers than in the ambient CO₂ chambers for all five of the plant species that accounted for over 98% of the total plant biomass of the ecosystem. In addition, the response to elevated CO₂ was the same across all plant species. Also, they reported that more *host-plant-induced mortality* was found for all miners on all plants in elevated CO₂ than in ambient CO₂. These effects were so powerful, in fact, that in addition to the *relative* densities of insect herbivores being reduced in the CO₂-enriched chambers, and even though there were more leaves on most plant species in the elevated CO₂ chambers, the *total* densities of leaf miners in the high-CO₂ chambers were also lower for all plant species. An interesting implication of these findings, as expressed by Stiling *et al.*, is that "reductions in herbivore loads in elevated CO₂ could boost plant growth beyond what might be expected based on pure plant responses to elevated CO₂," which is truly an exciting thing to contemplate.

In another 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 CO₂ alone (to 560 ppm during daylight hours), O₃ alone (to 46.4-55.5 ppb during daylight hours), and CO₂ and O₃ together on the forest tent caterpillar (*Malacosoma disstria*), a common leaf-chewing lepidopteran found in North American hardwood forests. By itself, elevated CO₂ *reduced* caterpillar performance by *reducing* female pupal mass; while elevated O₃ alone *improved* caterpillar performance by *increasing* female pupal mass. When

both gases were applied together, however, the elevated CO₂ *completely counteracted* the enhancement of female pupal mass caused by elevated O₃. Hence, either alone or in combination with undesirable increases in the air's O₃ concentration, elevated CO₂ tended to reduce the performance of the forest tent caterpillar. This finding is particularly satisfying because, in the words of Percy *et al.*, "historically, the forest tent caterpillar has defoliated more deciduous forest than any other insect in North America," and because "outbreaks can reduce timber yield up to 90% in one year, and increase tree vulnerability to disease and environmental stress."

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 CO₂ concentrations of 350 and 600 ppm. During the course of their experiment, two generations of the xylem-feeding insect were produced; and in each case, elevated CO₂ reduced the survival of nymphal stages by an average of 24%. Brooks and Whittaker suggest that this reduction in survival rate may have been caused by CO₂-induced reductions in stomatal conductance and transpirational water loss, which may have reduced xylem nutrient-water availability. Whatever the mechanism, the results of this study bode well for the future survival of these species-poor grasslands as the air's CO₂ content continues to rise.

Finally, we report one last study that has nothing to do with CO₂ directly, but with global warming, which climate-alarmists claim is caused by elevated levels of atmospheric CO₂. In this work of Thomas *et al.* (2001), it is demonstrated that, in response to regional warming in the British Isles over the last two decades of the 20th century, there was an unusually rapid northward expansion of the ranges of two species of cricket: the long-winged cone-head (*Conocephalus discolor*) and Roesel's bush cricket (*Metriopectera roeselii*). The reason for this increased rate of range expansion, according to Thomas *et al.*, resides in the fact that, *in response to the regional warming*, the crickets produced "increased fractions of longer-winged (dispersive) individuals in recently founded populations" that "resulted in about 3- to 15-fold increases in expansion rates, allowing these insects to cross habitat disjunctions that would have represented major or complete barriers to dispersal before the expansions started."

In summing up the implications of the various phenomena described in this section, it would appear that both CO₂-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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6.3.4. Interaction of CO₂ and Light on Plant Growth

Is the growth-enhancing effect of atmospheric CO₂ enrichment reduced when light intensities are less than optimal? 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 CO₂ caused greater relative biomass increases in shade-tolerant species than in shade-intolerant or sun-loving species. In fact, in more than half of the studies analyzed, shade-tolerant species experienced CO₂-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 CO₂ concentrations increased the relative growth response of shade-tolerant and shade-intolerant woody species by an average of 51 and 18%, respectively. Moreover, 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. Low light intensity, therefore, is by no means a roadblock to the benefits that come to plants as a consequence of an increase in the air's CO₂ content.

Of course, most general rules do have their exceptions. In one such study, a 200-ppm increase in the air's CO₂ concentration enhanced the photosynthetic rates of sunlit and shaded leaves of sweetgum trees by 92 and 54%, respectively, at one time of year, and by 166 and 68% at another time (Herrick and Thomas, 1999). Likewise, Naumburg and Ellsworth (2000) reported that a 200-ppm increase in the air's CO₂ content boosted steady-state photosynthetic rates in leaves of four hardwood understory species by an average of 60 and 40% under high and low light intensities, respectively. Thus, even though these photosynthetic responses were significantly less in shaded leaves, they were still substantial, with mean increases ranging from 40 to 68% for a 60% increase in atmospheric CO₂ concentration. And that's anything but shabby!

Under *extremely* low light intensities, the benefits arising from atmospheric CO₂ enrichment may be small, but oftentimes they are very important in terms of plant carbon budgeting. In the study of Hattenschwiler (2001), for example, seedlings of five temperate forest species subjected to an additional 200-ppm CO₂ under light intensities that were only 3.4 and 1.3% of full sunlight exhibited CO₂-induced biomass increases that ranged from 17 to 74%. Similarly, in the study of Naumburg *et al.* (2001), a 200-ppm increase in the air's CO₂ 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% of full sunlight.

In a final study we have reviewed on our web site, in which potato plantlets inoculated with an arbuscular mycorrhizal fungus were grown at various light intensities and *super* CO₂ enrichment of approximately 10,000 ppm, Louche-Tessandier *et al.* (1999) found that the unusually high CO₂ concentration produced an unusually high degree of root colonization by the beneficial mycorrhizal fungus, which typically helps supply water and nutrients to plants. 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 CO₂ content of the air is increased, so too are the various biological processes that lead to plant robustness also increased. Less than optimal light intensities, therefore, clearly do *not* negate the beneficial effects of atmospheric CO₂ 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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6.3.5. Interaction of CO₂ and O₃ on Plant Growth

Plants grown in CO₂-enriched air nearly always exhibit increased photosynthetic rates and biomass production relative to plants grown at the current ambient CO₂ concentration. In 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. Thus, 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 CO₂ and O₃ not discussed here, can be found at http://www.co2science.org/subject/o/subject_o.php under the heading Ozone.

6.3.5.1. Agricultural Species

Several studies have used soybean as a model plant to study the effects of elevated CO₂ and ozone on photosynthesis and growth. Reid *et al.* (1998), for example, grew soybeans for an

entire season at different combinations of atmospheric CO₂ and ozone, reporting that elevated CO₂ 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 CO₂ concentration exhibited far less foliar injury while maintaining significantly greater leaf chlorophyll contents than control plants exposed to elevated ozone and ambient CO₂ concentrations. By harvest time, these same plants (grown in the elevated ozone/elevated CO₂ treatment combination) had produced 53% more total biomass than their counterparts did at elevated ozone and ambient CO₂ concentrations (Miller *et al.*, 1998). Finally, in analyzing seed yield, it was determined that atmospheric CO₂ enrichment enhanced this parameter by 20% at ambient ozone, while it increased it by 74% at twice the ambient ozone concentration (Heagle *et al.*, 1998b). Thus, elevated CO₂ completely ameliorated the negative effects of elevated ozone concentration on photosynthetic rate and yield production in soybean.

Such ameliorating responses of elevated CO₂ to ozone pollution are not unique to soybeans; they have also been reported for various cultivars of spring and winter wheat. In the study of Tiedemann and Firsching (2000), for example, atmospheric CO₂ 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. Indeed, although infected plants displayed less *absolute* yield than non-infected plants at elevated ozone concentrations, atmospheric CO₂ enrichment caused the greatest *relative* yield increase in *infected* plants (57% vs. 38%).

McKee *et al.* (2000) reported that O₃-induced reductions in leaf rubisco contents in spring wheat were reversed when plants were simultaneously exposed to twice-ambient concentrations of atmospheric CO₂. 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 CO₂ concentrations, elevated ozone had absolutely 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 CO₂ concentrations. Similar results have been reported in spring wheat by Hudak *et al.* (1999) and in winter wheat by Heagle *et al.* (2000).

Other studies have observed similar responses in cotton and potato. Cotton plants grown at elevated ozone concentrations exhibited 25 and 48% 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 CO₂ concentrations, however, the reductions in these parameters were only 5 and 7%, 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 CO₂ 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 CO₂ 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, ultimately 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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6.3.5.2. Woody Species

6.3.5.2.1. ASPEN

Karnosky *et al.* (1999) grew O₃-sensitive and O₃-tolerant aspen clones in 30-m diameter plots at the Aspen FACE site near Rhinelander, Wisconsin, USA, which were maintained at atmospheric CO₂ concentrations of 360 and 560 ppm with and without exposure to elevated O₃ (1.5 times ambient ozone concentration). After one year of growth at ambient CO₂, elevated O₃ had caused visible injury to leaves of both types of aspen, with the average percent damage in O₃-sensitive clones being more than three times as great as that observed in O₃-tolerant clones (55% vs. 17%, respectively). In combination with elevated CO₂, however, O₃-induced damage to leaves of these same clones was only 38% and 3%, respectively. Thus, elevated CO₂ ameliorated much of the foliar damage induced by high O₃ concentrations.

King *et al.* (2001) studied the same plants for a period of two years, concentrating on belowground growth, where elevated O₃ alone had no effect on fine-root biomass. When the two aspen clones were simultaneously exposed to elevated CO₂ and O₃, however, there was an approximate 66% increase in the fine-root biomass of both of them.

Also in the same experiment, Noormets *et al.* (2001) studied the interactive effects of O₃ and CO₂ on photosynthesis, finding that elevated CO₂ increased rates of photosynthesis in both clones at all leaf positions. Maximum rates of photosynthesis were increased in the O₃-tolerant clone by averages of 33 and 49% due to elevated CO₂ alone and in combination with elevated O₃, respectively, while in the O₃-sensitive clone they were increased by 38% in both situations. Hence, CO₂-induced increases in maximal rates of net photosynthesis were typically maintained, and sometimes even *increased*, during simultaneous exposure to elevated O₃.

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 CO₂ 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 in the case of these leaf properties, simultaneous

exposure of the ozone-stressed trees to elevated CO₂ *more* than compensated for the ozone-induced reductions.

After *four* years of growing *five* aspen clones with varying degrees of tolerance to ozone under the same experimental conditions, McDonald *et al.* (2002) developed what they 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 CO₂ growth response of the various clones as modified by ozone. In general, elevated O₃ reduced aspen growth independent of competitive status, while the authors noted an "apparent convergence of competitive performance responses in +CO₂ +O₃ 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."

By itself, Percy *et al.* found that elevated O₃ decreased tree height and trunk diameter, increased rust occurrence by nearly fourfold, improved tent caterpillar performance by increasing female pupal mass by 31%, and had a strong negative effect on the natural enemies of aphids. The addition of the extra CO₂, however, *completely ameliorated* the negative effects of elevated O₃ on tree height and trunk diameter, *reduced* the O₃-induced enhancement of rust development from nearly fourfold to just over twofold, *completely ameliorated* the enhancement of female tent caterpillar pupal mass caused by elevated O₃, and *completely ameliorated* the reduction in the abundance of natural enemies of aphids caused by elevated O₃.

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 (O₃-sensitive and O₃-tolerant) alone and in combination for one full growing season; and they too found that elevated O₃ improved tent caterpillar performance under ambient CO₂ conditions, *but not in CO₂-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 CO₂ often *completely eliminates* the negative impacts of elevated O₃. Hence, if the tropospheric O₃ concentration continues to rise as expected (Percy *et al.* note that "damaging O₃ concentrations currently occur over 29% of the world's temperate and subpolar forests but are predicted to affect fully 60% by 2100"), we had better hope that the air's CO₂ content continues to rise as well. If it doesn't, aspen trees will be in a world of hurt; for Percy *et al.* additionally report that "since the mid-1990s, aspen use has increased almost exponentially in the US Great Lakes Region and in the boreal mixed wood region of Canada, where the resource is now almost fully utilized."

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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6.3.5.2.2. BEECH

In discussing the problem of elevated tropospheric ozone (O₃) 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)." Hence, in our quest to determine how the ongoing rise in the atmosphere's CO₂ concentration might impact this unfortunate situation, we here briefly summarize the results of studies that have examined the issue as it pertains to European beech (*Fagus sylvatica* L.) trees.

Liu *et al.* (2005) grew 3- and 4-year-old European beech seedlings for five months in well watered and fertilized soil in containers located within walk-in phytotrons maintained at either ambient or ambient + 300 ppm CO₂ (each subdivided into ambient and double-ambient O₃ concentration treatments, with maximum ozone levels restricted to <150 ppb), in both monoculture and in competition with Norway spruce, after which they examined the effects of each treatment on leaf non-structural carbohydrate levels (soluble sugars and starch). In doing so, they found that the effects of elevated O₃ alone on non-structural carbohydrate levels were small when the beech seedlings were grown in monoculture. When they were grown in mixed culture, however, the elevated O₃ slightly enhanced leaf sugar levels, but reduced starch levels by 50%.

With respect to elevated CO₂ alone, for the beech seedlings grown in both monoculture and mixed culture, levels of sugar and starch were significantly enhanced. Hence, when elevated O₃ and CO₂ significantly affected non-structural carbohydrate levels, elevated CO₂ tended to enhance them, whereas elevated O₃ tended to reduce them. In addition, the combined effects of elevated CO₂ and O₃ acting together were such as to produce a significant increase in leaf non-structural carbohydrates in both mixed and monoculture conditions. As a result, the researchers concluded that "since the responses to the combined exposure were more similar to elevated pCO₂ than to elevated pO₃, apparently elevated pCO₂ overruled the effects of elevated pO₃ on non-structural carbohydrates."

In a slightly longer study, Grams *et al.* (1999) grew European beech seedlings in glasshouses maintained at average atmospheric CO₂ 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 CO₂ concentrations the seedlings were exposed to either ambient or twice-ambient levels of O₃. This protocol revealed that elevated O₃ significantly reduced photosynthesis in beech seedlings grown at ambient CO₂ concentrations by a factor of approximately three. In contrast, in the CO₂-enriched air the seedlings did not exhibit *any* photosynthetic reduction due to the doubled

O₃ concentrations. In fact, the photosynthetic rates of the CO₂-enriched seedlings actually *rose by 8%* when simultaneously fumigated with elevated O₃, leading the researchers to conclude that "long-term acclimation to elevated CO₂ supply does counteract the O₃-induced decline of photosynthetic light and dark reactions."

Last of all, in a still longer study, Liu *et al.* (2004) grew 3- and 4-year-old beech seedlings for *two* growing seasons under the same experimental conditions as Liu *et al.* (2005) after the seedlings had been pre-acclimated for one year to either the ambient or elevated CO₂ treatment. At the end of the study, the plants were harvested and fresh weights and dry biomass values were determined for leaves, shoot axes, coarse roots and fine roots, as were carbohydrate (starch and soluble sugar) contents and concentrations for the same plant parts. This work falsified the hypothesis that "prolonged exposure to elevated CO₂ 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 CO₂."

These results are certainly good news for the biosphere (and especially for beech trees), as well as for human activities that result in CO₂ being emitted to the atmosphere. In addition to the latter activities having their own "excuse for being," they have the doubly good fortune of producing a byproduct that goes on to fight -- and *overpower* -- the deleterious consequences of one of the world's most devastating air pollutants.

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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6.3.5.2.3. 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 belowground 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%.

One year later at the same FACE facility, Oksanen *et al.* (2001) observed O_3 -induced injuries in the thylakoid membranes of the chloroplasts of the birch trees' leaves; but 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 CO₂ in combination with 30 and 50 ppb O₃ for two growing seasons, after which it was noted that the extra O₃ had significantly decreased branching in the trees' crowns. This malady, however, was almost completely ameliorated by a doubling of the air's CO₂ concentration. In addition, after one more year of study, Eichelmann *et al.* (2004) reported that, by itself, the increase in the air's CO₂ content increased the average net photosynthetic rates of both clones by approximately 16%, while the increased O₃ by itself caused a 10% 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% increase in net photosynthesis, as if the extra O₃ had had no effect when applied in the presence of the extra CO₂.

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 O₃ were found mainly in ambient CO₂, not in elevated CO₂." In fact, whereas doubling the air's O₃ concentration decreased total biomass production by 13% across both clones, simultaneously doubling the air's CO₂ concentration *increased* total biomass production by 30%, thereby *more* than compensating for the deleterious consequences of doubling the atmospheric ozone concentration.

In commenting on this ameliorating effect of elevated CO₂, 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 CO₂, or decreased stomatal conductance and thus decreasing O₃ uptake in elevated CO₂ conditions (e.g., Rao *et al.*, 1995)." They also noted that "the ameliorating effect of elevated CO₂ is in accordance with the results of single-season open-top chamber and growth chamber studies on small saplings of various deciduous tree species (Mortensen 1995; Dickson *et al.*, 1998; Loats and 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 CO₂ and O₃ concentrations on the accumulation of 27 phenolic compounds in the leaves of the trees, finding that elevated CO₂ increased the concentration of phenolic acids (+25%), myricetin glycosides (+18%), catechin derivatives (+13%) and soluble condensed tannins (+19%). Elevated O₃, on the other hand, increased the concentration of one glucoside by 22%, chlorogenic acid by 19%, and flavone aglycons by 4%. *However*, Peltonen *et al.* say that this latter O₃-induced production of antioxidant phenolic compounds "did not seem to protect the birch leaves from detrimental O₃ effects on leaf weight and area, but may have even exacerbated them." Last of all, in the combined elevated CO₂ and O₃ treatment, they found that "elevated CO₂ did seem to protect the leaves from elevated O₃ because all the O₃-derived effects on the leaf phenolics and traits were prevented by elevated CO₂."

Meanwhile, back at the FACE facility near Rhinelander, Wisconsin, USA, Agrell *et al.* (2005) examined the effects of ambient and elevated concentrations of atmospheric CO₂ and O₃ on the foliar chemistry of birch and aspen trees, plus the consequences of these effects for host plant preferences of forest tent caterpillar larvae. 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 CO₂ or O₃ treatment was in general also the one for which average levels of condensed tannins were most positively (or least negatively) affected by that treatment."

In this regard, it is of interest to note that the mean condensed tannin concentration of birch leaves was 18% higher in the elevated CO₂ and O₃ treatment. Consequently, as atmospheric concentrations of CO₂ and O₃ continue to rise, the increases in condensed tannin concentrations likely to occur in the foliage of birch trees should lead to their leaves becoming less preferred for consumption by the dreaded forest tent caterpillar, which according to Agrell *et al.* is "an eruptive generalist defoliator in North American hardwood forests, causing extensive damage during outbreak years (Fitzgerald, 1995)." Also, because the amount of methane expelled in the breath of ruminants is an inverse function of the condensed tannin concentration of the foliage they consume (see Tannins in our Subject Index), the increased foliage tannin concentrations likely to exist in a high-CO₂ world of the future should result in less methane being released to the atmosphere via ruminants ingesting such foliage, which phenomenon would tend to decrease the impetus for methane-induced global warming.

Concurrent with the work of Agrell *et al.*, King *et al.* (2005) evaluated the effect of CO₂ enrichment alone, O₃ enrichment alone, and the net effect of both CO₂ and O₃ enrichment together on the growth of the Rhinelander birch trees, finding that relative to the ambient-air control treatment, elevated CO₂ increased total biomass by 45% in the aspen-birch community, while elevated O₃ caused a 13% reduction in total biomass relative to the control. Of most interest of all, the combination of elevated CO₂ and O₃ resulted in a total biomass increase of 8.4% relative to the control aspen-birch community. King *et al.* thus concluded that "exposure to even moderate levels of O₃ significantly reduces the capacity of net primary productivity to respond to elevated CO₂ in some forests." Consequently, they suggested it makes sense to move forward with technologies that reduce anthropogenic precursors to photochemical O₃ 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 CO₂ concentration.

One final paper to come out of the Finnish silver birch study was that of Kostianen *et al.* (2006), who studied the effects of elevated CO₂ and O₃ on various wood properties. Their work revealed that the elevated CO₂ treatment had no effect on wood structure, but that it increased annual ring width by 21%, woody biomass by 23% and trunk starch concentration by 7%. Elevated O₃, on the other hand, decreased stem vessel percentage in one of the clones by 10%; but it had no effect on vessel percentage in the presence of elevated CO₂.

In discussing their results, Kostianen *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 O₃ may affect water transport," obviously lowering it. *However*, as they continue, "elevated CO₂ ameliorated the O₃-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)." Hence, they conclude that "starch accumulation observed under elevated CO₂ in this study indicates a surplus of carbohydrates produced by enhanced photosynthesis of the same trees (Riikonen *et al.*, 2004)." In addition, they report 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." Considering these several responses, therefore, it can be appreciated that the ongoing rise in the air's CO₂ content should be a boon to silver birch (and likely many other trees) in both summer *and* winter in both pristine *and* ozone-polluted air.

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% under elevated CO₂ but only 40% under elevated O₃. Likewise, with respect to the quantity of flowers produced, they found that elevated CO₂ led to a 262% increase, while elevated O₃ led to only a 75% increase. They also determined that elevated CO₂ had significant positive effects on birch catkin size, weight, and germination success rate, with elevated CO₂ increasing the germination rate of birch by 110%, decreasing seedling mortality by 73%, increasing seed weight by 17% and increasing new seedling root length by 59%. On the other hand, they found that just the *opposite* was true of elevated O₃, as it decreased the germination rate of birch by 62%, decreased seed weight by 25%, and increased new seedling root length by only 15%.

In discussing their findings, Darbah *et al.* additionally report that "the seeds produced under elevated O₃ had much less stored carbohydrate, lipids, and proteins for the newly developing seedlings to depend on and, hence, the slow growth rate." As a result, they conclude that "seedling recruitment will be enhanced under elevated CO₂ but reduced under elevated O₃," which is another important reason to hope that the atmosphere's CO₂ concentration continues to climb as long as the air's O₃ content is in a significantly ascending mode.

In summary, from their crowns to their roots, birch trees are generally negatively affected by rising ozone concentrations. When the air's CO₂ 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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6.3.5.2.4. YELLOW-POPLAR

Scherzel *et al.* (1998) grew yellow-poplar seedlings in open-top chambers for four years at three different combinations of atmospheric O₃ and CO₂ -- (1) ambient O₃ and ambient CO₂, (2) doubled O₃ and ambient CO₂, and (3) doubled O₃ and doubled CO₂ -- 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 O₃ and elevated CO₂ air decomposed at a significantly slower rate, such that even after two years of decomposition, litter from the elevated O₃ and elevated CO₂ treatment still contained about 12% more biomass than litter produced in the other two treatments. This reduced rate of decomposition under elevated O₃ and CO₂ conditions 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 CO₂ concentration, air with twice the ambient O₃ concentration, and air with twice the ambient CO₂ and O₃ concentrations to determine the effects of elevated CO₂ and O₃ on photosynthesis and growth in this deciduous tree species. In doing so, they found that doubling the air's CO₂ concentration increased the rate of net photosynthesis by 55% in ambient O₃ air, and that at twice the ambient level of O₃ it stimulated net photosynthesis by an average of 50%. Similarly, the doubled CO₂ concentration significantly increased total biomass by 29%, while the doubled O₃ concentration had little impact on growth.

Last of all, 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 O₃, (2) ambient O₃, (3) 1.5 times ambient O₃, and (4) 1.5 times ambient O₃ plus 350 ppm CO₂ above ambient CO₂, 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% when the trees were grown in ambient O₃-air and by 14% when they were grown in elevated O₃-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 O₃ and elevated CO₂ was 57-80% higher than it was in the trees exposed to elevated O₃ alone. There was also no evidence of any photosynthetic down regulation in the trees exposed to the elevated O₃ and CO₂ air, with some of the highest rates being observed during the final growing season. Consequently, Rebbeck *et al.* concluded that "elevated CO₂ may ameliorate the negative effects of increased tropospheric O₃ on yellow-poplar." In fact, their results suggest that a nominally doubled atmospheric CO₂ concentration *more* than compensates for the deleterious effects of a 50% increase in ambient O₃ levels ... and by several times over.

As the air's CO₂ content continues to rise, therefore, earth's yellow-poplar trees will likely display substantial increases in photosynthetic rate and biomass production, even under conditions of elevated O₃ concentrations; and the soils in which the trees grow should 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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6.3.6. Low Temperature Tolerance

Only a handful of studies have attempted to determine what relationship, if any, exists between atmospheric CO₂ enrichment and the ability of plants to withstand the rigors of cold temperatures. Nevertheless, some tantalizing things have been learned.

Loik *et al.* (2000) grew three *Yucca* species (*brevifolia*, *schidigera*, and *whipplei*) in pots placed within glasshouses maintained at atmospheric CO₂ concentrations of 360 and 700 ppm and day/night air temperatures of 40/24°C for seven months, after which some of the plants were subjected to a two-week day/night air temperature treatment of 20/5°C. In addition, leaves from each *Yucca* species were removed and placed in a freezer 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 CO₂ lowered the air temperature at which 50% low-temperature-induced cell mortality occurred by 1.6, 1.4 and 0.8°C in *brevifolia*, *schidigera* and *whipplei*, respectively. And on the basis of the result obtained for *Y. brevifolia*, Dole *et al.* (2003) estimated that "the increase in freezing tolerance caused by doubled CO₂ would increase the potential habitat of this species by 14%."

In contrast to these positive results, Obrist *et al.* (2001) observed just the opposite response. In an open-top chamber study of a temperate grass ecosystem growing on a nutrient-poor calcareous soil in northwest Switzerland, portions of which had been exposed to atmospheric CO₂ concentrations of 360 and 600 ppm for a period of six years, they determined that the average temperature at which 50% 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 CO₂ employed in their experiment.

Most relevant investigations, however, have produced evidence of *positive* CO₂ 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 CO₂ concentrations for a period of three years, finding that elevated CO₂ tended to hasten the end of the growing season. This effect was interpreted as enabling the seedlings to better avoid the severe cold-induced dieback of newly-produced tissues that often occurs with the approach of winter in this region. Likewise, Wayne *et al.* (1998) found that yellow birch seedlings grown at an atmospheric CO₂ concentration of 800 ppm exhibited greater dormant bud survivorship at low air temperatures than did seedlings grown at 400 ppm CO₂.

Schwanz and Polle (2001) investigated the effects of elevated CO₂ on chilling stress in micropropagated hybrid poplar clones that were subsequently potted and transferred to growth chambers maintained at either ambient (360 ppm) or elevated (700 ppm) CO₂ for 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 CO₂ as compared with those from ambient CO₂." 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 CO₂ treatment. This CO₂-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 CO₂-enriched air is suggested by the study of Sgherri *et al.* (1998), who reported that raising the air's CO₂ 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% increase in atmospheric CO₂ enhanced overall thylakoid lipid concentration by about 25%, while it increased the degree of unsaturation of the two main lipids by approximately 17% and 24%. Under conditions of water stress, these responses were found to be even greater, as thylakoid lipid concentration rose by approximately 92%, while the degree of unsaturation of the two main lipids rose by about 22% and 53%.

What do these observations have to do with a plant's susceptibility to chilling injury? According to a number of studies conducted over the past decade, *a lot*.

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, for example, they observed "dramatic reductions in chloroplast size, membrane content, and organization in developing leaves." Furthermore, 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 plants against low-temperature photoinhibition "by accelerating the recovery of the photosystem II protein complex." Likewise, Kodama *et al.* (1995), also working with transgenic tobacco plants, showed 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."

These observations are laden with significance for earth's agro-ecosystems. Many economically important crops, such as rice, maize and soybeans, are classified as *chilling-sensitive*; and they experience injury or death at temperatures between 0 and 15°C (Lyons, 1973). If atmospheric CO₂ enrichment enhances their production and degree-of-unsaturation of thylakoid lipids, as it does in alfalfa, a continuation of the ongoing rise in the air's CO₂ content could increase the abilities of these critically important agricultural species to withstand periodic exposure to debilitating low temperatures; and this phenomenon could provide the extra boost in food production that will be needed to sustain our increasing numbers in the years and decades ahead.

Earth's natural ecosystems would also benefit from a CO₂-induced increase in thylakoid lipids containing more-highly-unsaturated fatty acids. Many plants of tropical origin, for example, suffer cold damage when temperatures fall below 20°C (Graham and Patterson, 1982); and with improved lipid characteristics provided by the ongoing rise in the air's CO₂ content, such plants would be able to expand their ranges both poleward and upward in a higher-CO₂ world.

Clearly, 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 CO₂ enrichment on the properties of thylakoid lipids in a greater variety of plants; and, *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/frosthardeness.php>.

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6.3.7. Nitrogen

Numerous studies have investigated the effects of different soil nitrogen (N) concentrations on plant responses to increases in the air's CO₂ 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 CO₂. 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 CO₂ enrichment at low levels of soil N, while some will. In fact, some plants respond equally well to increases in the air's CO₂ content when growing in soils exhibiting a whole range of N concentrations. Most common of all, however, is the observation that plants respond ever better to rising atmospheric CO₂ concentrations as soil N concentrations rise. Interestingly, the current state of earth's atmosphere and land surface is one of jointly increasing CO₂ and N concentrations, respectively. 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 CO₂ 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.

6.3.7.1. Crops

6.3.7.1.1. 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 CO₂?

In exploring this question, Weerakoon *et al.* (1999) grew seedlings of two rice cultivars for 28 days in glasshouses maintained at atmospheric CO₂ concentrations of 373, 545, 723 and 895 ppm under conditions of low, medium and high soil nitrogen content. After four weeks of treatment, photosynthesis was found to significantly increase with increasing nitrogen availability and atmospheric CO₂ concentration. Averaged across all nitrogen regimes, plants grown at 895 ppm CO₂ exhibited photosynthetic rates that were 50% greater than those observed in plants grown at ambient CO₂. Total plant dry weight also increased with increasing atmospheric CO₂. In addition, the percentage growth enhancement resulting from CO₂ enrichment increased with increasing soil nitrogen; from 21% at the lowest soil nitrogen concentration to 60% at the highest concentration.

Using a different CO₂ enrichment technique, Weerakoon *et al.* (2000) grew rice in open-top chambers maintained at atmospheric CO₂ concentrations of approximately 350 and 650 ppm during a wet and dry growing season and under a range of soil nitrogen contents. Early in both growing seasons, plants exposed to elevated atmospheric CO₂ concentrations intercepted significantly more sunlight than plants fumigated with ambient air, due to CO₂-induced increases in leaf area index. This phenomenon occurred regardless of soil nitrogen content, but 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% greater in CO₂-enriched vs. ambiently-grown plants and tended to increase with increasing soil nitrogen content.

Utilizing yet a third approach to enriching the air about a crop with elevated levels of atmospheric CO₂, Kim *et al.* (2003) grew rice crops from the seedling stage to maturity at atmospheric CO₂ concentrations of ambient and ambient plus 200 ppm using FACE technology and three levels of applied nitrogen -- low (LN, 4 g N m⁻²), medium (MN, 8 and 9 g N m⁻²) and high (HN, 15 g N m⁻²) -- for three cropping seasons (1998-2000). They report that "the yield response to elevated CO₂ in crops supplied with MN (+14.6%) or HN (+15.2%) was about twice that of crops supplied with LN (+7.4%)," confirming the importance of nitrogen availability to the response of rice to atmospheric CO₂ enrichment previously determined by Kim *et al.* (2001) and Kobaysahi *et al.* (2001).

In light of these observations, it would appear that the maximum benefits of elevated levels of atmospheric CO₂ for the growth and grain production of rice cannot be realized in soils that are highly deficient in nitrogen, but that increasing nitrogen concentrations above what is considered adequate may not result in proportional gains in CO₂-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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6.3.7.1.2. WHEAT

Smart *et al.* (1998) grew wheat from seed for 23 days in controlled environment chambers maintained at atmospheric CO₂ concentrations of 360 and 1000 ppm and two concentrations of soil nitrate, finding that the extra CO₂ increased average plant biomass by approximately 15%, irrespective of soil nitrogen content. In a more realistic FACE experiment, however, Brooks *et al.* (2000) grew spring wheat for two seasons at atmospheric CO₂ concentrations of 370 and 570 ppm at both high and low levels of nitrogen fertility; and they obtained *twice* the yield enhancement (16% vs. 8%) 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 CO₂ 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 CO₂ treatment increased total plant dry weight by 44, 29 and 12% at the high, medium and low soil nitrogen levels, respectively. In addition, although elevated ozone alone reduced plant biomass, the simultaneous application of elevated CO₂ completely ameliorated its detrimental effects on biomass production, irrespective of soil nitrogen supply.

So why do the plants of some studies experience a major reduction in the relative growth stimulation provided by atmospheric CO₂ enrichment under low soil nitrogen conditions, while other studies find the aerial fertilization effect of elevated CO₂ to be independent of root-zone nitrogen concentration? Based on studies of both potted and hydroponically-grown plants, Farage *et al.* (1998) determined that low root-zone nitrogen concentrations need not lead to photosynthetic acclimation (less than maximum potential rates of photosynthesis) in elevated CO₂, as long as root-zone nitrogen *supply* is adequate to meet plant nitrogen *needs* to maintain the enhanced relative growth rate that is made possible by atmospheric CO₂ enrichment. When supply cannot meet this need, as is often the case in soils with limited nitrogen reserves, the aerial fertilization effect of atmospheric CO₂ enrichment begins to be reduced and less-than-potential CO₂-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 CO₂ enrichment tends to increase the growth and yield of wheat under a wide range of soil nitrogen concentrations, including some that are very low, considerably greater CO₂-induced enhancements are possible when more soil nitrogen is

available, 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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6.3.7.1.3. 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 CO₂ concentrations of 360 and 700 ppm. The extra CO₂ of the CO₂-enriched chambers reduced average rates of root nitrogen uptake by about 25%, which reduction, by itself, would normally tend to reduce tissue nitrogen contents and the relative growth rates of the seedlings. However, the elevated CO₂ also increased photosynthetic nitrogen-use efficiency by an average of 50%, which increase normally tends to increase the relative growth rates of seedlings. Of these two competing effects, the latter was by far the more powerful, ultimately leading to an increase in whole plant biomass. After the one month of the study, for example, the CO₂-enriched plants exhibited whole plant biomass values that were 44, 13 and 115% 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 CO₂ enrichment, particularly if photosynthetic nitrogen-use efficiency is enhanced, which is typically the case, as it was in this study. Nevertheless, the greatest CO₂-induced growth increase of Zerihun *et al.*'s study was exhibited by the plants growing in the high soil nitrogen treatment.

Deng and Woodward (1998) grew strawberries in environment-controlled glasshouses maintained at atmospheric CO₂ concentrations of 390 and 560 ppm for nearly three months. In addition, the strawberries were supplied with fertilizers containing three levels of nitrogen. The extra CO₂ increased rates of net photosynthesis and total plant dry weight at all three nitrogen levels, but the increases were not significant. Nevertheless, they provided the CO₂-enriched plants with enough additional sugar and physical mass to support significantly greater numbers of flowers and fruits than the plants grown at 390 ppm CO₂. This effect consequently led to total fresh fruit weights that were 42 and 17% greater in the CO₂-enriched plants that received the highest and lowest levels of nitrogen fertilization, respectively, once again indicating a greater growth response at higher nitrogen levels.

Newman *et al.* (2003) investigated the effects of two levels of nitrogen fertilization and an approximate doubling of the air's CO₂ concentration on the growth of tall fescue, 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 CO₂ concentration and half of which were maintained at an approximately doubled CO₂ concentration of 700 ppm. In addition, half of the pots in each CO₂ treatment received 0.0673 kg N m⁻² applied over a period of three consecutive days, 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. As to what was learned, Newman *et al.* report that the plants grown in the high-CO₂ air photosynthesized 15% more and produced 53% more dry matter (DM) under low N conditions and 61% more DM under high N conditions. In addition, they report that the % organic matter (OM) was little changed, except under elevated CO₂ and high N, when %OM (as %DM) increased by 3%. 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 CO₂ 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 CO₂ 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 CO₂ of this study enhanced total plant biomass by 13 and 25% in the low and high nitrogen treatments, respectively. In addition, it increased root biomass by 12 and 26% for the same situations. Thus, as was the case with sunflowers, strawberries and tall fescue, elevated CO₂ 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 CO₂ concentrations of 350 and 700 ppm, while fertilizing them with three different levels of nitrate-nitrogen. In this study, the plants grown in CO₂-enriched air exhibited rates of net photosynthesis that were approximately 50% greater than those displayed by the plants grown in ambient air, regardless of soil nitrate availability. These CO₂-induced increases in photosynthetic carbon uptake contributed to 60, 40 and 30% aboveground 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 CO₂ enrichment, displaying 10 and 30% increases in dry weight at one-half and standard nitrate levels, but no increase at the high soil nitrate concentration. In this study, therefore, the role of soil nitrogen fertility was clearly *opposite* to that observed in the four prior studies in the case of *aboveground* 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 CO₂ concentrations of either 360 or 650 ppm and either a high or low nitrogen fertilization regime; and in this case, as in the case of the aboveground biomass response of the sugar beets of Romanova *et al.*, the elevated CO₂ had the greatest relative impact on yield when the plants were grown under the *less-than-optimum low*-nitrogen regime, i.e., a 48% increase vs. 31% under high-nitrogen conditions.

Last of all, we report the pertinent results of the review and analysis of Kimball *et al.* (2002), who summarized the findings of most Free-Air CO₂ Enrichment (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 CO₂ concentration, rates of net photosynthesis in several C₃ grasses were enhanced by an average of 46% under conditions of ample soil nitrogen supply and by 44% when nitrogen was limiting to growth. With respect to aboveground biomass production, the differential was much larger, with the C₃ grasses wheat, rice and ryegrass experiencing an average increase of 18% at ample nitrogen but only 4% at low nitrogen; while with respect to belowground biomass production, they experienced an average increase of 70% at ample nitrogen and 58% at low nitrogen. Similarly, clover experienced a 38% increase in belowground biomass production at ample soil nitrogen, and a 32% increase at low soil nitrogen. Finally, with respect to agricultural yield, which is the bottom line in terms of food and fiber production, wheat and ryegrass experienced an average increase of 18% at ample nitrogen, while wheat experienced only a 10% 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 CO₂-induced relative (percentage) increases in net photosynthesis and biomass production when soil nitrogen concentrations are higher rather than lower.

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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6.3.7.2. 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 CO₂ and soil nitrogen concentrations. In this subsection, we review how various aspects of fungal-plant interactions are influenced by elevated CO₂ under varying soil nitrogen regimes.

In a one-year study conducted by Walker *et al.* (1998), ponderosa pine seedlings exposed to atmospheric CO₂ concentrations of 525 and 700 ppm displayed total numbers of ectomycorrhizal fungi on their roots that were 170 and 85% 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 CO₂ for four months displayed various root infection responses by arbuscular mycorrhizal fungi, which varied with soil nitrogen supply. At low soil nitrogen

contents, elevated CO₂ increased the percent root infection by this type of fungi in all five annual grassland species. 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 CO₂ and soil nitrogen status on fungal-plant interactions. First of all, after growing three-year-old shrubs at an atmospheric CO₂ concentration of 750 ppm for four months, they reported insignificant 19 and 9% increases in percent root infected by arbuscular mycorrhizal fungi at low and high soil nitrogen concentrations, respectively. However, elevated CO₂ significantly increased the percent root infection by arbuscules, which are the main structures involved in the symbiotic exchange of carbon and nutrients between a host plant and its associated fungi, by more than 14-fold at low soil nitrogen concentrations. In addition, the length of fungal hyphae more than doubled with atmospheric CO₂ enrichment in the low soil nitrogen regime. In the high soil nitrogen treatment, elevated CO₂ increased the percent root infection by vesicles, which are organs used by arbuscular mycorrhizal fungi for carbon storage, by approximately 2.5-fold.

In conclusion, these observations suggest that elevated CO₂ will indeed affect fungal-plant interactions in positive ways that often depend upon soil nitrogen status. Typically, it appears that CO₂-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 CO₂ 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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6.3.7.3. Grasses

Perennial ryegrass (*Lolium perenne* L.) has been used as a model species in many experiments to help elucidate grassland responses to atmospheric CO₂ enrichment and soil nitrogen availability. In the FACE study of Rogers *et al.* (1998), for example, plants exposed to 600 ppm CO₂ exhibited a 35% increase in their photosynthetic rates without regard to soil nitrogen availability. However, when ryegrass was grown in plastic ventilated tunnels at twice-ambient concentrations of atmospheric CO₂, the CO₂-induced photosynthetic response was about 3-fold greater in a higher, 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 CO₂ concentration of 700 ppm stimulated photosynthesis by 30% in this species when it was grown with moderate, but not low, soil nitrogen availability. Thus, CO₂-induced photosynthetic stimulations in perennial ryegrass can be influenced by soil nitrogen content, with greater positive responses typically occurring under higher, as opposed to lower, soil nitrogen availability.

With respect to biomass production, van Ginkel and Gorissen (1998) reported that a doubling of the atmospheric CO₂ concentration increased shoot biomass of perennial ryegrass by 28%, regardless of soil nitrogen concentration. In the more revealing six-year FACE study of Daepf *et al.* (2000), plants grown at 600 ppm CO₂ and high soil nitrogen availability continually increased their dry matter production over that observed in ambient-treatment plots, from 8% more in the first year to 25% more at the close of year six. When grown at a low soil nitrogen availability, however, CO₂-enriched plants exhibited an initial 5% increase in dry matter production, which dropped to a negative 11% in year two; but this negative trend was thereafter turned around, and it continually rose to ultimately reach a 9% stimulation at the end of the study. Thus, these data demonstrate that elevated CO₂ increases perennial ryegrass biomass, even under conditions of low soil nitrogen availability, especially under conditions of long-term atmospheric CO₂ enrichment.

If perennial ryegrass is indeed representative of most grassland species, one would anticipate the remainder of this summary to include similar positive effects of CO₂ on the photosynthesis and biomass of other grasses, even under low nitrogen conditions; and that is exactly what the data reveal. Lutze *et al.* (1998), for example, reported that microcosms of the C₃ grass *Danthonia richardsonii* grown for four years in glasshouses fumigated with air containing 720 ppm CO₂ displayed total photosynthetic carbon gains that were always 15-34% 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 CO₂ for two years were 12 and 38% greater than rates measured in control plants grown at 350 ppm CO₂ under high and low soil nitrogen regimes, respectively. In addition, they also reported CO₂-induced photosynthetic stimulations of 25 and 74% for *Trifolium repens* subjected to high and low soil nitrogen regimes, respectively. Thus, we see that the greatest CO₂-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 CO₂ increased biomass production of *Danthonia richardsonii*, *Phalaris aquatica*, *Lotus pedunculatus*, and *Trifolium repens* across a large soil nitrogen gradient. With slightly more detail, Cotrufo and Gorissen (1997) reported average CO₂-induced increases in whole-plant dry weights of *Agrostis capillaries* and *Festuca ovina* that were 20% 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 CO₂ and high soil nitrogen availability displayed similar increases in total plant dry mass that were about 28% greater than those of their respective ambiently-grown controls. At low nitrogen, however, elevated CO₂ 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 CO₂ 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 CO₂ 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 CO₂-induced growth responses. Thus, because the rising CO₂ content of the air is likely to continue for a long time to come, occasional nitrogen limitations on the aerial fertilization effect of atmospheric CO₂ enrichment of grasslands 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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6.3.7.4. Trees

6.3.7.4.1. 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 CO₂?

In exploring this question, Kubiske *et al.* (1998) grew cuttings of four quaking aspen genotypes for five months at CO₂ concentrations of 380 or 720 ppm and low or high soil nitrogen in open-top chambers in the field in Michigan, USA. They found that the elevated CO₂ treatment significantly increased net photosynthesis, regardless of soil nitrogen content, although there were no discernible increases in aboveground growth within the five-month study period. Belowground, however, elevated CO₂ 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 CO₂ 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-CO₂ treatment exhibited rates of net photosynthesis that were 128% and 31% 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 CO₂-induced biomass increases of the trees in the high- and low-nitrogen soils to be 38% and 16%, 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 CO₂ concentrations of 367 and 715 ppm in soils of low and high soil nitrogen concentrations. They report finding that elevated CO₂ increased the total biomass of the aspen cuttings by 50% and 26% in the high and low soil nitrogen treatments, respectively, and that it increased coarse root biomass by 78% and 24% in the same respective treatments.

Last of all, 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 CO₂ 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 CO₂-induced increase in total biomass (58% and 66% in the high- and low-nitrogen soils, respectively), while in the female cuttings the difference was much greater (82% and 22% 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 CO₂ enrichment on the growth of aspen trees by promoting a greater CO₂-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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6.3.7.4.2. 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 CO₂ enrichment in both species were negligible. For moderate soil nitrogen deficiencies, however, a doubling of the air's CO₂ content sometimes boosted growth by as much as 1,000%. In addition, atmospheric CO₂ enrichment mitigated the negative growth response of ponderosa pine to extremely high soil nitrogen concentrations.

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 CO₂ concentrations of 350, 525 and 700 ppm on soils of low, medium and high nitrogen content. They report that elevated CO₂ had little effect on most growth parameters after the first growing season, the one exception being belowground biomass, which increased with both CO₂ and soil nitrogen. After two growing seasons, however, elevated CO₂ significantly increased all growth parameters, including tree height, stem diameter, shoot weight, stem volume and root volume, with the greatest responses typically occurring at the highest CO₂ concentration in the highest soil nitrogen treatment. Root volume at 700 ppm CO₂ and high soil nitrogen, for example, exceeded that of all other treatments by at least 45%, as did shoot volume by 42%. Similarly, at high CO₂ and soil nitrogen, coarse root and shoot weights exceeded those at ambient CO₂ and high nitrogen by 80 and 88%, respectively.

Walker *et al.* (2000) published another paper on the same trees and treatments after five years of growth. At this time, the trees exposed to the twice-ambient levels of atmospheric CO₂ had heights that were 43, 64 and 25% 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% 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 CO₂ concentrations of 365 or 720 ppm, finding that the elevated CO₂ caused no overall change in whole-plant biomass at low soil nitrogen, but that at high soil nitrogen, it increased it by 42%. After two years of these treatments, Runion *et al.* (1999) also reported that rates of net photosynthesis were about 50% greater in the high CO₂ treatment, irrespective of soil nitrogen content ... and water content too.

Last of all, 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 CO₂. In commencing this study, they had originally hypothesized that "the increase in carbon fluxes to the microbial community under elevated CO₂ would increase the rate of N immobilization over mineralization," leading to a decline in

the significant CO₂-induced stimulation of forest net primary production that developed over the first two years of the experiment (DeLucia *et al.*, 1999; Hamilton *et al.*, 2002). Quite to the contrary, however, they discovered "there was no statistically significant change in the cycling rate of N derived from soil organic matter under elevated CO₂." Neither was the rate of net N mineralization significantly altered by elevated CO₂, nor was there any statistically significant difference in the concentration or net flux of organic and inorganic N in the forest floor and top 30-cm of mineral soil after 5 years of CO₂ 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 CO₂ 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 does indeed impact the aerial fertilization effect of atmospheric CO₂ enrichment on the growth of pine trees by promoting a greater CO₂-induced growth enhancement 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 that higher N concentrations may sometimes even reduce the forest growth response to elevated CO₂.

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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6.3.7.4.3. 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 CO₂ concentrations of 370 or 570 ppm and low or high soil nitrogen contents. They found that elevated CO₂ generally stimulated light-saturated rates of photosynthesis under all conditions by as much as 35%, regardless of genotype, which consistently led to increased aboveground 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 CO₂ 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 CO₂ increased the seedlings' light-saturated rates of net photosynthesis by 19% and 33% in the low- and high-nitrogen treatments, respectively, while it increased their total biomass by 0% and 37% in these same treatments. Nevertheless, Murray *et al.* note there was a reallocation of biomass from aboveground 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 CO₂-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 CO₂ 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 CO₂ 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 CO₂ concentrations for two more years in larger open-top chambers either with or without extra nitrogen being supplied to the soil. After the first three years of the study, they determined that the CO₂-enriched trees possessed 11.6% more total biomass than the ambient-treatment trees. At the end of the next two years, however, the CO₂-enriched trees supplied with extra nitrogen had 15.6% more total biomass than their similarly-treated ambient-air counterparts, while the CO₂-enriched trees receiving no extra nitrogen had 20.5% more biomass than their ambient-treatment counterparts.

In light of these several observations, it would appear that the degree of soil nitrogen availability can indeed alter the aerial fertilization effect of atmospheric CO₂ enrichment on the growth of spruce trees by promoting a greater CO₂-induced growth enhancement in soils of adequate, as opposed to insufficient, nitrogen content. As in the cases of aspen and pine, however, there is evidence to suggest that at some point the response of spruce trees to increasing soil nitrogen also saturates, and that higher nitrogen concentrations may possibly even reduce the growth response to elevated CO₂ 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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6.3.7.4.4. OTHER

Maillard *et al.* (2001) grew pedunculate oak seedlings for three to four months in greenhouses maintained at atmospheric CO₂ concentrations of either 350 or 700 ppm under conditions of either low or high soil nitrogen concentration. The elevated CO₂ of their study stimulated belowground growth in the seedlings growing in the nitrogen-poor soil, significantly increasing their root-to-shoot ratios. However, it increased both the below- *and* above-ground biomass of seedlings growing in nitrogen-*rich* soil. In fact, the CO₂-enriched seedlings growing in the nitrogen-rich soil produced 217 and 533% more stem and coarse-root biomass, respectively, than their ambient-air counterparts growing in the same fertility treatment. Overall, the doubled CO₂ concentration of the air in their study enhanced *total* seedling biomass by approximately 30 and 140% under nitrogen-poor and nitrogen-rich soil conditions, respectively.

Schortemeyer *et al.* (1999) grew seedlings of *Acacia melanoxylon* (a leguminous nitrogen-fixing tree native to south-eastern Australia) in hydroponic culture for six weeks in growth cabinets, where the air was maintained at CO₂ concentrations of either 350 or 700 ppm and the seedlings were supplied with water containing nitrogen in a number of 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 CO₂ 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 N₂-fixing tree - *Alnus glutinosa* (the common alder) - seedlings of which had been grown for three years in open-top chambers in either ambient or elevated (ambient + 350 ppm) concentrations of atmospheric CO₂ and one of two soil nitrogen regimes (full nutrient solution or no fertilizer). 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 CO₂ 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 CO₂ concentration increased total seedling biomass by 134% in the low nitrogen treatment but by a smaller 98% in the high nitrogen treatment. In addition, the elevated CO₂ led to greater root growth in the low nitrogen treatment, as indicated by a 33% higher root:shoot ratio.

In light of these several results, it is clear that different species of trees may respond in qualitatively different ways to atmospheric CO₂ enrichment in terms of their growth stimulation being greater or smaller under conditions of low vs. high soil nitrogen fertility. In the majority of cases, however, as may be discerned by reviewing the results of similar studies conducted on aspen, pine and spruce trees, the most common response is for the growth-promoting effects of atmospheric CO₂ enrichment to be expressed to a greater degree when soil nitrogen fertility is optimal as opposed to less-than-optimal.

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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6.3.8. Salinity Effects

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 CO₂ 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 CO₂ concentration, but only when exposed to salinity levels that were 25%, but not 75%, of full-strength seawater. However, Mavrogianopoulos *et al.* (1999) reported that atmospheric CO₂ concentrations of 800 and 1200 ppm stimulated photosynthesis in parnon melons by 75 and 120%, respectively, regardless of soil salinity, which ranged from 0 to 50 mM NaCl. Moreover, the authors noted that atmospheric CO₂ enrichment partially alleviated the negative effects of salinity on melon yield, which increased with elevated CO₂ at all salinity levels. Furthermore, Maggio *et al.* (2002) grew tomatoes at 400 and 900 ppm in combination with varying degrees of soil salinity and noted that plants grown in elevated CO₂ tolerated an average root-zone salinity threshold value that was about 60% greater than that exhibited by plants grown at 400 ppm CO₂ (51 vs. 32 mmol dm⁻³ Cl).

In conclusion, it is clear that elevated CO₂ may alleviate some of the negative impacts of high soil salinity on plant growth. In addition, as indicated in the review of Poorter and Perez-Soba (2001), there appear to be no changes in the effect of elevated CO₂ 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). Hence, plants should respond positively to future increases in the air's CO₂ content, even in areas 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/salinitystress.php>.

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6.3.9. Temperature

As the air's CO₂ content continues to rise, most plants will exhibit increased rates of photosynthesis and biomass production. Consequently, this phenomenon should enhance the amount of food, fiber and timber products that can be used to feed, clothe and shelter earth's expanding human population. However, some climate alarmists have predicted that the growth-promoting effects of atmospheric CO₂ enrichment may be negated by global warming, which could compromise our ability to sustain greater human populations without increasing arable land acreage. We thus turn to the scientific literature to see if plants will continue to exhibit CO₂-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 within this context.

6.3.9.1. Agricultural Crops

In order to better understand the issues being addressed in this review, one must realize that the optimum growth temperature for several plants has already been shown to rise substantially with increasing levels of atmospheric CO₂ (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 C₃ plants should increase their optimum growth temperature by approximately 5°C for a 300 ppm increase in the air's CO₂ content. One would thus also expect plant photosynthetic rates to rise with concomitant increases in the air's CO₂ concentration and temperature, as has indeed been previously shown to be true by Idso and Idso (1994). Hence, we here proceed to see if these positive CO₂ x temperature interactions are still being supported in the recent scientific literature.

In the study of Zhu *et al.* (1999), pineapples grown at 700 ppm CO₂ assimilated 15, 97 and 84% more total carbon than pineapples grown at the current ambient CO₂ concentration in day/night air temperature regimes of 30/20 (which is optimal for pineapple growth at ambient CO₂), 30/25, and 35/25 °C, respectively. Similarly, Taub *et al.* (2000) demonstrated that net photosynthetic rates of cucumbers grown at twice-ambient levels of atmospheric CO₂ and air temperatures of 40°C were 3.2 times greater than those displayed by control plants grown at ambient CO₂ and this same elevated air temperature. Thus, at air temperatures normally considered to be deleterious to plant growth, rates of photosynthesis are typically considerably greater for CO₂ enriched vs. ambiently-grown plants.

Other studies report similar results. Reddy *et al.* (1999), for example, 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 CO₂ displayed photosynthetic rates that were 137 to 190% greater than those displayed by plants exposed to ambient CO₂ concentrations across this temperature spectrum. Similarly, Cowling and Sage (1998) reported that a 200-ppm increase in the air's CO₂ concentration boosted photosynthetic rates of young bean plants by 58 and 73% at growth temperatures of 25 and 36°C, respectively. In addition, Bunce (1998) grew wheat and barley at 350 and 700 ppm CO₂ across a wide range of temperatures and reported that elevated CO₂ stimulated photosynthesis in these species by 63 and 74%, respectively, at an air temperature of 10°C and by 115 and 125% at 30°C. Thus, the percentage increase in photosynthetic rate resulting from atmospheric CO₂ enrichment often increases substantially with increasing air temperature.

On another note, elevated CO₂ 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 CO₂ 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 CO₂-enriched plants attained photosynthetic rates that were 72% of their unstressed controls, while stressed plants grown at ambient CO₂ attained photosynthetic rates that were only 52% of their respective controls.

CO₂-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 CO₂ content boosted total plant biomass for wheat and barley by a combined average of 59 and 200% at air temperatures of 25 and 36°C. Similarly, Ziska (1998) reported that a doubling of the atmospheric CO₂ concentration increased the total dry weight of soybeans by 36 and 42% at root zone temperatures of 25 and 30°C, respectively. Likewise, Hakala (1998) noted that spring wheat grown at 700 ppm CO₂ attained total biomass values that were 17 and 23% 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 CO₂-induced growth responses of winter wheat into plant growth models, Alexandrov and Hoogenboom (2000) predicted 12 to 49% increases in wheat yield in Bulgaria even if air temperatures rise by as much as 4°C. Finally, in the study of Reddy *et al.* (1998), it was shown that elevated CO₂ (700 ppm) increased total cotton biomass by 31 to 78% across an air temperature range from 20 to 40°C. Thus, the beneficial effects of elevated CO₂ on agricultural crop yield is often enhanced due to elevated air temperature.

In some cases, however, elevated CO₂ does *not* interact with air temperature to further increase the growth-promoting effects of atmospheric CO₂ 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 CO₂ attained 25% 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 CO₂ 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 CO₂ content increased total biomass by 52%, regardless of air temperature.

Finally, even if the air's CO₂ 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 CO₂ had essentially no effect on the yield of French bean. However, a 4°C increase in air temperature increased yield by approximately 50%.

In conclusion, the recent scientific literature continues to indicate that as the air's CO₂ content continues to rise, 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 CO₂ enrichment will likely rise right along with it, becoming more and more robust in agreement with the experimental observations reviewed by Idso and Idso (1994). Thus, the biosphere's ability to continue producing the food and fiber needed to feed and clothe the increasing population of humanity looks good indeed ... as long, that is, as the CO₂ content of the air continues its 350-year habit of rising hand-in-hand with the population of the planet.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <http://www.co2science.org/subject/g/tempco2aq.php>.

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6.3.9.2. Grassland Species

In the study of Lilley *et al.* (2001), swards of *Trifolium subterraneum* were grown at 380 and 690 ppm CO₂ 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 CO₂ increased foliage growth by 19% at ambient air temperature. At elevated air temperature, however, plants grown at ambient CO₂ exhibited a 28% *reduction* in foliage growth, while CO₂-enriched plants still displayed a growth *enhancement* of 8%. Similarly, Morgan *et al.* (2001) reported that twice-ambient levels of atmospheric CO₂ increased aboveground biomass in native shortgrass steppe ecosystems by an average of 38%, 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 CO₂ content boosted photosynthesis and aboveground biomass by 22 and 17%, respectively, independent of air temperature. Thus, at elevated air temperature, CO₂-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 CO₂ displayed average photosynthetic rates that were 36 and 70% greater, respectively, than average rates exhibited by control plants subjected to ambient CO₂ concentrations. Moreover, the average CO₂-induced biomass increase for these five species rose dramatically with increasing air temperature: from only 8% at 18°C to 95% at 28°C. Thus, the beneficial effects of elevated CO₂ on grassland productivity is often significantly enhanced by elevated air temperature.

Finally, even if the air's CO₂ 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 Norton *et al.* (1999), where elevated CO₂ 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, the recent scientific literature continues to indicate that as the air's CO₂ content rises, grassland plants 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 does rise, the growth-promoting effects of atmospheric CO₂ enrichment will likely rise right along with it, becoming more and more robust in agreement with the experimental observations reviewed by Idso and Idso (1994). The future ability of grasslands to produce increasingly greater amounts of forage, and perhaps reclaim areas of barren ground in certain environments, thus looks promising indeed, as long as the air's CO₂ 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/g/tempco2grass.php>.

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6.3.9.3. Trees

In the study of Kellomaki and Wang (2001), birch seedlings were grown at atmospheric CO₂ 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 CO₂-enriched seedlings were 21 and 28% greater than those displayed by their ambiently-grown counterparts at ambient and elevated air temperatures, respectively. In another study, Carter *et al.* (2000) observed that a 300 ppm increase in the air's CO₂ content allowed leaves of sugar maple seedlings to remain green and non-chlorotic when exposed to air temperatures 3°C above ambient air temperature. 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 CO₂-enriched as opposed to ambiently-grown trees.

Other studies report similar results. Sheu *et al.* (1999), for example, grew a sub-tropical tree at day/night temperatures of 25/20 (ambient) and 30/25°C (elevated) for six months and reported that seedlings exposed to 720 ppm CO₂ displayed photosynthetic rates that were 20 and 40% higher, respectively, than that of their ambiently-grown controls. In addition, the CO₂-induced increases in total dry weight for this species were 14 and 49%, respectively, at ambient and elevated air temperatures. Likewise, Maherali *et al.* (2000) observed that a 5°C increase in ambient air temperature increased the CO₂-induced biomass enhancement resulting from a 750

ppm CO₂ enrichment of ponderosa pine seedlings from 42 to 62%. Moreover, 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 CO₂ increased the CO₂-induced increase in biomass from 60 to 227%. Thus, the beneficial effects of elevated CO₂ on tree species photosynthesis and growth is often enhanced due to elevated air temperatures, which 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 CO₂ 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 CO₂ concentrations of 580 ppm, they reported average increases in photosynthetic rates of 28%, regardless of temperature, which varied from 18 to 30°C. After analyzing the CO₂-induced increases in dry mass for these seedlings, Tjoelker *et al.* (1998b) further reported that dry mass values were about 50 and 20% greater for the deciduous and coniferous species, respectively, regardless of air temperature.

In conclusion, the recent scientific literature continues to indicate that as the air's CO₂ content rises, trees will likely exhibit enhanced rates of photosynthesis and biomass production that will not be negated by any global warming that might occur concurrently. In fact, if the ambient air temperature rises, the growth-promoting effects of atmospheric CO₂ enrichment will likely rise right along with it, in agreement with the experimental observations reviewed by Idso and Idso (1994). Thus, the future ability of earth's trees to produce greater amounts of biomass and, hence, more timber products to meet the increasing needs of an expanding human population looks promising indeed, as long as the CO₂ content of the air 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/g/tempco2trees.php>.

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6.3.9.4. 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 CO₂ concentration, it predicted a 25% 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 CO₂ and *low* air temperatures (between 15 and 25°C) displayed photosynthetic rates that were 10 to 30% 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 CO₂ appears to be capable of significantly increasing the photosynthetic prowess of certain of the native plants of earth's natural ecosystems.

In the real world, Stirling *et al.* (1998) grew five fast-growing native species at various atmospheric CO₂ concentrations and air temperatures, finding that twice-ambient levels of atmospheric CO₂ increased photosynthetic rates by 18-36% for all species regardless of air temperature, which was up to 3°C higher than ambient air temperature. In addition, atmospheric CO₂ enrichment increased average plant biomass by 25%, 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 CO₂ enrichment would do for these species!

On another note, 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 CO₂, as compared to 350 ppm, which would likely favor enhanced rates of photosynthesis as well.

In conclusion, the recent scientific literature continues to indicate that as the air's CO₂ content rises, the native plants of earth's natural ecosystems will likely exhibit enhanced rates of photosynthesis and biomass production that will not be diminished by any realistic increase in air temperature. In fact, if the ambient air temperature does rise somewhat, the growth-promoting effects of atmospheric CO₂ enrichment will likely rise right along with it, in agreement with the experimental observations reviewed by Idso and Idso (1994). Thus, the productivity of earth's natural ecosystems will likely continue its upward trend, even in the face of modest global warming, as long as the air's CO₂ content is in an ascending mode 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/g/tempco2growthres.php>.

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6.3.10. 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; Nouges *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)." Similar concern has been expressed in the CRDs, but the subject is treated there only lightly. In light of the above observations, it is important to clarify for the EPA's endangerment ruling how the ongoing rise in the air's CO₂ content might impact 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 CO₂ concentrations of 360 or 720 ppm from emergence until three weeks past first-flower stage under three levels of UV-B radiation (0, 8 and 16 kJ m⁻² d⁻¹); and on five dates between 21 and 62 days after emergence, they measured a number of plant physiological processes and parameters. Over the course of the experiment, the mean net photosynthetic rate of the upper-canopy leaves in the CO₂-enriched chambers was increased -- relative to that in the ambient-air chambers -- by 38.3% in the low UV-B treatment (from 30.3 to 41.9 m m⁻² s⁻¹), 41.1% in the medium UV-B treatment (from 28.7 to 40.5 m m⁻² s⁻¹), and 51.5% in the high UV-B treatment (from 17.1 to 25.9 m m⁻² s⁻¹). In the medium UV-B treatment, the growth stimulation from the elevated CO₂ was sufficient to raise net photosynthesis rates 33.7% above the rates experienced in the ambient air and no UV-B treatment (from 30.3 to 40.5 m m⁻² s⁻¹); but in the high UV-B treatment the radiation damage was so great that even with the help of the 51.5% increase in net photosynthesis provided by the doubled-CO₂ air, the mean net photosynthesis rate of the cotton leaves was 14.5% 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, however, 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% 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 CO₂ concentration and the current UV-B radiation level would reduce the net photosynthetic rate of cotton leaves by just under 10% (from 28.7 to 25.9 m m⁻² s⁻¹), whereas in the absence of a doubling of the air's CO₂ content, a doubling of the UV-B radiation level would reduce cotton net photosynthesis by just over 40% (from 28.7 to 17.1 m m⁻² s⁻¹).

Viewed in this light, it can be seen that a doubling the current atmospheric CO₂ 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; and it may possibly do even 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 CO₂ totally compensated for the negative effects of equally high UV-B radiation.

In another study (Qaderi and Reid, 2005), well watered and fertilized plants were grown from seed to maturity in pots within controlled environment chambers maintained at either 370 or

740 ppm CO₂ with and without a daily dose of UV-B radiation in the amount of 4.2 kJ m⁻², 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 CO₂, with UV-B). Doubling the CO₂ concentration increased yield by 25.5% to 1.23 g/plant. Alternatively, removing the UV-B radiation flux increased yield by 91.8% to 1.88 g/plant. Doing both (doubling the CO₂ concentration while simultaneously removing the UV-B flux) increased final seed yield most of all, by 175.5% to 2.7 g/plant. Viewed from a different perspective, doubling the air's CO₂ concentration in the *presence* of the UV-B radiation flux enhanced final seed yield by 25.5%, while doubling CO₂ in the *absence* of the UV-B radiation flux increased seed yield by 43.6%. In concluding their paper, the authors note that "previous studies have shown that elevated CO₂ 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 CO₂ 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 (*Brassica napus* L.) 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 UVB radiation or no such radiation in air of either 370 or 740 ppm CO₂, 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 UVB radiation, the experimental doubling of the air's CO₂ concentration led to a 29% increase in siliqua net photosynthesis, an 18% decrease in siliqua transpiration, and a 58% increase in siliqua water use efficiency; while for the plants exposed to *no* UVB radiation, siliqua net photosynthesis was increased by a *larger* 38%, transpiration was decreased by a *larger* 22% and water use efficiency was increased by a *larger* 87% in the CO₂-enriched air.

Although UV-B radiation levels are projected to increase in the near future as a result of stratospheric ozone depletion, in the slightly more distant future, however, when stratospheric ozone levels are projected to decline as a result of the worldwide ban on stratospheric-ozone-depleting substances, the biologically-beneficial effects of the ongoing rise in the air's CO₂ content will likely become *ever greater* as UVB levels at the earth's surface begin their anticipated long-term decline. As a result, the long-term agricultural and biospheric benefits of atmospheric CO₂ enrichment may well be significantly greater than what has been suggested by past and current open-top chamber and FACE experiments.

In another noteworthy study, Deckmyn *et al.* (2001) grew white clover plants for four months in four small greenhouses, two of which allowed 88% of the incoming UV-B radiation to pass through their roofs and walls and two of which allowed 82% to pass through, while one of the two greenhouses in each of the UV-B treatments was maintained at ambient CO₂ (371 ppm) and the other at elevated CO₂ (521 ppm). At the mid-season point of their study, they found that the 40% increase in atmospheric CO₂ concentration stimulated the production of flowers in

the low UV-B treatment by 22% and in the slightly higher UV-B treatment by 43%; while at the end of the season, the extra CO₂ was determined to have provided no stimulation of biomass production in the low UV-B treatment, but it significantly stimulated biomass production by 16% in the high UV-B treatment.

The results of this study indicate that the positive effects of atmospheric CO₂ enrichment on flower and biomass production in white clover are greater at more realistic or natural values of UV-B radiation than those found in many greenhouses. 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 CO₂ 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 CO₂ content.

The interactive effects of CO₂ and UV-B radiation has also been the subject of analysis. 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 CO₂ 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/m²/day). Results led this group of authors to report that "elevated CO₂ partially compensated [for] the damaging effects on vegetative growth and physiology caused by negative stressors such as high temperatures and enhanced UV-B radiation levels in soybean," specifically noting, in this regard, CO₂'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 CO₂ concentrations of 370 and 550 ppm and two levels of soil moisture (50 and 100% of potential evapotranspiration). They found that leaves of plants grown in elevated CO₂ had 14% 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 thus be conducted to see how general this beneficial response may be throughout the plant world.

In a study of UV-B and CO₂ 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% stratospheric ozone depletion -- and atmospheric CO₂ concentration -- ambient (around 365 ppm) and

enriched (around 600 ppm) -- after which they determined the amounts of microbial carbon (C_{mic}) and nitrogen (N_{mic}) in the soils of the plots.

When the plots were exposed to the enhanced UV-B radiation, the amount of C_{mic} in the soil was reduced to only 37% of what it was at the ambient UV-B level when the air's 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%. The story with respect to N_{mic} was both similar and different at one and the same time. In this case, when the plots were exposed to the enhanced level of UV-B radiation, the amount of N_{mic} in the soil experienced a 69% *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 a whopping 138%.

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)." Hence, the 138% increase in soil microbial N observed in this study to accompany a 15% reduction in stratospheric ozone and a 64% increase in atmospheric 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/uvradiation.php>.

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6.3.11. Water Stress

As the CO₂ content of the air continues to rise, nearly all of earth's plants will exhibit increases in photosynthesis and biomass production; but climate alarmists periodically 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 CO₂-induced stimulation of plant productivity. In fact, they found that the CO₂-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.

6.3.11.1. Agricultural Species

During times of water stress, atmospheric CO₂ 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% increase in lateral root dry weights of water-stressed wheat grown at 550 ppm CO₂, while De Luis *et al.* (1999) reported a 269% increase in root-to-shoot ratio of water-stressed alfalfa growing at 700 ppm CO₂. Thus, elevated CO₂ elicits stronger-than-usual positive root responses in agricultural species under conditions of water stress.

Elevated levels of atmospheric CO₂ also tend to reduce the openness of stomatal pores on leaves, thus decreasing plant stomatal conductance. This phenomenon, in turn, reduces the amount of water lost to the atmosphere by transpiration and, consequently, lowers overall plant water use. Indeed, Serraj *et al.* (1999) report that water-stressed soybeans grown at 700 ppm CO₂ reduced their total seasonal water loss by 10% relative to that of water-stressed control plants grown at 360 ppm CO₂. In addition, Conley *et al.* (2001) noted that a 200-ppm increase in the air's CO₂ concentration reduced cumulative evapotranspiration in water-stressed sorghum by approximately 4%.

Atmospheric CO₂ 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.

CO₂-induced increases in root development together with CO₂-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), for example, have reported that leaf water potential, which is a good indicator of overall plant water status, was 30% higher (less negative and therefore more favorable) in water-stressed alfalfa grown at an atmospheric CO₂ concentration of 600 ppm CO₂ versus 340 ppm CO₂. In addition, Wall (2001) reports that leaf water potentials were similar in CO₂-enriched water-stressed plants and ambiently-grown well-watered control plants, which implies a complete CO₂-induced amelioration of water stress in the CO₂-enriched plants. Similarly, Lin and Wang (2002) demonstrated that elevated CO₂ caused a several-day delay in the onset of the water stress-induced production of the highly reactive oxygenated compound H₂O₂ in spring wheat.

If atmospheric CO₂ 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% in plants growing in ambient air, while plants growing in air containing 600 ppm CO₂ only experienced a 30% reduction in net photosynthesis (Rabha and Uprety, 1998). In another manifestation of this phenomenon, 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 CO₂ 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 only to be expected that plant biomass production would be enhanced by elevated CO₂ concentrations under drought conditions. In exploring this idea, Ferris *et al.* (1999) reported that water-stressed soybeans grown at 700 ppm CO₂ attained seed yields that were 24% greater than those of similarly water-stressed plants grown at ambient CO₂ concentrations, while Hudak *et al.* (1999) reported that water-stress had no effect on yield in CO₂-enriched spring wheat.

In some cases, the CO₂-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 CO₂ content increased lower stem grain weights in water-stressed and well-watered spring wheat by 24 and 14%, respectively. Similarly, spring wheat grown in air containing an additional 280 ppm CO₂ exhibited 57 and 40% increases in grain yield under water-stressed and well-watered conditions, respectively (Schutz and Fangmeier, 2001). Likewise, Ottman *et al.* (2001) noted that elevated CO₂ increased plant biomass in water-stressed sorghum by 15%, 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 CO₂ 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. Indeed, in predicting maize and winter wheat yields in Bulgaria under increased air temperature and decreased precipitation scenarios, Alexandrov and Hoogenboom (2000) noted that yield losses were likely to occur if the atmospheric CO₂ concentration remained unchanged. However, if the atmospheric CO₂ concentration doubled, then maize and winter wheat yields would likely increase even under the stresses of elevated temperature and reduced rainfall. Thus, future increases in the air's CO₂ content will likely lead to increased crop growth and yield production, even in areas where reduced soil moisture availability leads to plant water stress.

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

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6.3.11.2. Grassland Species

Elevated levels of atmospheric CO₂ tend to reduce the area of open stomatal pore space on leaf surfaces, thus reducing plant stomatal conductance. This phenomenon, in turn, effectively reduces the amount of water lost to the atmosphere via transpiration. In the study of Leymarie

et al. (1999), for example, twice-ambient levels of atmospheric CO₂ 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 CO₂ concentrations (600 ppm) consistently exhibited reduced stomatal conductance, regardless of soil moisture availability. Thus, atmospheric CO₂ enrichment clearly reduces stomatal conductance and, hence, plant transpiration and soil water depletion in grassland ecosystems.

CO₂-induced increases in root development together with CO₂-induced reductions in stomatal conductance often combine to maintain a more favorable plant water status during times of drought. In the case of four grassland species comprising a pasture characteristic of New Zealand, for example, Clark *et al.* (1999) 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 CO₂ concentrations. Similarly, leaf water potentials of the water-stressed C₄ grass *Panicum coloratum* grown at 1000 ppm CO₂ 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 CO₂-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 CO₂ 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% reductions in the photosynthetic rates of two CO₂-enriched grassland species; yet their rates of carbon fixation were still greater than those observed under ambient CO₂ conditions.

In view of the fact that elevated CO₂ enhances photosynthetic rates during times of water stress, one would expect that plant biomass production would also be enhanced by elevated CO₂ 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 CO₂ 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 CO₂ content of the air increased shoot biomass in two C₄ grasses by 57%, regardless of soil water content. Moreover, Seneweera *et al.* (2001) reported that a 640-ppm increase in the air's CO₂ content increased shoot dry mass in a C₄ grass by 44 and 70% under well-watered and water-stressed conditions, respectively. Likewise, Volk *et al.* (2000) grew calcareous grassland assemblages at 360 and 600 ppm CO₂ and documented 18 and 40% CO₂-induced increases in whole-community biomass under well-watered and water-stressed conditions, respectively.

In summary, the peer-reviewed scientific literature indicates that the ongoing rise in the air's CO₂ 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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6.3.11.3. Woody Species

During times of water stress, atmospheric CO₂ 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 CO₂ helped them effectively deal with the reduced availability of moisture; and these trees eventually produced just as much biomass as well-watered controls exposed to ambient air containing 400 ppm CO₂. In addition, Polley *et al.* (1999) note that water-stressed honey mesquite trees subjected to an atmospheric CO₂ concentration of 700 ppm produced 37% more root biomass than water-stressed control seedlings growing at 370 ppm.

Elevated levels of atmospheric CO₂ also tend to reduce the area of open stomatal pore space on leaf surfaces, thus reducing plant stomatal conductance. This phenomenon, in turn, reduces the amount of water lost to the atmosphere via transpiration. Tognetti *et al.* (1998), for example, determined that stomatal conductances of mature oak trees growing near natural CO₂ springs in central Italy were significantly lower than those of similar trees growing further away from the springs during periods of severe summer drought.

CO₂-induced increases in root development together with CO₂-induced reductions in stomatal conductance often contribute to the maintenance of a more favorable plant water status during times of drought. In the case of three Mediterranean shrubs, 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 CO₂ concentrations. Similarly, leaf water potentials of water-stressed mesquite seedlings grown at 700 ppm CO₂ were 40% higher than those of their water-stressed counterparts growing in ambient air (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 CO₂, respectively (Hamerlynck *et al.*, 2000).

If atmospheric CO₂ enrichment thus allows plants to maintain better water status during times of water stress, it is only logical to expect that plants will exhibit CO₂-induced increases in photosynthesis, even under conditions of low soil moisture availability. It is not surprising, therefore, that Palanisamy (1999) observed water-stressed *Eucalyptus* seedlings grown at 800 ppm CO₂ to display greater net photosynthetic rates than their ambiently-grown and water-stressed counterparts. In fact, Runion *et al.* (1999) observed the CO₂-induced photosynthetic stimulation of water-stressed pine seedlings grown at 730 ppm CO₂ to be nearly 50% greater than that of similar water-stressed pine seedlings grown at 365 ppm CO₂. Similarly, Centritto *et al.* (1999a) found that water-stressed cherry trees grown at 700 ppm CO₂ displayed net photosynthetic rates that were 44% greater than those of water-stressed trees grown at 350 ppm CO₂. And Anderson and Tomlinson (1998) found that a 300-ppm increase in the air's CO₂ concentration boosted photosynthetic rates in well-watered and water-stressed red oak seedlings by 34 and 69%, respectively, demonstrating that the CO₂-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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ conditions, whereas ambiently-growing plants displayed net carbon *losses*. In addition, Polley *et al.* (2002) reported that seedlings of five woody species grown at twice-ambient CO₂ concentrations survived 11 days longer (on average) than control seedlings when subjected to maximum drought conditions. Thus, in some cases of water stress, enriching the air with CO₂ can actually mean the difference between a plant's growing or not growing. And if such conditions persist too long, that difference may translate into an actual life-or-death difference.

In view of the fact that elevated CO₂ thus enhances photosynthetic rates during times of water stress, one would expect that plant biomass production would also be enhanced by elevated CO₂ concentrations under drought conditions; and so it is, as demonstrated by Arp *et al.* (1998), who reported that six perennial plants common to the Netherlands increased their biomass under CO₂-enriched conditions even when suffering from lack of water. In other cases, the CO₂-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 CO₂-induced biomass increase for paper birch was 27% and 130% for well-watered and water-stressed seedlings, respectively. Similarly, Schulte *et al.* (1998) noted that the CO₂-induced biomass increase of oak seedlings was greater under water-limiting conditions than under well-watered conditions (128% vs. 92%), as did Centritto *et al.* (1999b) for basal trunk area in cherry seedlings (69% vs. 22%).

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 CO₂ concentration was around 340 ppm, than they did from 1900-1930, when the atmospheric CO₂ 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 CO₂ concentration was factored into their mechanistic model, a 25% *increase* in primary productivity was projected.

In summary, the peer-reviewed scientific literature indicates that the ongoing rise in the air's CO₂ 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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6.4. Acclimation

Plants grown in elevated CO₂ 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 CO₂-enriched air. These downward

adjustments result from modest long-term decreases in the activities and/or amounts of the primary plant carboxylating enzyme *rubisco*. Acclimation is said to be present when the photosynthetic rates of long-term CO₂-enriched plants are found to be lower than those of long-term *non*-CO₂-enriched plants when the normally CO₂-enriched plants are measured during brief exposures to ambient CO₂ concentrations. Nevertheless, rates of photosynthesis displayed by plants grown and measured at elevated CO₂ concentrations are often greater than those exhibited by plants grown and measured at ambient CO₂ concentrations, leading to enhanced growth in CO₂-enriched air. 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.

6.4.1. Agricultural Species

Several studies have examined the effects of elevated CO₂ on acclimation in agricultural crops. Ziska (1998), for example, reported that soybeans grown at an atmospheric CO₂ concentration of 720 ppm initially exhibited photosynthetic rates that were 50% greater than those observed in control plants grown at 360 ppm. However, after the onset of photosynthetic acclimation, CO₂-enriched plants displayed subsequent photosynthetic rates that were only 30% greater than their ambiently-grown counterparts. In another study, Theobald *et al.* (1998) grew spring wheat at twice-ambient atmospheric CO₂ concentrations and determined that elevated CO₂ reduced the amount of *rubisco* required to sustain enhanced rates of photosynthesis, which led to a significant increase in plant photosynthetic nitrogen-use efficiency. CO₂-induced increases in photosynthetic nitrogen-use efficiency 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 CO₂ 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 CO₂ concentration of 550 ppm in a FACE experiment with optimal soil nutrition and unlimited rooting volume, Garcia *et al.* (1998) could find no evidence of photosynthetic acclimation.

CO₂-induced photosynthetic acclimation often results from insufficient plant sink strength, which can lead to carbohydrate accumulation in source leaves and the triggering of photosynthetic end product feedback inhibition, which reduces net photosynthetic rates. Indeed, Gesch *et al.* (1998) reported that rice plants -- which have relatively limited potential for developing additional carbon sinks -- grown at an atmospheric CO₂ concentration of 700 ppm exhibited increased leaf carbohydrate contents, which likely reduced *rbcS* mRNA levels and ultimately *rubisco* protein content. Similarly, Sims *et al.* (1998) reported that photosynthetic acclimation was induced in CO₂-enriched soybean plants from the significant accumulation of nonstructural carbohydrates in their leaves. However, in growing several

different *Brassica* species at 1,000 ppm CO₂, Reekie *et al.* (1998) demonstrated that CO₂-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 CO₂ enrichment but rather an indirect effect of low sink strength, which results in leaf carbohydrate accumulation that can trigger acclimation.

In some cases, plants can effectively increase their sink strength, and thus reduce the magnitude of CO₂-induced acclimation, by forming symbiotic relationships with certain species of soil fungi. Under such conditions, photosynthetic down regulation is not triggered as rapidly, or as frequently, by end product feedback inhibition, as excess carbohydrates are mobilized out of source leaves and sent belowground to symbiotic fungi. Indeed, Louche-Tessandier *et al.* (1999) report that photosynthetic acclimation in CO₂-enriched potatoes was less apparent when plants were simultaneously colonized by a mycorrhizal fungus. Thus, CO₂-induced acclimation appears to be closely related to the source:sink balance that exists within plants, being triggered when sink strength falls below, and source strength rises above, critical thresholds in a species-dependent manner.

Acclimation is generally regarded as a process that reduces the amount of rubisco and/or other photosynthetic proteins, which effectively increases the amount of nitrogen available for enhancing sink development or stimulating other nutrient-limited processes. In the study of Watling *et al.* (2000), for example, the authors reported a 50% CO₂-induced reduction in the concentration of PEP-carboxylase, the primary carboxylating enzyme in C₄ plants, within sorghum leaves. Similarly, Maroco *et al.* (1999) documented CO₂-induced decreases in both PEP-carboxylase and rubisco in leaves of the C₄ crop maize.

In some cases, however, acclimation to elevated CO₂ is manifested by an "up-regulation" of certain enzymes. When Gesch *et al.* (2002) took rice plants from ambient air and placed them in air 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 CO₂ concentration of 660 ppm displayed 20% more SPS activity during the growing season than did ambiently-grown rice plants. Such increases in the activity of this enzyme could allow CO₂-enriched plants to avoid the onset of photosynthetic acclimation by synthesizing and subsequently exporting sucrose from source leaves into sink tissues before they accumulate and trigger end product feedback inhibition.

In an interesting experiment, Gesch *et al.* (2000) took ambiently-growing rice plants and placed them in an atmospheric CO₂ concentration of 175 ppm, which reduced photosynthetic rates by 45%. However, after five days exposure to this sub-ambient CO₂ concentration, the plants manifested an up-regulation of rubisco, which stimulated photosynthetic rates by 35%. Thus, plant acclimation responses can involve both an increase or decrease in specific enzymes, depending on the atmospheric CO₂ concentration.

In summary, many peer-reviewed studies suggest that as the CO₂ content of the air slowly but steadily rises, agricultural species may not necessarily exhibit photosynthetic acclimation, even under conditions of low soil nitrogen; for if a plant can maintain a balance between its sources and sinks for carbohydrates at the whole-plant level, acclimation should not be necessary. In addition, because earth's atmospheric CO₂ 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 CO₂-induced increase in leaf carbohydrate production. However, in the event that a plant cannot initially balance its sources and sinks for carbohydrates at the whole-plant level, CO₂-induced acclimation represents a beneficial secondary mechanism for achieving that balance through redistributing limiting resources away from the plant's photosynthetic machinery to strengthen sink development or enhance other 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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6.4.2. Chaparral and Desert Species

Roberts *et al.* (1998) conducted a FACE experiment in southern California, USA, exposing *Adenostoma fassiculatum* shrubs to atmospheric CO₂ concentrations of 360 and 550 ppm while they studied the nature of gas-exchange in this chaparral species. After six months of CO₂ fumigation, photosynthetic acclimation occurred. However, because of reductions in stomatal conductance and transpirational water loss, the CO₂-enriched shrubs exhibited leaf water potentials that were less negative (and, hence, less stressful) than those of control plants. This CO₂-induced water conservation phenomenon should enable this woody perennial to better withstand the periods of drought that commonly occur in this southern California region, 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 CO₂ concentrations of 350 and 550 ppm. The elevated CO₂ 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 CO₂-enriched plants. However, elevated CO₂ had no consistent effect on stomatal conductance in this species. In contrast, *Eriogonum* plants growing at 550 ppm CO₂ exhibited significant photosynthetic acclimation, especially late in the season, which led to similar rates of net photosynthesis in these plants in both CO₂ treatments. But in this species, elevated CO₂ *did* reduce stomatal conductance over most of the growing season. Hence, although both desert plants exhibited different stomatal and photosynthetic responses to elevated CO₂, both experienced significant CO₂-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 CO₂ 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 CO₂ displayed photosynthetic acclimation, as maximum rubisco activity in the plants growing in the CO₂-enriched air was 19% lower than in the plants growing in ambient air. Also, the elevated CO₂ did not significantly impact rates of photosynthesis. Leaf stomatal conductance, on the other hand, was consistently about 27% lower in the plants grown in the CO₂-enriched air; and during the last month of the spring growing season, the plants in the elevated CO₂ plots displayed leaf water potentials that were less negative than those exhibited by the control plants growing in ambient air. Hence, as the CO₂ 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. Moreover, 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 CO₂ 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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6.4.3. Grassland Species

In nearly every reported case of photosynthetic acclimation in CO₂-enriched plants, rates of photosynthesis displayed by grassland species *grown and measured at elevated CO₂ concentrations* are typically greater than those exhibited by control plants *grown and measured at ambient CO₂ concentrations* (Davey *et al.*, 1999; Bryant *et al.*, 1998).

As mentioned in prior sections, CO₂-induced photosynthetic acclimation often results from insufficient plant sink strength, which can lead to carbohydrate accumulation in source leaves and the triggering of photosynthetic end-product feedback inhibition, which reduces 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 CO₂ concentration of 600 ppm and *low* soil nitrogen exhibited leaf carbohydrate contents and rubisco activities that were 100% greater and 25% less, respectively, than those observed in control plants grown at 360 ppm CO₂, prior to a cutting event. Following the cutting, which effectively reduced the source:sink ratio of the plants, leaf carbohydrate contents in CO₂-enriched plants decreased and rubisco activities increased, completely ameliorating the photosynthetic acclimation in this species. However, at *high* soil nitrogen, photosynthetic acclimation to elevated CO₂ did *not* occur. Thus, photosynthetic acclimation appears to result from the inability of plants to develop adequate sinks at low soil nitrogen, and is not necessarily induced directly by atmospheric CO₂ enrichment.

In some cases, plants can effectively increase their sink strength and thus reduce the magnitude of CO₂-induced acclimation by forming symbiotic relationships with certain species of soil fungi. Under such conditions, photosynthetic down regulation is not triggered as rapidly, or as frequently, by end-product feedback inhibition, as excess carbohydrates are mobilized out of source leaves and sent belowground to symbiotic fungi. Indeed, Staddon *et al.* (1999) reported that photosynthetic acclimation was not induced in CO₂-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, CO₂-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 CO₂ 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 ultimately 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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6.4.4. Tree Species

Trees grown for long periods of time in elevated CO₂ 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 CO₂-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 CO₂-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), for example, grew one-year-old Scots pine seedlings for two additional years at twice-ambient atmospheric CO₂ concentrations and reported that the elevated CO₂ increased the trees' mean rate of net photosynthesis by 64%. However, when measured during a brief return to ambient CO₂ concentrations, the normally-CO₂-enriched seedlings exhibited an approximate 21% 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 CO₂ concentration boosted rates of net photosynthesis in fifteen-year-old Norway spruce trees by 78%; but when net photosynthesis in the normally-CO₂-enriched trees was measured at a temporary atmospheric CO₂ concentration of 350 ppm, an 18% reduction was observed relative to what was observed in comparable trees that had always been grown in ambient air. In fact, after reviewing the results of 15 different atmospheric CO₂ enrichment studies of European forest species growing in field environments maintained at twice-ambient CO₂ concentrations, Medlyn *et al.* (1999) found that the mean photosynthetic acclimation effect in the CO₂-enriched trees was characterized by an average reduction of 19% in their rates of net photosynthesis when measured at temporary ambient CO₂ 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 CO₂-induced photosynthetic acclimation in trees, the photosynthetic rates of trees *growing and measured in CO₂-enriched air* have still been *much greater* than those exhibited by trees *growing and measured in ambient air*.

CO₂-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 CO₂ concentration of 1600 ppm had foliar starch concentrations *17-fold greater* than those observed in leaves of seedlings grown at 360 ppm CO₂, 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 CO₂-enriched silver birch seedlings (100% 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 CO₂ 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% increases in foliar glucose levels.

In some cases, trees can effectively increase their sink strength, and thus reduce the magnitude of CO₂-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 CO₂-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 CO₂-enriched seedlings. Thus, CO₂-induced acclimation appears to be closely related to the source:sink balance that exists within plants; and it appears to be triggered when sink strength falls below, and source strength rises above, certain critical thresholds in a species-dependent manner.

During acclimation to elevated CO₂, 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, in the study of Blaschke *et al.* (2001), the authors reported that a doubling of the atmospheric CO₂ concentration reduced foliar rubisco concentrations by 15 and 30% in two mature oak species growing near CO₂-emitting springs. Similarly, a 200-ppm increase in the air's CO₂ content reduced foliar rubisco concentrations in young aspen and birch seedlings by 39% (Takeuchi *et al.*, 2001) and 24% (Tjoelker *et al.*, 1998), respectively. Also, in two *Pinus radiata* studies, seedlings fumigated with air containing 650 ppm CO₂ displayed 30 to 40% 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 CO₂-enriched Norway spruce and Scots pines have documented CO₂-induced reductions in foliar chlorophyll contents of 17% (Spunda *et al.*, 1998) and 26% (Gielen *et al.*, 2000), respectively. And in the study of Gleadow *et al.* (1998), elevated CO₂ 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 CO₂-enriched air and subsequently grew them at ambient and twice-ambient atmospheric CO₂ concentrations. They discovered that seedlings derived from acorns produced on CO₂-enriched trees exhibited less-pronounced photosynthetic acclimation to elevated CO₂ than did seedlings derived from acorns produced on ambiently-grown trees, suggesting the possibility of generational adaptation to higher atmospheric CO₂ concentrations over even longer periods of time.

In summary, these many peer-reviewed scientific studies suggest that as the air's CO₂ 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 CO₂ 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 *ultimately* 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% complete (in the studies reviewed here it was on the order of 20%), so that tree growth is almost always significantly enhanced in CO₂-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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6.5. Competition

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.

6.5.1. C₃ vs C₄ Plants

C₃ plants typically respond better to atmospheric CO₂ enrichment than do C₄ 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 CO₂ concentration, C₃ plants may out-compete C₄ plants and displace them, thereby decreasing the biodiversity of certain ecosystems. However, the story is much more complex than 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 C₃ species that were colonized by the fungi was the same as that of the non-inoculated C₃ species, but that the fungal-colonized C₄ species produced, on average, 85% *more* dry matter than the non-inoculated C₄ species. This finding is of pertinence to the relative responsiveness of C₃ and C₄ plants to atmospheric CO₂ enrichment; for elevated levels of atmospheric CO₂ tend to enhance the mycorrhizal colonization of plant roots [see Fungi (Grasses and Herbaceous Plants)], which is known to make soil minerals and water more available for plant growth (see Nutrient Acquisition). Hence, this CO₂-induced fungal-mediated growth advantage, which from this study appears to be more readily available to C₄ plants, could well counter the inherently greater biomass response of C₃ plants relative to that of C₄ plants, leveling the playing field relative to their competition for space in any given ecosystem.

Another advantage that may come to C₄ plants as a consequence of the ongoing rise in the air's CO₂ content was elucidated by BassiriRad *et al.* (1998), who found that elevated CO₂ enhanced the ability of the perennial C₄ grass *Bouteloua eriopoda* to increase its uptake of NO₃⁻ and PO₄³⁻ considerably more than the perennial C₃ shrubs *Larrea tridentata* and *Prosopis glandulosa*. Hence, it is not surprising that in an eight-year study of the effects of twice-ambient atmospheric CO₂ concentrations on a pristine tallgrass prairie in Kansas, Owensby *et al.* (1999) found that the elevated CO₂ did not affect the basal coverage of its C₄ species or their relative contribution to the composition of the ecosystem.

Then, of course, there is the well-known *antitranspirant effect* of atmospheric CO₂ enrichment (Pospisilova and Catsky, 1999), which is often more strongly expressed in C₄ plants than in C₃ plants and that typically allows C₄ plants to better cope with water stress. In a study of the C₃ dicot *Abutilon theophrasti* and the C₄ dicot *Amaranthus retroflexus*, for example, Ward *et al.*

(1999) found that *Amaranthus retroflexus* exhibited a greater relative recovery from drought than did the C₃ species, which suggests, in their words, that "the C₄ species would continue to be more competitive than the C₃ species in regions receiving more frequent and severe droughts," which basically characterizes regions where C₄ 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 CO₂ concentrations of 360 and 720 ppm for two six-month growing seasons. In spite of an average air temperature increase of 2.6°C, which was caused by the presence of the open-top chambers, the elevated CO₂ increased aboveground biomass production by an average of 38% in both years of the study; and when 50% of the standing green plant biomass was defoliated to simulate grazing halfway through the growing season, atmospheric CO₂ enrichment still increased aboveground biomass by 36%. It was also found that the communities enriched with CO₂ 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 CO₂-enriched plants. Last of all, the elevated CO₂ did not preferentially stimulate the growth of C₃ species over that of C₄ species in these communities. Hence, elevated CO₂ did not significantly affect the percentage composition of C₃ and C₄ species in these grasslands; and they maintained their original level of vegetative biodiversity.

In light of these several observations, we believe it to be highly unlikely that the ongoing rise in the air's CO₂ content will lead to C₃ plants replacing C₄ plants in the vast majority of earth's ecosystems. This would also appear to be the take-home message 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 C₃ and C₄ grasses to elevated CO₂. On average, they found photosynthetic enhancements of 33 and 25%, respectively, for C₃ and C₄ plants, along with biomass enhancements of 44 and 33%, respectively, for a doubling of the air's CO₂ concentration. These larger-than-expected growth responses in the C₄ species led them to conclude that "it may be premature to predict that C₄ grass species will lose their competitive advantage over C₃ grass species in elevated CO₂."

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 great body of research, they concluded that the "growth of C₄ species is about as responsive to CO₂ concentration as [is that of] C₃ species when water supply restricts growth, as is usual in grasslands containing C₄ species." Hence, the work of this group of scientists also provides no evidence for the suggestion that C₃ plants may out-compete C₄ plants and thereby replace them in a high-CO₂ 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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6.5.2. 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 did indeed give 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 that there was no difference between the minimal to non-existent growth responses of N-fixing and non-N-fixing species to elevated levels of atmospheric CO₂. In addition, in a study of mixed plantings of the grass *Lolium perenne* and the legume *Medicago sativa*, Matthies and Egli (1999) found that elevated CO₂ did not influence the competition between the two plants, either directly or indirectly via its effects upon the root hemiparasite *Rhinanthus alectorolophus*; and in a study of mixed plantings of two grasses and two legumes, Navas *et al.* (1999) observed that plant responses to atmospheric CO₂ 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 and eliminate them from any ecosystems.

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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6.5.3. Weeds vs. Non-Weeds

Elevated CO₂ typically stimulates the growth of nearly all plant species in monoculture, including those deemed undesirable by humans, i.e., weeds. Consequently, it is important to determine how future increases in the air's CO₂ content may influence relationships between weeds and non-weeds when they grow competitively in mixed-species stands.

Dukes (2002) grew model serpentine grasslands common to California, USA, in competition with the invasive forb *Centaurea solstitialis* at atmospheric CO₂ concentrations of 350 and 700 ppm for one year, determining that elevated CO₂ increased the biomass proportion of this weedy species in the community by a mere 1.2%, while total community biomass increased by 28%. Similarly, Gavazzi *et al.* (2000) grew loblolly pine seedlings for four months in competition with both C₃ and C₄ weeds at atmospheric CO₂ concentrations of 260 and 660 ppm, reporting that elevated CO₂ increased pine biomass by 22% while eliciting *no response at all* from either type of weed. Likewise, in a study of pasture ecosystems near Montreal, Canada, Taylor and Potvin (1997) found that elevated CO₂ concentrations did not influence the number of native species returning after their removal (to simulate disturbance), even in the face of the *introduced* presence of the C₃ weed *Chenopodium album*, which normally competes quite effectively with several slower-growing crops in ambient air. In fact, atmospheric CO₂ enrichment did not impact the growth of this weed in any measurable way.

Ziska *et al.* (1999) also studied the C₃ weed *C. album*, along with the C₄ weed *Amaranthus retroflexus*, in glasshouses maintained at atmospheric CO₂ concentrations of 360 and 720 ppm. They determined that elevated CO₂ significantly increased the photosynthetic rate and total dry weight of the C₃ weed, but that it had *no effect at all* on the C₄ weed. Also, they found that the growth response of the C₃ weed to a doubling of the air's CO₂ content was approximately 51%, which is about the same as the average 52% growth response tabulated by Idso (1992), and that obtained by Poorter (1993) for rapidly-growing wild C₃ species (54%), which finding suggests there is no enhanced dominance of the C₃ weed over other C₃ plants in a CO₂-enriched environment.

Wayne *et al.* (1999) studied another agricultural weed, field mustard (*Brassica kaber*), which was sown in pots at six densities, placed in atmospheric CO₂ concentrations of 350 and 700 ppm, and sequentially harvested during the growing season. Early in stand development, elevated CO₂ increased aboveground weed biomass in a density-dependent manner; with the greatest stimulation of 141% occurring at the lowest density (corresponding to 20 plants per square meter) and the smallest stimulation of 59% occurring at the highest density (corresponding to 652 plants per square meter). However, as stands matured, the density-dependence of the CO₂-induced growth response disappeared, and CO₂-enriched plants exhibited an average aboveground biomass that was 34% greater than that of ambiently-grown plants across a broad range of plant densities. Moreover, this final growth stimulation was similar to that of most other herbaceous plants exposed to atmospheric CO₂ enrichment (30 to 50% biomass increases for a doubling of the air's CO₂ content), once again evidencing that atmospheric CO₂ 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 CO₂ concentrations of 370 and 570 ppm and normal or high levels of soil fertility. They found that the high CO₂ treatment

consistently increased rates of net photosynthesis by 30 to 70%, depending on soil fertility and time of year. However, elevated CO₂ 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 CO₂ on bracken growth was observed in the normal nutrient regime, where elevated CO₂ actually *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 CO₂ concentration of 700 ppm was 65% 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% in ambient air of 360 ppm CO₂, while it only reduced it by 20% in air of 550 ppm CO₂.

These several studies suggest that, contrary to what is claimed by the alarmists, the ongoing rise in the air's CO₂ content likely will *not* favor the growth of weedy species over that of crops and native plants. In fact, it may well provide non-weeds greater protection against weed-induced decreases in their productivity and growth. Thus, future increases in the air's CO₂ 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/weedsvsnw.php>.

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6.6. Respiration

Nearly all of earth's plants respond favorably to increases in the air's CO₂ concentration by exhibiting enhanced rates of net photosynthesis and biomass production. In many cases, observed increases in these parameters (especially biomass production) are believed to be due, in part, to CO₂-induced reductions in carbon losses via respiration, which seems only logical (albeit appearances may sometimes be deceiving), for with less carbon being respired under CO₂-enriched conditions, rates of net carbon assimilation and its incorporation into plant organic matter would be expected to rise, as they indeed do in most cases when the air's CO₂ content is increased. In this section, therefore, 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.

6.6.1. Herbaceous Plants

6.6.1.1. Crops

Baker *et al.* (2000) grew rice in Soil-Plant-Atmosphere Research (SPAR) units at atmospheric CO₂ concentrations of 350 and 700 ppm during daylight hours. Under these conditions, rates of dark respiration decreased in both CO₂ treatments with short-term increases in the air's CO₂ concentration at night. However, when dark respiration rates were measured at the CO₂ growth concentrations of the plants, they were *not* significantly different from each other.

Cousins *et al.* (2001) grew sorghum at atmospheric CO₂ concentrations of 370 and 570 ppm within a Free-Air CO₂-Enrichment (FACE) facility near Phoenix, Arizona, USA. Within six days of planting, the photosynthetic rates of the second leaves of the CO₂-enriched plants were 37% greater than those of the second leaves of the ambiently-grown plants. However, this CO₂-induced photosynthetic enhancement slowly declined with time, stabilizing at approximately 15% between 23 and 60 days after planting. In addition, when measuring photosynthetic rates at a reduced oxygen concentration of 2%, they observed 16 and 9% increases in photosynthesis for the ambient and CO₂-enriched plants, respectively. These observations suggest that the extra 200 ppm of CO₂ was reducing photorespiratory carbon losses, although this phenomenon did not account for all of the CO₂-induced stimulation of photosynthesis.

Das *et al.* (2002) grew tropical nitrogen-fixing mungbean plants in open-top chambers maintained at atmospheric CO₂ concentrations of either 350 or 600 ppm for two growing

seasons, with the extra CO₂ being provided between either days 0 and 20 or days 21 and 40 after germination. This work revealed that the elevated CO₂ decreased rates of respiration by 54-62%, with the greatest declines occurring during the first 20 days after germination.

Wang *et al.* (2004) grew well-watered and fertilized South American tobacco plants from seed in 8.4-liter pots (one plant per pot) filled with sand and housed in controlled-environment growth chambers maintained at atmospheric CO₂ concentrations of either 365 or 730 ppm for 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 CO₂-enriched environment but had risen by only 58% 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 CO₂ more efficiently as they mature."

Bunce (2005) grew soybeans in the field in open-top chambers maintained at atmospheric CO₂ concentrations of ambient and ambient +350 ppm at the Beltsville Agricultural Research Center in Maryland (USA), where net carbon dioxide exchange rate measurements were performed on a total of 16 days between 18 July and 11 September of 2000 and 2003, during the flowering to early pod-filling stages of the growing season. Averaged over the course of the study, he found that daytime net photosynthesis per unit leaf area was 48% greater in the plants growing in the CO₂-enriched air, while nighttime respiration per unit leaf area was unaffected by elevated CO₂. However, because the extra 350 ppm of CO₂ increased leaf dry mass per unit area by an average of 23%, respiration per unit of mass was significantly lower for the leaves of the soybeans growing in the CO₂-enriched air.

Wang and Curtis (2002) conducted a meta-analysis of the results of 45 area-based dark respiration (Rda) and 44 mass-based dark respiration (Rdm) assessments of the effects of a doubling of the air's CO₂ concentration on 33 species of plants derived from 37 scientific studies. This work revealed that the mean leaf Rda of the suite of herbaceous plants studied was significantly *higher* (+29%, $P < 0.01$) at elevated CO₂ than at ambient CO₂. However, when the herbaceous plants were separated into groups that had experienced durations of CO₂ 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% ($P < 0.05$), while the long-term studies exhibited *no effect*. Hence, for conditions of *continuous* atmospheric CO₂ enrichment, herbaceous plants would likely experience no change in leaf Rda. In addition, the two researchers found that plants exposed to elevated CO₂ for < 100 days "showed significantly less of a reduction in leaf Rdm due to CO₂ enrichment (-12%) than did plants exposed for longer periods (-35%, $P < 0.01$)." Hence, for long-term conditions of *continuous* atmospheric CO₂ enrichment, herbaceous crops would likely experience an approximate 35% 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 CO₂ 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 CO₂ 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 CO₂ concentration." As a result, and irrespective of whatever mechanisms may have been involved in eliciting the responses observed, Bunce logically concluded that "the parallel responses of translocation and nitrate reduction for both the temperature and CO₂ treatments make it unlikely that the response of respiration to one variable [CO₂] was an artifact while the response to the other [temperature] was real." Hence, there is reason to believe that the oft-observed decreases in dark respiration experienced by plants exposed to elevated levels of atmospheric CO₂, as per the review and analysis studies of Drake *et al.* (1999) and Wang and Curtis (2002), are indeed real and not the result of measurement system defects.

In light of these several findings, it can probably be validly concluded that the balance of evidence suggests that the growth of herbaceous crops is generally not only enhanced by CO₂-induced increases in net photosynthesis during the light period of the day, it is also enhanced by CO₂-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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6.6.1.2. Other

In this section we review the results of a smattering of studies of non-crop herbaceous plants in an attempt to determine if atmospheric CO₂ 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 CO₂ concentrations and adequate or inadequate soil moisture levels. Their work revealed that the elevated CO₂ concentration reduced leaf dark respiration rates by about 25% in both soil moisture treatments, which suggests that a greater proportion of the increased carbohydrate pool in the CO₂-enriched plants remained within them to facilitate increases in growth and development.

Ziska and Bunce (1999) grew four C₄ plants in controlled environment chambers maintained at either full-day (24-hour) atmospheric CO₂ concentrations of 350 and 700 ppm or a nocturnal-only CO₂ concentration of 700 ppm (with 350 ppm CO₂ during the day) for about three weeks. In this particular study, 24-hour CO₂ enrichment caused a significant increase in the photosynthesis (+13%) and total dry mass (+21%) of only one of the four C₄ species (*Amaranthus retroflexus*). However, there was *no significant effect* of nocturnal-only CO₂ enrichment on this species, indicating that the observed increase in biomass, resulting from 24-hour atmospheric CO₂ enrichment, was *not* facilitated by greater carbon conservation stemming from a CO₂-induced reduction in dark respiration.

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 CO₂ concentrations of 280, 440 and 600 ppm for five months. This study also revealed that atmospheric CO₂ 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 CO₂ 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 CO₂ reduced rates of dark respiration consistently throughout the study by 40 to 60%. In a final multi-species study, Gonzalez-Meler *et al.* (2004) reviewed the scientific literature pertaining to the effects of atmospheric CO₂ 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 CO₂." Nevertheless, they note that "whole ecosystem studies show that canopy respiration does not increase proportionally to increases in biomass in response to elevated CO₂," which suggests that *respiration per unit biomass* is likely somewhat *reduced* by atmospheric CO₂ enrichment. However, they also find that "a larger proportion of respiration takes place in the root system [when plants are grown in CO₂-enriched air]," which once again obfuscates the issue.

The three researchers ultimately conclude that "fundamental information is still lacking on how respiration and the processes supported by it are physiologically controlled, thereby preventing sound interpretations of what seem to be species-specific responses of respiration to elevated CO₂." Hence, they refreshingly state that "the role of plant respiration in augmenting the sink capacity of terrestrial ecosystems is still uncertain," setting an example of wise restraint that many climate alarmists and politicians would do well to follow with respect to questions about many other aspects of CO₂ effects (and non-effects!) on climate and biology.

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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6.6.2. Woody Plants

6.6.2.1. 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 CO₂ concentrations of either 350 or 750 ppm for two years; and to make the experiment even more representative of the natural world, they applied no nutrients or irrigation water to the soils in which the trees grew for the duration of the study. After two years of growth under these conditions, dark respiration on a needle mass basis in the CO₂-enriched seedlings was 27% and 33% lower in current-year and one-year-old needles, respectively, with the greater reduction in the older needles being thought to arise from the greater duration of elevated CO₂ exposure experienced by those needles.

Hamilton *et al.* (2001) studied the short- and long-term respiratory responses of loblolly pines in a free-air CO₂-enrichment (FACE) study that was established in 1996 on 13-year-old trees in a North Carolina (USA) plantation, where the CO₂-enriched trees were exposed to an extra 200 ppm of CO₂. This modest increase in the atmosphere's CO₂ concentration produced no significant short-term suppression of *dark* respiration rates in the trees' needles. Neither did long-term exposure to elevated CO₂ alter *maintenance* respiration, which is the amount of CO₂ respired to maintain existing plant tissues. However, *growth* respiration, which is the amount of CO₂ respired when constructing new tissues, was reduced by 21%.

McDowell *et al.* (1999) grew five-month-old seedlings of western hemlock in root boxes subjected to various root-space CO₂ concentrations (ranging from 90 to 7000 ppm) for periods of several hours to determine the effects of soil CO₂ concentration on growth, maintenance and total root respiration. In doing so, they found that although elevated CO₂ had no effect on growth respiration, it significantly impacted maintenance and total respiration. At a soil CO₂ concentration of 1585 ppm, for example, total and maintenance respiration rates of roots were 55% and 60% lower, respectively, than they were at 395 ppm. In fact, the impact of elevated CO₂ on maintenance respiration was so strong that it exhibited an exponential decline of about 37% for every doubling of soil CO₂ concentration. The implications of this observation are especially important, since maintenance respiration comprised 85% of total root respiration in this study.

The results of these experiments suggest that both above and below the soil surface, coniferous trees *might* exhibit reductions in total respiration in a high-CO₂ world of the future. Three studies of but three species, however, is no guarantee of anything. Hence, it is important to consider the findings described in this summary within the broader context provided by the results of experiments conducted on other woody plants, as well as herbaceous plants, as summarized here.

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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6.6.2.2. 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 CO₂ concentrations of 380 and 765 ppm, finding that gender had little effect on dark respiration rates, but that elevated CO₂ *increased* them, by 6% and 32% in the low and high soil nitrogen treatments, respectively. On the other hand, Karnosky *et al.* (1999) grew both O₃-sensitive and O₃-tolerant aspen clones for one full year in free-air CO₂-enrichment (FACE) plots maintained at atmospheric CO₂ concentrations of 360 and 560 ppm, finding that the extra CO₂ *decreased* dark respiration rates by 24%.

Gielen *et al.* (2003) measured stem respiration rates of white, black and robusta poplar trees in a high-density forest plantation in the third year of a FACE experiment in which the CO₂ concentration of the air surrounding the trees was increased to a value of approximately 550 ppm. 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 R_m [maintenance respiration, which is related to the sustaining of existing cells] and R_g [growth respiration, which is related to the synthesis of new tissues]."

Hamilton *et al.* (2001) studied respiratory responses of sweetgum trees growing in the understory of a loblolly pine plantation (but occasionally reaching the top of the canopy) to an extra 200 ppm of CO₂ in a FACE study conducted in North Carolina, USA. As a result of their measurement program, they determined that the modest increase in atmospheric CO₂

concentration did not appear to alter maintenance respiration to any significant degree, but that it reduced dark respiration by an average of 10% and growth respiration of leaves at the top of the canopy by nearly 40%.

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 CO₂ enrichment, as well as cases of *no change* in respiration. Hence, as we concluded to be the situation with conifers, more data are needed before any general conclusions may safely be drawn about the effects of atmospheric CO₂ enrichment on the respiration rates of deciduous trees.

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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6.6.2.3. 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 CO₂ concentration surrounding individual leaves was stabilized at 400 ppm for 15 minutes, whereupon their respiration rates were measured for 30 minutes, after which the CO₂ concentration in the leaf chamber was raised to 800 ppm for 15 minutes and respiration data were again recorded for the same leaves. This protocol revealed that elevated CO₂ had little effect on leaf dark respiration rates. In fact, the extra 400 ppm of CO₂ within the measurement cuvette decreased the median respiration rate by only 1.5% across the nine tree species. This observation thus led Amthor to state that the "rising atmospheric CO₂ 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 thus concluded that "future direct effects of increasing CO₂ 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] CO₂."

Amthor's conclusion, however, is debatable, for it is based upon the extrapolation of the short-term respiratory responses of *individual leaves*, exposed to elevated CO₂ *for only an hour or two*, to that of *entire trees*, many of which will experience rising CO₂ levels *for over a century or more* during their lifetimes. Trees are long-lived organisms that should not be expected to reveal the ultimate nature of their long-term responses to elevated atmospheric CO₂ concentrations on as short a time scale as that employed by Amthor. Indeed, their initial respiratory responses may change significantly with the passage of time, as they acclimate and optimize their physiology and growth patterns to the gradually-rising CO₂ content of earth's atmosphere, as evidenced by the findings of 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 CO₂ 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 CO₂. However, there *was* an effect on mean leaf Rdm, and it was determined to be *time-dependent*. The woody plants exposed to elevated CO₂ for < 100 days, in the reviewing scientists' words, "showed significantly less of a reduction in leaf Rdm due to CO₂ enrichment (-12%) than did plants exposed for longer periods (-35%, P < 0.01)." Hence, *for conditions of continuous long-term atmospheric CO₂ enrichment*, the results of Wang and Curtis' analysis suggest that woody plants may well experience an approximate 35% *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 CO₂ concentrations on plant respiration rates. In doing so, they found that atmospheric CO₂ enrichment typically decreased respiration rates in mature foliage, stems, and roots of CO₂-enriched plants relative to rates measured in plants grown in ambient air; and when normalized on a biomass basis, they determined that a doubling of the atmosphere's CO₂ concentration would likely reduce plant respiration rates by an average of 18%. 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% CO₂-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.

More recently, however, Davey *et al.* (2004) have reversed our view of the subject yet again. "Averaged across many previous investigations," as they put it, "doubling the CO₂ concentration has frequently been reported to cause an instantaneous reduction of leaf dark respiration measured as CO₂ efflux." However, as they continue, "no known mechanism accounts for this effect, and four recent studies [Amthor (2000); Amthor *et al.* (2001); Jahnke (2001); Jahnke and Krewitt (2002)] have shown that the measurement of respiratory CO₂ efflux is prone to experimental artifacts that could account for the reported response."

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 O₂ uptake of nine different species of plants in response to a short-term increase in atmospheric CO₂ concentration, as well as the response of seven species to long-term elevation of the air's CO₂ content in four different field experiments. In doing so, they found that "over six hundred separate measurements of respiration failed to reveal any decrease in respiratory O₂ uptake with an instantaneous increase in CO₂." Neither could they detect any response to a five-fold increase in the air's CO₂ concentration nor to the total removal of CO₂ from the air. They also note that "this lack of response of respiration to elevated CO₂ was independent of treatment method, developmental stage, beginning or end of night, and the CO₂ concentration at which the plants had been grown." In the long-term field studies, however, there *was* a respiratory response; but it was *small* (7% on a leaf mass basis), and it was *positive*, not negative.

So what is one to ultimately conclude about the matter? Perhaps the most reasonable conclusion would be that atmospheric CO₂ 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, one way or the other.

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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6.7. Other Benefits

6.7.1. Isoprene

Isoprene (C₅H₈ 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. In fact, it has been calculated by Poisson *et al.* (2000) 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% in the marine boundary-layer and 50-60% over land, and that the current tropospheric ozone content extends the atmospheric lifetime of methane -- one of the world's most powerful greenhouse gases -- by approximately 14%. Consequently, it can be appreciated that anything that reduces isoprene emissions from vegetation is something to be desired; and in this section we briefly review what has been learned in this regard about the ongoing rise in the atmosphere's CO₂ concentration.

Although a few experiments conducted on certain plant species have suggested that elevated concentrations of atmospheric CO₂ 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 CO₂-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). Short synopses of several *other* such studies are therefore briefly described in the following paragraphs, along with some of the implications of their more robust findings.

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 CO₂ 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% and 82%, respectively, while their production of isoprene was *decreased* by 21% and 41%, 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 CO₂ spring in central Italy. At the specific locations they chose to make their measurements, atmospheric CO₂ concentrations of approximately 350, 400, 550 and 800 ppm had likely prevailed for the entire lifetimes of the plants. Across this CO₂ gradient, plant isoprene emissions dropped ever lower as the air's CO₂ concentration rose ever higher. Over the first 50-

ppm CO₂ increase, isoprene emissions were reduced to approximately 65% of what they were at ambient CO₂, while for CO₂ increases of 200 and 450 ppm, they were reduced to only about 30% and 7% of what they were in the 350-ppm-CO₂ 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 CO₂ generally inhibits the expression of isoprenoid synthesis genes and isoprene synthase activity which may, in turn, limit formation of every chloroplast-derived isoprenoid." Hence, they state that the "basal emission rate of isoprene is likely to be reduced under future elevated CO₂ 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 CO₂ concentration was increased by approximately 200 ppm. Their study demonstrated, in their words, that "isoprene emission is reduced in elevated CO₂, 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%. When isoprene emission was summed over the entire plant profile, however, the reduction was not nearly so great (only 6%), because of the greater number of leaves on the CO₂-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 CO₂ 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 CO₂." 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 CO₂ spring, mostly confirm that isoprene emission is inversely dependent on CO₂ [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 O₃-tolerant clone and an O₃-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 CO₂, 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 CO₂ *decreased* the mean isoprene emission rate by 11.7% in the O₃-tolerant aspen clone and by 22.7% in the O₃-sensitive clone, while for the trees growing in air with 1.5 times the ambient ozone concentration, the extra CO₂ also *decreased* the mean isoprene emission rate by 10.4% in the O₃-tolerant clone and by 32.7% in the O₃-sensitive clone. At the same time, and in the same order, net photosynthesis rates were *increased* by 34.9%, 47.4%, 31.6% and 18.9%.

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 CO₂ 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 CO₂ concentration reduced isoprene emissions by 63% on a leaf area basis and 64% on a biomass basis, while in the fertilized trees the extra CO₂ reduced isoprene emissions by 70% on a leaf area basis and 74% on a biomass basis. In addition, the extra CO₂ boosted leaf photosynthesis rates by 17% in the unfertilized trees and 13% in the fertilized trees. At one and the same time, therefore, the CO₂-enriched air of this experiment did a number of positive things. It (1) enhanced the photosynthetic rates of the trees' leaves, while it (2) reduced their rates of isoprene emission, which tends to (3) reduce the (a) lifetime and (b) atmospheric concentration of (i) methane and (ii) other radiatively active trace gases of the atmosphere, as well as (4) reduce the atmospheric concentration of radiatively-active and phytotoxic ozone, which accomplishments are rather astounding for a trace gas (CO₂) that climate alarmists are trying to characterize as a *pollutant*.

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 CO₂ 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. In doing so, 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] CO₂-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 CO₂, 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 CO₂ 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 CO₂ and the highest emission fluxes of isoprene were attained in the lowest CO₂ treatment." In more quantitative terms, it was determined that the elevated CO₂ treatment resulted in a 46% 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 CO₂ 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 CO₂ concentrations, and that the anti-transpirant effect of atmospheric CO₂ enrichment typically leads to *increases* in the moisture contents of soils beneath vegetation (see Soil Water Status Field Studies and Growth Chamber Studies in our Subject Index). Also, we note that over the latter decades of the 20th century, when climate alarmists claim 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 CO₂-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 will produce more or less biomass capable of emitting isoprene, and changes in climate will stimulate or inhibit emissions per unit of biomass." Hence, as they continue, "these models tend to ignore the discovery that there are direct effects of changes in the atmospheric CO₂ concentration on isoprene emission that tend to work *in the opposite direction* [our italics] to that of stimulated NPP," as has clearly been indicated in the research studies described above. Furthermore, their results *showed*, in their words, "that growth in an atmosphere of elevated CO₂ inhibited the emission of isoprene at levels that *completely compensate* [our italics] 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."

Fast forward a year later and we come to the study of Arneth *et al.* (2008), who used a mechanistic isoprene-dynamic vegetation model of European woody vegetation to "investigate the interactive effects of climate and CO₂ 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 CO₂-isoprene inhibition phenomenon we have described in the papers above. Not surprisingly, with the inclusion of this parameterization, the results of the study indicate that "across the model domain," the CO₂-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 many encouraging findings presented above, it would thus appear that the ongoing rise in the atmosphere's CO₂ concentration will lead to ever greater reductions in atmospheric isoprene concentrations; and as noted in the introductory paragraph of this section, such a consequence would be very welcome news for humanity and nature alike. Although these beneficial findings are important, we find no mention of them in the IPCC or other assessments on earth's rising atmospheric carbon dioxide concentration.

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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6.7.2. Microorganisms

Plants grown in CO₂-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 CO₂-induced increases in plant growth affect microorganisms, another important topic often omitted from discussion by climate alarmists.

Several studies have shown that atmospheric CO₂ 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 CO₂ 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 CO₂ enrichment.

Other studies, however, have found that elevated CO₂ can significantly impact soil microorganisms. Van Ginkel and Gorissen (1998), for example, observed that three months of elevated CO₂ exposure (700 ppm) increased soil microbial biomass beneath ryegrass plants by 42% relative to that produced under ambient CO₂ conditions, as did Van Ginkel *et al.* (2000). Likewise, soil microbial biomass was reported to increase by 15% beneath agricultural fields subjected to a two-year wheat-soybean crop rotation (Islam *et al.*, 2000); and in a study by Marilley *et al.* (1999), atmospheric CO₂ enrichment significantly increased bacterial numbers in the rhizospheres beneath ryegrass and white clover monocultures. Similarly, Lussenhop *et al.* (1998) reported CO₂-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 CO₂ 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 CO₂ caused shifts in soil microbial populations. In soils beneath their leguminous white clover, for example, elevated CO₂ 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 CO₂ 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 CO₂-induced shifts in bacterial populations that would likely optimize nutrient acquisition for specific host plant species.

In a non-related study, Montealegre *et al.* (2000) reported that elevated CO₂ 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 CO₂ concentrations were mixed together and grown with white clover at an atmospheric CO₂ concentration of 600 ppm, 17% more root nodules were formed by isolates previously determined to be favored by elevated CO₂.

In the interesting study of Hu *et al.* (2001), fertile sandstone grasslands subjected to five years of twice-ambient CO₂ concentrations 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 CO₂-induced increases in net carbon accumulation. Similarly, Williams *et al.* (2000) reported that microbial biomass carbon increased by 4% in a tallgrass prairie after five years exposure to twice-ambient CO₂ concentrations, which contributed to a total soil carbon enhancement of 8%.

In another study, Johnson *et al.* (2002) presented evidence that elevated levels of atmospheric CO₂ will also enhance soil microbes in the face of the enhanced receipt of solar ultraviolet-B radiation that would be expected to occur in response to a 15% depletion of the earth's stratospheric ozone layer. Johnson *et al.* conducted their landmark work on experimental plots of subarctic heath located close to the Abisko Scientific Research Station in Swedish Lapland (68.35°N, 18.82°E). The plots they studied were composed of open canopies of *Betula pubescens* ssp. *czerepanovii* and dense dwarf-shrub layers containing scattered herbs and grasses. For a period of five years, the scientists exposed the plots to factorial combinations of UV-B radiation - ambient and that expected to result from a 15% stratospheric ozone depletion - and atmospheric CO₂ concentration - ambient (around 365 ppm) and enriched (around 600 ppm) - after which they determined the amounts of microbial carbon (C_{mic}) and nitrogen (N_{mic}) in the soils of the plots.

When the plots were exposed to the enhanced UV-B radiation level expected to result from a 15% depletion of the planet's stratospheric ozone layer, the researchers found that the amount of C_{mic} in the soil was reduced to only 37% of what it was at the ambient UV-B level when the air's CO₂ content was maintained at the ambient concentration. When the UV-B increase was accompanied by the CO₂ increase, however, not only was there *not* a decrease in C_{mic}, there was an actual *increase* of fully 37%.

The story with respect to N_{mic} was both similar and different at one and the same time. In this case, when the plots were exposed to the enhanced level of UV-B radiation, the amount of N_{mic} in the soil experienced a 69% *increase* when the air's CO₂ content was maintained at the ambient concentration. When the UV-B increase was accompanied by the CO₂ increase, however, N_{mic} rose even more, experiencing a whopping 138% increase.

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)." Hence, the 138% increase in soil microbial N observed in this study to accompany a 15% reduction in stratospheric ozone and a concomitant 64% increase in atmospheric CO₂ concentration (experienced in going from 365 ppm to 600 ppm) should do wonders in enhancing 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." Indeed, in a previous essay in this series, wherein we discussed the findings of the literature review of Berg and Matzner (1997), we found that such is truly the case. 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 resulting more recalcitrant carbon compounds can be successfully stored in the soil for many millennia.

In summation, it is clear from the published literature that as the CO₂ content of the air continues to rise, earth's vegetation will likely respond with increasing photosynthetic rates and biomass production. As a consequence of these phenomena, more organic carbon will be returned 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). Moreover, it is conceivable that 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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6.7.3. Nitrogen Use Efficiency

Long-term exposure to elevated atmospheric CO₂ concentrations often, but not always, elicits photosynthetic acclimation or down regulation in plants, which is typically accompanied by reduced amounts of rubisco and/or other photosynthetic proteins that are typically present in excess amounts in ambient air. As a consequence of this latter phenomenon, foliar nitrogen concentrations often decrease with atmospheric CO₂ enrichment, as nitrogen is mobilized out of leaves and into other areas of the plant to increase its availability for enhancing sink development or stimulating other nutrient-limited processes.

In reviewing the literature in this area, one quickly notices that in spite of the fact that photosynthetic acclimation has occurred, CO₂-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 CO₂-enriched plants.

In the study of Davey *et al.* (1999), for example, CO₂-induced reductions in foliar nitrogen contents and concomitant increases in photosynthetic rates led to photosynthetic nitrogen-use efficiencies in the CO₂-enriched (to 700 ppm CO₂) grass *Agrostis capillaris* that were 27 and 62% greater than those observed in control plants grown at 360 ppm CO₂ under moderate and low soil nutrient conditions, respectively. Similarly, elevated CO₂ enhanced photosynthetic nitrogen-use efficiencies in *Trifolium repens* by 66 and 190% under moderate and low soil nutrient conditions, respectively, and in *Lolium perenne* by 50%, regardless of soil nutrient status. Other researchers have found comparable CO₂-induced enhancements of photosynthetic nitrogen-use efficiency in wheat (Osborne *et al.*, 1998) and in *Leucadendron* species (Midgley *et al.*, 1999).

In some cases, researchers report nitrogen-use efficiency in terms of the amount of biomass produced per unit of plant nitrogen. Niklaus *et al.* (1998), for example, reported that intact swards of CO₂-enriched calcareous grasslands grown at 600 ppm CO₂ attained total biomass values that were 25% greater than those of control swards exposed to ambient air while extracting the same amount of nitrogen from the soil as ambiently-grown swards. 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 CO₂ were 23 and 17% 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 CO₂ 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. In addition, enhanced rates of photosynthetic carbon uptake invariably lead to greater biomass production, which often occurs without increasing soil nitrogen uptake and thus enhances growth nitrogen-use efficiency as well. Hence, as overall plant nitrogen-use efficiency increases with the ongoing rise in the atmosphere's CO₂ concentration, it is likely that plants will grow ever better on soils containing less-than-optimal levels of this important soil nutrient.

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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6.7.4. Nutrient Acquisition

Most species of plants respond to increases in the air's CO₂ 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 CO₂-enriched conditions, which further stimulates plant growth and development. In this summary, we thus review how the acquisition of plant nutrients - primarily nitrate and phosphate - is impacted by atmospheric CO₂ enrichment. We do not discuss the effects of elevated CO₂ on nitrogen fixation, however, as we address this subject elsewhere on our website (see Nitrogen Fixation).

In the study of Zak *et al.* (2000), aspen seedlings grown for 2.5 years at twice-ambient CO₂ concentrations displayed an average total seedling nitrogen content that was 13% greater than that displayed by control seedlings grown in ambient air, in spite of an average reduction in tissue nitrogen concentration of 18%. Thus, elevated CO₂ enhanced total nitrogen uptake from the soil, even though tissue nitrogen concentrations in the CO₂-enriched plants were diluted by the enhanced biomass of the much larger CO₂-enriched seedlings.

On a per-unit-biomass basis, Smart *et al.* (1998) noted there were no differences in the total amounts of nitrogen within CO₂-enriched and ambiently-grown wheat seedlings after three weeks of exposure to atmospheric CO₂ concentrations of 360 and 1,000 ppm. Nevertheless, the CO₂-enriched seedlings exhibited greater rates of soil nitrate extraction than did the ambiently-grown plants. Similarly, BassiriRad *et al.* (1998) reported that a doubling of the atmospheric CO₂ concentration doubled the uptake rate of nitrate in the C₄ grass *Bouteloua eriopoda*. However, they also reported that elevated CO₂ had no effect on the rate of nitrate uptake in *Prosopis*, and that it actually decreased the rate of nitrate uptake by 55% in *Larrea*. Nonetheless, atmospheric CO₂ enrichment increased total biomass in these two species by 55 and 69%, respectively. Thus, although the uptake rate of this nutrient was depressed under elevated CO₂ conditions in the latter species, the much larger CO₂-enriched plants likely still extracted more total nitrate from the soil than did the ambiently-grown plants of the experiment.

It is also interesting to note that 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 CO₂ for 2.5 months exhibited total plant phosphorus contents that were much greater than those displayed by plants grown at 400 ppm CO₂, due to the fact that atmospheric CO₂ 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 CO₂ 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 can also occur due to CO₂-induced increases in root absorptive surface area or enhancements in specific enzyme activities. In addressing the first of these phenomena, BassiriRad *et al.* (1998) reported that a doubling of the atmospheric CO₂ concentration significantly increased the belowground biomass of *Bouteloua eriopoda* and doubled its uptake rate of phosphate. However, elevated CO₂ had no effect on uptake rates of phosphate in *Larrea* and *Prosopis*. Because the CO₂-enriched plants grew so much bigger, however, they still removed more phosphate from the soil on a per-plant basis. With respect to the second phenomenon, phosphatase - which is the primary enzyme responsible for the conversion of organic phosphate into usable inorganic forms - had its activity increased by 30 to 40% in wheat seedlings growing at twice-ambient CO₂ concentrations (Barrett *et al.*, 1998).

In summary, as the CO₂ content of the air increases, the experimental data that have been accumulated to date suggest that much of earth's vegetation will likely display increases in biomass; and there is considerable evidence suggestive of the further likelihood that the larger plants thereby produced will develop more extensive root systems and 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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6.7.5. Pathogens

As the air's CO₂ 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 CO₂ 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 CO₂ 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."

Adding to this impressive list, Chakraborty and Datta elucidated yet another way in which atmospheric CO₂ enrichment may tip the scales in favor of plants in a study of the aggressiveness of the fungal anthracnose pathogen *Colletotrichum gloeosporioides*, wherein 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 CO₂ concentrations in controlled environment chambers. This protocol revealed that "at twice-ambient CO₂ 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 CO₂, but resistance in Seca remains largely unchanged." Simultaneously, however, pathogen *fecundity* was found to *increase* at twice-ambient CO₂. Of this finding, they report that their results "concur with the handful of studies that have demonstrated increased pathogen fecundity at elevated CO₂ (Hibberd *et al.*, 1996a; Klironomos *et al.*, 1997; Chakraborty *et al.*, 2000)." How this happened in the situation they investigated, as they describe it, is that the overall increase in fecundity at high CO₂ "is a reflection of the altered canopy environment," wherein "the 30% larger *S. scabra* plants at high CO₂ (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 CO₂ in this specific study - reduced aggressiveness but increased fecundity - it is difficult to know the ultimate outcome of atmospheric CO₂ 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. What is more, results could also differ under different climatic conditions. Nevertheless, the large number of ways in which elevated CO₂ has been demonstrated to increase plant resistance to pathogen attack suggests that plants may well gain the advantage over pathogens as the air's CO₂ content continues to climb in the years ahead; and in the paragraphs that follow, we review the results of a number of studies that support this assessment of the issue.

A good place to begin is the study of McElrone *et al.* (2005) who "assessed how elevated CO₂ affects a foliar fungal pathogen, *Phyllosticta minima*, of *Acer rubrum* [red maple] growing in the understory at the Duke Forest free-air CO₂ enrichment experiment in Durham, North Carolina, USA ... in the 6th, 7th, and 8th years of the CO₂ exposure." Surveys conducted in those years, 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 CO₂ "also significantly reduced disease severity in infected plants in all years (e.g. mean lesion area reduced 35%, 50%, and 10% in 2002, 2003, and 2004, respectively)."

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 CO₂ on the fungal pathogen, McElrone *et al.* performed some side experiments in controlled environment chambers. However, they found that the elevated CO₂ 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 CO₂ enrichment, but that "stomatal conductance was reduced by 21-36% under elevated CO₂, providing smaller openings for infecting germ tubes." In addition, they concluded that reduced disease severity under elevated CO₂ was also likely due to altered leaf chemistry, as elevated CO₂ increased total leaf phenolic concentrations by 15% and tannin concentrations by 14%.

Because the phenomena they found to be important in reducing the amount and severity of fungal pathogen infection (leaf spot disease) of red maple have been demonstrated to be operative in most other plants as well, McElrone *et al.* say these CO₂-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." And because of their insightful work, that future is looking particularly bright in terms of the never-ending struggle between earth's plants and the pathogens that prey upon them. Although elevated CO₂ helps *both* sides of the conflict, it helps plants *more* and in *more ways*.

Malmstrom and Field (1997) grew individual oat plants for two months in pots within phytocells maintained at CO₂ concentrations of 350 and 700 ppm, while a third of each CO₂ 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 CO₂ stimulated net photosynthesis rates in all plants, but with the greatest increase occurring in diseased individuals (48% vs. 34%). In addition, atmospheric CO₂ enrichment decreased stomatal conductance by 34% in healthy plants, but by 50% in infected ones, thus reducing transpirational water losses more in infected plants. Together, these two phenomena contributed to a CO₂-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 CO₂ was greatest in the diseased plants. After 60 days of CO₂ enrichment, for example, total plant biomass increased by 36% in infected plants, while it increased by only 12% in healthy plants. In addition, while elevated CO₂ had little effect on root growth in healthy plants, it increased root biomass in infected plants by up to 60%. In their concluding remarks, therefore, Malmstrom and Field say that CO₂ enrichment "may reduce losses of infected plants to drought" and "may enable diseased plants to compete better with healthy neighbors."

Tiedemann and Firsching (2000) grew spring wheat from germination to maturity in controlled environment chambers maintained at either ambient (377 ppm) or enriched (612 ppm) atmospheric CO₂ concentrations and either ambient (20 ppb) or enriched (61 ppb) atmospheric ozone (O₃) 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 CO₂ enrichment but strongly reduced by elevated O₃. With respect to *photosynthesis*, elevated CO₂ increased rates in inoculated plants by 20 and 42% at ambient and elevated O₃ concentrations, respectively. Although inoculated plants produced lower yields than non-inoculated plants, atmospheric CO₂ enrichment still stimulated yield in infected plants, increasing it by fully 57% at high O₃. Consequently, the beneficial effects of elevated CO₂ on wheat photosynthesis and yield continue to be expressed in the presence of both O₃ and pathogenic stresses.

In another joint CO₂/O₃ study, Percy *et al.* (2002) grew the most widely distributed North American tree species - trembling aspen - in twelve 30-m-diameter FACE rings near Rhinelander, Wisconsin, USA in air maintained at ambient CO₂ and O₃ concentrations, ambient O₃ and elevated CO₂ (560 ppm during daylight hours), ambient CO₂ and elevated O₃ (46.4-55.5 ppb during daylight hours), and elevated CO₂ and O₃ over the period of each growing season from 1998 through 2001. Throughout 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 CO₂ alone did not alter rust occurrence, but that elevated O₃ alone increased it by nearly fourfold. When applied together, however, elevated CO₂ reduced the enhancement of rust development caused by elevated O₃ 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 CO₂ concentrations of 350 and 700 ppm. At week five of their study, half of the plants growing in each CO₂ concentration were infected with the fungal pathogen *Phytophthora parasitica*, which attacks plant roots and induces water stress that ultimately decreases plant growth and yield. This infection procedure ultimately reduced total plant biomass by nearly 30% at both atmospheric CO₂ concentrations. However, the elevated CO₂ treatment increased the total biomass of healthy and infected plants by the same percentage, so that infected tomato plants grown at 700 ppm CO₂ exhibited biomass values similar to those of healthy tomato plants grown at 350 ppm CO₂. Consequently, atmospheric CO₂ 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 CO₂ 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 CO₂, reflecting the development of a level of resistance in susceptible cv. Fitzroy at high CO₂." In fact, with respect to plants inoculated at twelve 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 CO₂." Last of all, 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 CO₂, 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 CO₂."

Finally, according to Plesl *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 CO₂ enrichment on this pathogen, Plesl *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 CO₂ 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 CO₂ "dramatically reduced symptom development," including *extent of necrosis* (down by 44% four days after inoculation and 65% five days after inoculation), *area of sporulation* (down by 100% four days after inoculation and 61% five days after inoculation), and *sporulation intensity* (down by 73% four days after inoculation and 17% five days after inoculation). Thus, Plesl *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 CO₂," 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 CO₂." These similar observations bode well for both potato and tomato cultivation in a CO₂-enriched world of the future.

In conclusion, the balance of evidence obtained to date appears to demonstrate an enhanced ability of plants to withstand pathogen attacks in CO₂-enriched as opposed to ambient-CO₂ air. Hence, as the atmosphere's CO₂ concentration continues to rise in the years, decades and centuries to come, earth's vegetation should fare ever better in its eternal battle to better withstand the ravages that have historically been inflicted upon it by a myriad of 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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6.7.6. Parasites

Parasitic plants obtain energy, water and nutrients from their host plants and cause widespread reductions in harvestable yields around the globe. Hence, it is important to understand how rising atmospheric CO₂ levels may impact the growth of parasitic plants and the relationships that exist between them and their host plants. Here, we review the findings of several papers that have investigated this important subject.

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 CO₂ 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 CO₂ enrichment *decreased* mean parasite biomass by an average of 16%, while at *high* nutrient supply it *increased* parasite biomass by an average of 123%. Nevertheless, the extra 215 ppm of CO₂ increased host plant biomass in both situations: by 29% under high soil nutrition and by 18% 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 CO₂ concentrations of either 360 or 550 ppm for 75 days in controlled-environment growth cabinets. The elevated CO₂ 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% less biomass than uninfected plants growing in ambient air, infected plants growing at 550 ppm CO₂ exhibited final dry weights that were only 20% less than those displayed by uninfected plants growing in the CO₂-enriched air,

indicative of a significant CO₂-induced partial alleviation of parasite-induced biomass reductions in the white clover host plants.

Watling and Press (1997) infected several C₄ sorghum plants with *Striga hermonthica* and *Striga asiatica* (parasitic C₃ weeds of the semi-arid tropics that infest many grain crops) and grew them, along with uninfected control plants, for approximately two months in controlled-environment cabinets maintained at atmospheric CO₂ concentrations of 350 and 700 ppm. In the absence of parasite infection, the extra 350 ppm of CO₂ increased sorghum biomass by approximately 36%. When infected with *S. hermonthica*, however, the sorghum plants grown at ambient and elevated CO₂ concentrations only produced 32 and 43% of the biomass displayed by their respective uninfected controls. Infection with *S. asiatica* was somewhat less stressful and led to host biomass production that was about half that of uninfected controls in both ambient and CO₂-enriched air. The end result was that the doubling of the air's CO₂ content employed in this study increased sorghum biomass by 79% and 35% in the C₄ sorghum plants infected with *S. hermonthica* and *S. asiatica*, respectively.

Hwangbo *et al.* (2003) grew Kentucky Bluegrass (*Poa pratensis* L.) with and without infection by the C₃ 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) CO₂ concentrations. At the end of the study, the parasite's biomass (when growing on its host) was 47% greater in the CO₂-enriched chambers, while its host exhibited only a 10% CO₂-induced increase in biomass in the parasite's absence but a nearly doubled 19% 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 CO₂ 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% of what it was in the absence of the parasite; whereas in air enriched with CO₂ the presence of the parasite reduced the biomass of infected plants to but 73% of what it was in the absence of the parasite.

In summary, these several observations suggest that the rising CO₂ 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 CO₂ generally tends to reduce the negative effects of parasitic infection, so that infected host plants continue to exhibit positive growth responses to elevated CO₂. Thus, it is likely that whatever the scenario with regard to parasitic infection, host plants will fare better under higher atmospheric CO₂ 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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6.7.7. Roots

In reviewing the scientific literature pertaining to atmospheric CO₂ enrichment effects on belowground plant growth and development, Weihong *et al.* (2000) briefly summarize what is known about this subject. They report that atmospheric CO₂ enrichment typically enhances the growth rates of roots, especially those of fine roots, and that CO₂-induced increases in root production eventually lead to increased carbon inputs to soils, due to enhanced root turnover and exudation of various organic carbon compounds, which can 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 CO₂ 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. In pursuing this protocol, the scientists learned that the CO₂-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 CO₂-induced stimulation of mitotic activity, accelerated cortical cell expansion, and increased cell wall plasticity.

In another unique study, Gouk *et al.* (1999) grew an orchid plantlet, Mokara Yellow, in plastic bags flushed with 350 and 10,000 ppm CO₂ for three months to study the effects of elevated CO₂ on this epiphytic CAM species. They determined that the super-elevated CO₂ 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 CO₂ -- by 64% in young leaves and by 118% in young roots. This phenomenon permitted greater light harvesting during photosynthesis and likely led to the tissue starch contents of the CO₂-enriched plantlets rising nearly 20-fold higher than those of the control-plantlets. In spite of this large CO₂-induced accumulation of starch, however, no damage or disruption of chloroplasts was evident in the leaves and roots of the CO₂-enriched plants.

A final question that has periodically intrigued researchers is whether plants take up carbon through their roots in addition to through their leaves. Although a definitive answer 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 CO₂ (Stolwijk *et al.*, 1957; Skok *et al.*, 1962; Splittstoesser, 1966), a number of experiments have produced significant increases in root growth (Erickson, 1946; Leonard and Pinckard, 1946; Geisler, 1963; Yorgalevitch and Janes, 1988), as well as yield itself (Kursanov *et al.*, 1951; Grinfeld, 1954; Nakayama and Bucks, 1980; Baron and Gorski, 1986), with CO₂-enriched irrigation water. Early on, Misra (1951) suggested that this beneficent effect may be related to CO₂-induced changes in soil nutrient availability; and this hypothesis may well be correct. Arteca *et al.* (1979), for example, have observed K, Ca and Mg to be better absorbed by potato roots when the concentration of CO₂ in the soil solution is increased; while Mauney and Hendrix (1988) found Zn and Mn to be better absorbed by cotton under such conditions, and Yurgalevitch and Janes (1988) found an enhancement of the absorption of Rb by tomato roots. In all cases, large increases in either total plant growth or ultimate yield accompanied the enhanced uptake of nutrients. Consequently, as it has been suggested that CO₂ concentration plays a major role in determining the porosity, plasticity and charge of cell membranes (Jackson and Coleman, 1959; Mitz, 1979), which could thereby alter ion uptake and organic acid production (Yorgalevitch and Janes, 1988), it is possible that some such suite of mechanisms may well be responsible for the plant productivity increases often observed to result from enhanced concentrations of CO₂ in the soil solution."

Although much is thus known about many aspects of root responses to atmospheric CO₂ enrichment, much remains to be learned. In this next section we review such responses 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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6.7.7.1. Crops

How do the roots of the crops we eat respond to atmospheric CO₂ enrichment? Unless the roots are the edible portion of the plant, we probably give the question little thought: "out of sight, out of mind," as the saying goes. But it is the *roots* that acquire the water and nutrients that sustain the plant; and so the question is of more than academic interest, providing a significant impetus for scientists to look beneath the surface of the subject *and the ground*. Hence, we here review what a few of them have found.

Hodge and Millard (1998) grew narrowleaf plantain (*Plantago lanceolata*) seedlings for a period of six weeks in controlled environment growth rooms maintained at atmospheric CO₂ concentrations of either 400 or 800 ppm. By the end of this period, the plants in the 800-ppm air exhibited increases in shoot and root dry matter production that were 159% and 180% 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-CO₂ treatment. Thus, these investigators found that the belowground growth stimulation provided by atmospheric CO₂ enrichment was greater than that experienced aboveground.

Wechsung *et al.* (1999) grew spring wheat (*Triticum aestivum*) in rows in a FACE study employing atmospheric CO₂ concentrations of 370 and 550 ppm and irrigation treatments that periodically replaced either 50% or 100% of prior potential evapotranspiration in an effort to determine the effects of elevated CO₂ and water stress on root growth. They found that elevated CO₂ increased *in-row* root dry weight by an average of 22% during the growing season under both the wet and dry irrigation regimes. In addition, during the vegetative growth phase, atmospheric CO₂ enrichment increased *inter-row* root dry weight by 70%, indicating that plants

grown in elevated CO₂ developed greater lateral root systems than plants grown at ambient CO₂.

During the reproductive growth phase, elevated CO₂ stimulated the branching of lateral roots into inter-row areas, but only when water was limiting to growth. In addition, the CO₂-enriched plants tended to display greater root dry weights at a given depth than did ambiently-grown plants. This study thus suggests that as the CO₂ content of the air continues to rise, spring wheat plants will likely develop larger and more extensively branching root systems that may help them to better cope with periods of reduced soil moisture availability.

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 CO₂ concentration, the root biomass of wheat, ryegrass and rice experienced an average increase of 70% at ample water and nitrogen, 58% at low nitrogen and 34% at low water, while clover experienced a 38% increase at ample water and nitrogen, plus a 32% increase at low nitrogen. Outdoing all of the other crops was *cotton*, which exhibited a 96% increase in root biomass at ample water and nitrogen.

In a radically different type of study, Zhao *et al.* (2000) germinated pea (*Pisum sativum*) seeds and exposed the young plants to various atmospheric CO₂ concentrations in controlled environment chambers to determine if elevated CO₂ impacts root border cells, which are major contributors of root exudates in this and most other agronomic plants. They found that elevated CO₂ did indeed increase the production of root border cells in pea seedlings. In fact, in going from ambient air to air enriched to 3,000 and 6,000 ppm CO₂, border-cell numbers increased by over 50% and 100%, respectively. Hence, as the CO₂ 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. Last of all, this chain of events should make the soil environment even more favorable for plant growth and development in a high-CO₂ world of the future.

In concluding this brief review, we revisit the study of van Ginkel *et al.* (1996), who grew perennial ryegrass (*Lolium perenne*) plants from seed in two growth chambers for 71 days under continuous ¹⁴CO₂-labeling of the atmosphere at CO₂ concentrations of 350 and 700 ppm at two 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 CO₂ flowing through it, and one of which had air of 706 ppm CO₂ flowing through it. Several of the containers were then seeded with more *Lolium perenne*, others were similarly seeded the following year, and still others were kept bare for two years. 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 of all, that shoot and root growth were enhanced by 13 and 92%, respectively, by the extra CO₂ in the initial 71-day portion of the experiment, once again demonstrating the significantly greater benefits that are often conferred upon plant roots by atmospheric CO₂ enrichment. Secondly, it was found that the decomposition of the high-CO₂-grown roots in the high-CO₂ wind tunnel was 19% lower than that of the low-CO₂-grown roots in the low-CO₂ wind tunnel at the end of the first year, and that it was 14% lower at the end of the second year *in the low-nitrogen-grown plants* but equivalent in the high-nitrogen-grown plants. It was also determined 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 CO₂ combined with a decrease in root decomposition will lead to a longer residence time of C in the soil and probably to a higher C storage."

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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6.7.7.2. Trees

Trees figure prominently in political and economic schemes designed to promote the biospheric sequestration of carbon as a means for slowing the rate of rise of the air's CO₂ content and thereby reducing the supposed severity of CO₂-induced global warming. Nature also employs trees for this purpose, but without any of the burdensome strings that come attached to the

plans of man. In *both* instances, however, it is useful to learn whatever we can about the potential for the world's forests to perform this important function.

In this regard, one can readily see and measure the carbon that goes into the aboveground components of forests. But what about the underground components? And how does the ongoing rise in the atmosphere's CO₂ concentration, which is the supposed cause of the pseudo-problem, contribute to its pseudo-resolution? In this brief review we summarize the findings of some recent studies of *trees* that address this question.

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 CO₂, finding that the extra CO₂ increased total root length by 122% and total root dry mass by 135%. In a similar study that employed close to the same degree of enhancement of the air's CO₂ 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 aboveground parts of these seedlings only experienced a growth enhancement of 20%. The *root* biomass of the trees, however, was increased by *more than three times as much* (62%).

Working with FACE technology, Pritchard *et al.* (2001b) studied 14-year-old loblolly pine trees after a year of exposure to an extra 200 ppm of CO₂, finding that total standing root length and root numbers were 16 and 34% greater, respectively, in the CO₂-enriched plots than in the ambient-air plots. In addition, the elevated CO₂ increased the diameter of living and dead roots by 8 and 6%, respectively, while annual root production was found to be 26% greater in the CO₂-enriched plots. For the degree of CO₂ enrichment employed in the prior two studies, this latter enhancement corresponds to a root biomass increase of approximately 45%.

In an open-top chamber study of a model ecosystem composed of a mixture of spruce and beech seedlings, Wiemken *et al.* (2001) investigated the effects of a 200 ppm increase in the air's CO₂ concentration that prevailed for a period of four years. On nutrient-poor soils, the extra CO₂ led to a 30% increase in fine-root biomass, while on nutrient-rich soils it led to a 75% increase. As before, these numbers correspond to increases of about 52% and 130%, respectively, for atmospheric CO₂ enhancements on the order of those employed by Janssens *et al.* (1998) and Pritchard *et al.* (2001a).

Another interesting aspect of the Wiemken *et al.* study was their finding that the extra CO₂ increased the amount of symbiotic fungal biomass associated with the trees' fine roots by 31% on nutrient-poor soils and by 100% on nutrient-rich soils, which for the degree of atmospheric CO₂ enrichment used in the studies of Janssens *et al.* (1998) and Pritchard *et al.* (2001a) translate into increases of about 52% and 175%, respectively.

Berntsen and Bazzaz (1998) removed intact chunks of soil from the Hardwood-White Pine-Hemlock forest region of New England and placed them in plastic containers within controlled environment glasshouses maintained at either 375 or 700 ppm CO₂ for a period of two years in

order to study the effects of elevated CO₂ 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% of which was supplied by yellow and white birch tree seedlings) was found to be 31% higher in the elevated CO₂ treatment than in ambient air, with a mean enhancement of 23% aboveground and 62% belowground. The extra CO₂ also increased the mycorrhizal colonization of root tips by 45% in white birch and 71% in yellow birch; and the CO₂-enriched yellow birch seedlings exhibited 322% greater root length and 305% more root surface area than did the yellow birch seedlings growing in ambient air.

Kubiske *et al.* (1998) grew cuttings of four quaking aspen genotypes in open-top chambers for five months at atmospheric CO₂ concentrations of either 380 or 720 ppm and low or high soil nitrogen concentrations. They found, surprisingly, that the cuttings grown in elevated CO₂ displayed no discernible increases in aboveground growth. However, the extra CO₂ significantly increased fine-root length and root turnover rates at high soil nitrogen by increasing fine-root production, which would 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 aboveground growth as well. That this reasoning is indeed correct may be verified by perusing the many positive aboveground growth responses of quaking aspen trees to atmospheric CO₂ enrichment that are listed in the biomass portion of the Plant Growth Data section of our website (see *Populus tremuloides* Michx.).

Expanding on this study, Pregitzer *et al.* (2000) grew six quaking aspen genotypes for 2.5 growing seasons in open-top chambers maintained at atmospheric CO₂ concentrations of 350 and 700 ppm with both adequate and inadequate supplies of soil nitrogen. This work demonstrated that the trees exposed to elevated CO₂ developed thicker and longer roots than the trees growing in ambient air, and that the fine-root biomass of the CO₂-enriched trees was enhanced by 17% in the nitrogen-poor soils and by 65% in the nitrogen-rich soils.

Yet another study of quaking aspen conducted by King *et al.* (2001) demonstrated that trees exposed to an atmospheric CO₂ concentration 560 ppm in a FACE experiment produced 133% more fine-root biomass than trees grown in ambient air of 360 ppm, which roughly equates to 233% more fine-root biomass for the degree of CO₂ enrichment employed in the prior study of Pregitzer *et al.* 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 CO₂ was still as great as 66%, or roughly 115% when extrapolated to the greater CO₂ 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% and rates of whole-plant growth by 37%, 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 CO₂ concentration, air temperature and soil nitrogen content all enhance their belowground growth, which positively impacts their aboveground growth. And it is important to note that all of these environmental changes have been imputed to occur as a consequence of the burning of fossil fuels.

Turning our attention to other deciduous trees, we focus next on the study of Gleadow *et al.* (1998), who grew eucalyptus seedlings for six months in glasshouses maintained at atmospheric CO₂ concentrations of either 400 or 800 ppm, fertilizing them twice daily with low or high nitrogen solutions. The elevated CO₂ of their experiment increased total plant biomass by 98 and 134% relative to plants grown at ambient CO₂ in the high and low nitrogen treatments, respectively. In addition, in the low nitrogen treatment, elevated CO₂ stimulated greater root growth, as indicated by a 33% higher root:shoot ratio.

In a more complex study, Day *et al.* (1996) studied the effects of elevated CO₂ on fine-root production in open-top chambers erected over a regenerating oak-palmetto scrub ecosystem in Florida, USA, determining that a 350-ppm increase in the atmosphere's CO₂ concentration increased fine-root length densities by 63% while enhancing the distribution of fine roots at 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 CO₂ 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 CO₂-enhanced biomass production in the years and decades ahead.

In another study that employed CO₂, 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 CO₂ concentrations of 350 and 700 ppm and air temperatures of 26°C (ambient) and 30°C, with either some or no additional nitrogen fertilization, finding that the extra CO₂ increased total seedling biomass by 14%, that the elevated temperature increased it by 55%, and that nitrogen fertilization increased it by 157%. With respect to root exudation, a similar pattern was seen. Plants grown in elevated CO₂ exuded 20% more organic carbon compounds than plants grown in ambient air, while elevated temperature and fertilization increased root exudation by 71 and 55%, respectively. Hence, as the air's CO₂ content continues to rise, black locust trees 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 CO₂ concentration; and 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 a somewhat different type of study, McDowell *et al.* (1999) grew five-month-old seedlings of western hemlock in root boxes, subjecting them for several hours to various root-space CO₂ concentrations, ranging from approximately 90 to 7000 ppm, in order to determine the effect of soil CO₂ concentration on growth, maintenance and total root respiration. Although they could detect no effect of atmospheric CO₂ enrichment on growth respiration, it significantly impacted maintenance and total respiration rates. At a soil CO₂ concentration of 1585 ppm, for example, total and maintenance respiration rates were 55 and 60% lower, respectively, than they were at a soil CO₂ concentration of 395 ppm. In fact, the impact of elevated soil CO₂ on maintenance respiration (which comprised 85% of the total respiration in this study) was so strong that it exhibited an exponential decline of about 37% for every doubling of the soil CO₂ concentration.

In light of these several experimental findings, it can confidently be concluded that the ongoing rise in the air's CO₂ content, together with possible concurrent increases in air temperature and nitrogen deposition, will likely help earth's woody plants to become ever more robust and productive as atmospheric CO₂ concentrations rise higher and higher.

This brief sampling of the scientific literature suggests that the ongoing rise in the air's CO₂ content bodes well for the growth of earth's coniferous forests and their ability to sequester carbon. These consequences have great virtue in and of themselves and are worthy of being pursued on the basis of their own intrinsic value; and as they comprise a potentially powerful negative feedback on CO₂-induced global warming, there is yet a *third* reason for lauding their existence.

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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6.7.8. Seeds

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.

6.7.8.1. Crops

When dealing with agricultural commodities such as grain crops, seeds comprise the yield; and in such cases, the biomass of one is the biomass of the other. Hence, when looking for effects of elevated CO₂ on the *seeds* of such crops, one is naturally interested in something more than just their final biomass; and in this brief synopsis of pertinent papers we have reviewed, we consider a number of the *sources* of biomass production, as well as seed properties that go *beyond biomass*.

In a greenhouse study of the various *components* of seed biomass production, Palta and Ludwig (2000) grew narrow-leafed lupin in pots filled with soil within Mylar-film tunnels maintained at either 355 or 700 ppm CO₂. They found that the extra CO₂ 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 CO₂-induced improvements to key physiological processes resulted in 47 to 56% increases in dry matter per plant, which led to increases of 44 to 66% in seed yield per plant.

Sanhewe *et al.* (1996) grew winter wheat in polyethylene tunnels maintained at atmospheric CO₂ concentrations of 380 and 680 ppm from the time of seed germination to the time of plant maturity, while maintaining a temperature gradient of approximately 4°C in each tunnel. In addition to the elevated CO₂ increasing seed yield per unit area, they found it also increased seed weight, but not seed survival or germination. Increasing air temperature, on the other hand, increased seed longevity across the entire range of temperatures investigated (14 to 19°C).

Thomas *et al.* (2003) grew soybean plants to maturity in sunlit controlled-environment chambers under sinusoidally-varying day/night-max/min temperatures of 28/18, 32/22, 36/26, 40/30 and 44/34°C and two levels of atmospheric CO₂ concentration (350 and 700 ppm). 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 CO₂." In this regard, however, they note that "Heagle *et al.* (1998) observed a positive significant effect of CO₂ 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. They also found that "32/22°C is optimum for producing the highest oil concentration in soybean seed," and that "the degree of fatty acid saturation in soybean oil was significantly increased by increasing temperature." In addition, they determined that crude protein concentration increased with temperature to 40/30°C.

In commenting on these findings, 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." This being the case, the temperature-driven changes they identified in these parameters, as well as the CO₂ effect observed by Heagle *et al.*, bode well for the future production of this important crop and its value to society in a CO₂-enriched and warming world. They do note, however,

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 another soybean study, Ziska *et al.* (2001) grew one modern and eight ancestral genotypes in glasshouses maintained at atmospheric CO₂ concentrations of 400 and 710 ppm, finding that the extra CO₂ increased photosynthetic rates by an average of 75%. This enhancement in photosynthetic sugar production led to increases in seed yield that averaged 40% for all cultivars, except for one ancestral variety that exhibited an 80% increase in seed yield. Hence, if plant breeders were to utilize the highly CO₂-responsive ancestral cultivar identified in this study in their breeding programs, it is possible that soybean seed yields - and all of the other good things that go with it - 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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6.7.8.2. Grasslands

We begin this section review of elevated atmospheric CO₂ effects on seed production -- as well as the subsequent phenomena they trigger -- with the study of Steinger *et al.* (2000), who collected seeds from *Bromus erectus* plants that had been grown at atmospheric CO₂ concentrations of 360 and 650 ppm, and who germinated some of both groups of seeds under

those same two sets of conditions. In the first part of their study, they found that the elevated CO₂ treatment (1) increased individual seed mass by about 9% and (2) increased seed carbon-to-nitrogen ratio by almost 10%. 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 CO₂-enriched plants were germinated and grown in ambient air, there was no significant size difference between the two groups of resultant seedlings after a period of 19 days. Likewise, when the seeds produced from ambient or CO₂-enriched plants were germinated and grown in the high CO₂ treatment, there was also no significant difference between the sizes of the seedlings derived from the two groups of seeds. However, the CO₂-enriched seedlings produced from both groups of seeds were almost 20% larger than the seedlings produced from *both* groups of seeds grown in ambient air, demonstrating that the direct effects of elevated atmospheric CO₂ concentration on seedling growth and development were more important than the differences in seed characteristics produced by the elevated atmospheric CO₂ concentration in which their parent plants grew.

In another study conducted about the same time, Edwards *et al.* (2001) utilized a FACE experiment where daytime atmospheric CO₂ concentrations above a sheep-grazed pasture in New Zealand were increased by 115 ppm to study the effects of elevated CO₂ on seed production, seedling recruitment and species compositional changes. In the two years of their study, the extra daytime CO₂ increased seed production and dispersal in seven of the eight most abundant species, including the grasses *Anthoxanthum odoratum*, *Lolium perenne* and *Poa pratensis*, the legumes *Trifolium repens* and *T. subterranean*, and the herbs *Hypochaeris radicata* and *Leontodon saxatilis*. In some of these plants, elevated CO₂ increased the number of seeds per reproductive structure, while all of them exhibited CO₂-induced increases in the number of reproductive structures per unit of ground area. In addition, they determined that the CO₂-induced increases in seed production contributed in a major way to the increase in the numbers of species found within the CO₂-enriched plots.

In a five-year study of a nutrient-poor calcareous grassland in Switzerland, Thurig *et al.* (2003) used screen-aided CO₂ control (SACC) technology (Leadley *et al.*, 1997) to enrich the air over half of their experimental plots with an extra 300 ppm of CO₂, finding that "the effect of elevated CO₂ on the number of flowering shoots (+24%) and seeds (+29%) at the community level was similar to above ground biomass response." In terms of species functional groups, there was a 42% increase in the mean seed number of graminoids and a 33% increase in the mean seed number of forbs, but no change in legume seed numbers. In most species, mean seed weight also tended to be greater in plants grown in CO₂-enriched air (+12%); and Thurig *et al.* 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)."

Rounding out the papers we have reviewed on this subject, 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 CO₂ concentrations of either 365 or 730 ppm. In response to this doubling of the air's CO₂ content, the vegetative mass of both male and female plants

rose by approximately 39%. Reproductive mass, on the other hand, rose by 82% in male plants and by 97% in females. In the female plants, this feat was accomplished, in part, by increases of 36% and 44% in the number and mass of seeds per plant, and by a 15% increase in the mass of individual seeds, in harmony with the findings of Jablonski *et al.* (2002), which they derived from a meta-analysis of the results of 159 CO₂ enrichment experiments conducted on 79 species of agricultural and wild plants. Hence, 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-CO₂ world of the future, which ultimate result should bode well indeed 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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6.7.8.3. Trees

How does enriching the air with carbon dioxide impact the reproductive capacity of trees? LaDeau and Clark (2001) addressed this question in a major way when they determined the reproductive response of loblolly pine trees to atmospheric CO₂ 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 CO₂-enriched trees were twice as likely to be reproductively mature and produced three times more cones per tree. Similarly, the trees growing in the CO₂-enriched air produced 2.4 times more cones in the fall of 2000; and from August 1999 through July 2000, they collected three times as many seeds in the CO₂-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 CO₂-enriched trees were 91% heavier than those collected from the trees growing in ambient air, (2) the CO₂-enriched seeds had a lipid content that was 265% greater than that of the seeds produced on the ambient-treatment trees, (3) the germination success for seeds developed under atmospheric CO₂ enrichment was more than three times greater than that observed for control seeds developed at ambient CO₂, regardless of germination CO₂ concentration, (4) seeds from the CO₂-enriched trees germinated approximately five days earlier than their ambiently-produced counterparts, again regardless of germination CO₂ concentration, and (5) seedlings developing from seeds collected from CO₂-enriched trees displayed significantly greater root lengths and needle numbers than seedlings developing from trees exposed to ambient air, also regardless of growth CO₂ concentration.

What are the implications of these findings? The propensity for elevated levels of atmospheric CO₂ to hasten the production of more plentiful seeds on the trees of this valuable timber species bodes well for naturally-regenerated loblolly pine stands of the southeastern United States, where LaDeau and Clark report these trees "are profoundly seed-limited for at least 25 years." Hence, as the air's CO₂ content continues to climb, they conclude that "this period of seed limitation may be reduced," which is good news for this highly-prized tree. In addition, the observations of Hussain *et al.* suggest that loblolly pine trees in a CO₂-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 CO₂-enriched loblolly pine seedlings become photosynthetically-active, they will likely photosynthesize and produce biomass at greater rates than those exhibited by seedlings growing under current ambient CO₂ concentrations.

Another major study of the reproductive responses of trees to elevated levels of atmospheric CO₂ was conducted at the Kennedy Space Center, Florida, USA, where in 1996 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 CO₂ 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. So what did they find?

Acorn germination rate and degree of predation by weevils were unaffected by elevated CO₂, while acorn size was enhanced by a small amount: 3.6% for *Q. myrtifolia*, 7.0% for *Q. chapmanii*, and 7.7% for *Q. geminata*. Acorn number responses, on the other hand, were enormous, but for only two of the three species, as *Q. geminata* did not register any CO₂-induced increase in reproductive output, in harmony with its unresponsive overall growth rate. For *Q. myrtifolia*, however, Stiling *et al.* report "there were four times as many acorns per 100 twigs in elevated CO₂ as in ambient CO₂ and for *Q. chapmanii* the increase was over threefold." On the ground, the enhancement was greater still, with the researchers reporting that "the number of *Q. myrtifolia* acorns per meter squared in elevated CO₂ was over seven times greater than in ambient CO₂ and for *Q. chapmanii*, the increase was nearly sixfold."

Stiling *et al.* say that these results lead them to believe "there will be large increases in seedling production in scrub-oak forests in an atmosphere of elevated CO₂," 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. If other trees behave similarly, it would appear that the rising CO₂ content of earth's atmosphere will be a boon indeed to the regenerative prowess of the planet's forests. More research results from other tree species are thus anxiously awaited.

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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6.7.9. 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 trees respond to atmospheric CO₂ enrichment? We here briefly summarize the findings of several studies for aspen, birch and oak trees.

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.

6.7.9.1. Aspen Trees

In New Zealand, the Legume Lotus is a good source of condensed tannins; and scientists with the country's *AgResearch Grasslands* institute have additionally determined that sheep and cattle feeding on forage that contains this plant may see their methane emissions reduced by as much as 16%.

This latter finding is of special importance to New Zealanders, because the methane expelled in the breath of cattle and sheep - which is a by-product of the fermentation of feed in the rumen of these animals - accounts for close to 90% of the country's methane emissions. Consequently, a significant reduction in such a large national source of one of the atmosphere's most potent greenhouse gases would go a long way towards helping the country reduce its emissions of climate-altering substances, which would be, according to the press release that described this development, "very welcome." The press release also states that tannins "have a variety of other animal related benefits, such as improved milk yield, increased liveweight gain, decreased internal parasite burden and reduced occurrence of bloat, dags and fly strike."

In this regard, it is important to note that in addition to sheep and cattle, *ruminants*, as they are called, comprise a great group of animals (four-footed, hooved, even-toed, cud-chewing mammals that have a stomach consisting of four divisions or chambers) that includes antelope, bison, buffalo, camel, deer, giraffe, goat, llama, etc., and that these animals eat a number of other types of plants, which may also experience increases in leaf tannin production as the air's CO₂ content rises. In this Summary, therefore, we *begin* an investigation of this subject as it applies to aspen (*Populus tremuloides*) trees.

King *et al.* (2001) grew aspen seedlings for five months in open-top chambers maintained at atmospheric CO₂ concentrations of either 350 or 700 ppm. At the end of this period, naturally-senesced leaf *litter* was collected and analyzed; and it was found that the elevated CO₂ 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) CO₂ concentrations under conditions of either low or high light availability (half and full sunlight,

respectively) for 31 days after the mean date of bud break. In this case it was determined that under low light conditions, the CO₂-enriched seedlings exhibited an increase of approximately 15% in leaf condensed tannin concentration, while under high light conditions the CO₂-induced increase in leaf condensed tannin concentration was a whopping 175%.

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 CO₂ (360 ppm and 560 ppm, respectively) and O₃ (35-60 ppb and 52-90 ppb, respectively) on the foliar chemistry of more mature aspen trees of two different genotypes (216 and 259) growing out-of-doors at the Aspen Free Air CO₂ Enrichment (FACE) facility near Rhinelander, Wisconsin, USA, 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 CO₂ or O₃ treatment was in general also the one for which average levels of condensed tannins were most positively (or least negatively) affected by that treatment." In this regard, it is of interest to note that the mean condensed tannin concentrations of the aspen 216 and 259 genotypes were 25% and 57% higher, respectively, under the elevated CO₂ and O₃ combination treatment compared to the ambient CO₂ and O₃ combination treatment.

In light of these findings, it is logical to presume that as atmospheric concentrations of CO₂ and O₃ continue to rise, the increase in condensed tannin concentration likely to occur in the foliage of aspen trees should lead to their leaves becoming less preferred for consumption by the dreaded forest tent caterpillar, which according to Agrell *et al.* is "an eruptive generalist defoliator in North American hardwood forests, causing extensive damage during outbreak years (Fitzgerald, 1995)." Also, because the amount of methane expelled in the breath of ruminants is an inverse function of the condensed tannin concentration of the foliage they consume, the increased aspen foliage tannin concentrations likely to exist in a high-CO₂ world of the future should result in less methane being released to the atmosphere via ruminants browsing on aspen foliage, which phenomenon should act to decrease the impetus for methane-induced global warming.

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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6.7.9.2. 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 CO₂ 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) CO₂ concentrations under conditions of either low or high light availability (half and full sunlight, respectively) for 31 days after the mean date of bud break. In doing so, they determined that under low light conditions the CO₂-enriched seedlings exhibited an increase of approximately 15% in leaf condensed tannin concentration, while under high light conditions the CO₂-induced tannin increase was a whopping 175%.

Peltonen *et al.* (2005) studied the impacts of doubled atmospheric CO₂ and O₃ concentrations on the accumulation of 27 phenolic compounds, including soluble condensed tannins, in the leaves of two European silver birch clones in seven-year-old soil-grown trees that were exposed in open-top chambers for three growing seasons to ambient and twice-ambient atmospheric CO₂ and O₃ concentrations singly and in combination. This work, which was carried out in central Finland, revealed that elevated CO₂ increased the concentration of soluble condensed tannins in the leaves of the trees by 19%. In addition, they found that the elevated CO₂ protected the leaves from elevated O₃ because, as they describe it, "all the O₃-derived effects on the leaf phenolics and traits were prevented by elevated CO₂."

Kuokkanen *et al.* (2003) grew two-year-old silver birch seedlings in ambient air of 350 ppm CO₂ or air enriched to a CO₂ concentration of 700 ppm under conditions of either ambient temperature or ambient temperature plus 3°C for one full growing season in the field in closed-top chambers at the 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 CO₂-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 CO₂ nearly *tripled* condensed tannin concentrations in

the ambient-temperature air, while it increased their concentrations in the elevated-temperature air by a factor *in excess of 3.5*.

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 CO₂. This procedure revealed that the concentration of condensed tannins in the fine roots of the saplings was increased by 27% in the CO₂-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 CO₂-enriched (to 200 ppm above ambient) FACE plots in northern Wisconsin, USA, which were also maintained under ambient and O₃-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 (including nitrogen, which hastens leaf decay, and condensed tannins, which retard decay), and the remaining leaves were placed in 1-mm-aperture litterbags made of fiberglass cloth and left to decay upon the ground for the next twelve months under the same atmospheric conditions in which they were produced. Then, at the conclusion of the one-year litter-exposure period, the mass of remaining litter was measured and the time required to achieve 95% mass loss determined.

In following this protocol, the researchers learned that under ambient O₃ conditions, the *nitrogen* concentrations of the leaves in the CO₂-enriched plots at the time of litterfall were 31% *less* than those of the leaves in the ambient-CO₂ plots, while condensed tannin concentrations were 64% *greater* in the CO₂-enriched plots. Similarly, under the O₃-enriched conditions, leaf nitrogen concentrations were a nearly-identical 32% less, while condensed tannins concentrations a much-larger 99% greater.

These observations suggest that leaf decay rates in the CO₂-enriched plots should be lower than those in the ambient-CO₂ plots; and the mass-loss rates determined at the end of the one-year exposure period bore out this expectation, with Parsons *et al.* reporting that "for control litter, 5% of mass remained after 3.6 years, while CO₂-enriched litter took ~4.5 years to turn over 95% of its mass." Hence, it could well take 25% more time (4.5 years / 3.6 years) to lose an equivalent percentage of paper birch leaf litter from CO₂-enriched forests, independent of the air's O₃ concentration. And combining this fact with the facts that the CO₂-enriched trees, in the words of the researchers, "attained greater size, and a greater degree of canopy closure, and contributed more litterfall to the development of [the] forest floor than did trees in the control rings," it is clear that the ongoing rise in the atmosphere's CO₂ concentration should greatly augment the sequestration of carbon by paper birch tree stands as the air's CO₂ content climbs ever higher.

In another study conducted at the Wisconsin FACE site, Agrell *et al.* (2005) examined the effects of ambient and elevated concentrations of atmospheric CO₂ (360 ppm and 560 ppm) and O₃ (35-60 ppb and 52-90 ppb) on the foliar chemistry of paper birch trees, as well as the impacts of these effects on the host plant preferences of forest tent caterpillar larvae, finding that the mean condensed tannin concentration of the birch tree leaves was 18% greater in the elevated CO₂ and O₃ treatment than in the ambient CO₂ and O₃ treatment. In addition, they state 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 CO₂ or O₃ treatment was in general also the one for which average levels of condensed tannins were most positively (or least negatively) affected by that treatment."

In light of these findings, it is logical to presume that as atmospheric concentrations of CO₂ and O₃ continue to rise, the increase in condensed tannin concentration likely to occur in the foliage of birch trees should lead to their leaves becoming less preferred for consumption by the dreaded forest tent caterpillar, which according to Agrell *et al.* is "an eruptive generalist defoliator in North American hardwood forests, causing extensive damage during outbreak years (Fitzgerald, 1995)." Also, because the amount of methane expelled in the breath of ruminants is an inverse function of the condensed tannin concentration of the foliage they consume, the higher birch-foliage tannin concentrations likely to prevail in a high-CO₂ world of the future should result in less methane being released to the atmosphere via ruminants browsing on the foliage of birch trees, which phenomenon should act to decrease the impetus for methane-induced global warming.

In conclusion, it appears that elevated concentrations of atmospheric CO₂ tend to increase leaf and fine-root tannin concentrations of birch trees, and that this phenomenon tends to (1) protect the trees' foliage from predation by voracious insect herbivores, (2) protect the trees' roots from soil-borne pathogens and herbivores, (3) enhance the sequestration of carbon in forest soils, and (4) reduce methane emissions from ruminants that might nibble on the trees' foliage.

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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6.7.9.3. Oak Trees

How do rising air temperatures and atmospheric CO₂ concentrations affect the leaf tannin concentrations of oak trees? In this section we broach this question as it applies to several different species of oak, including myrtle oak (*Quercus myrtifolia* Wild.), pedunculate oak (*Quercus robur* L.), sand live oak (*Quercus geminata* Small) and Chapman's oak (*Quercus chapmanii* Sargent).

Dury *et al.* (1998) grew four-year-old pedunculate oak trees in pots within greenhouses maintained at ambient and twice-ambient atmospheric CO₂ concentrations in combination with ambient and elevated (ambient plus 3°C) air temperatures for approximately one year. This work revealed that elevated CO₂ 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 CO₂-enriched and warmer world of the future.

In a radically different type of experiment, Cornelissen *et al.* (2003) studied fluctuating asymmetry in the leaves of two species of sclerophyllous oaks - myrtle oak (*Quercus myrtifolia*) and sand live oak (*Quercus geminata*) - that dominate a native scrub-oak community at the Kennedy Space Center, Titusville, Florida (USA), which has served as the base of operations for a number of important open-top-chamber investigations of the effects of a 350-ppm increase in atmospheric CO₂ concentration on this unique ecosystem; and to provide a little background for their study, we note that *fluctuating asymmetry* is the terminology used to describe small variations from perfect symmetry in otherwise bilaterally symmetrical characters in an organism (Moller and Swaddle, 1997), 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 CO₂, and, when encountered, they were less asymmetric than leaves growing under ambient CO₂." In addition, they found that "*Q. myrtifolia* leaves under elevated CO₂ were 15.0% larger than in ambient CO₂ and *Q. geminata* leaves were 38.0% larger in elevated CO₂ conditions." As a bonus, they also determined that "elevated CO₂ 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*."

In commenting on their primary findings of *reduced percentages* of leaves experiencing asymmetry in the presence of elevated levels of atmospheric CO₂ and the *lesser degree* of asymmetry exhibited by affected leaves in the elevated CO₂ treatment, Cornelissen *et al.* say that "a possible explanation for this pattern is the fact that, in contrast to other environmental stresses, which can cause negative effects on plant growth, the predominant effect of elevated CO₂ on plants is to promote growth with consequent reallocation of resources (Docherty *et al.*, 1996)." Another possibility they discuss "is the fact that CO₂ acts as a plant fertilizer," and, as a result, that "elevated CO₂ ameliorates plant stress compared with ambient levels of CO₂," which is one of the well-documented biological benefits of atmospheric CO₂ enrichment (Idso and Idso, 1994).

With respect to the ancillary finding of CO₂-induced increases in tannin concentrations in the leaves of both oak species (a mean increase of approximately 35% for *Q. myrtifolia* and 43% for *Q. geminata*), we note that this phenomenon may provide the two species with greater

protection against herbivores, and that part of that protection may be associated with the observed CO₂-induced reductions in the amount and degree of asymmetry in the leaves of the CO₂-enriched trees. Consistent with this hypothesis, for example, Stiling *et al.* (1999, 2003) found higher abundances of leaf miners in the leaves of the trees in the ambient CO₂ chambers, where asymmetric leaves were more abundant, while in the current study it was determined that leaf miners attacked asymmetric leaves more frequently than would be expected by chance alone in both CO₂ treatments.

In a subsequent study conducted at the Kennedy Space Center's scrub-oak community, Hall *et al.* (2005b) evaluated foliar quality and herbivore damage in three oaks (*Q. myrtifolia*, *Q. chapmanii* and *Q. geminata*) plus the nitrogen-fixing legume *Galactia elliotii* 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 CO₂-enriched leaves, with across-species mean increases of 6.8% for condensed tannins, 6.1% for hydrolyzable tannins, 5.1% for total phenolics and 4.3% for lignin. In addition, there were large CO₂-induced decreases in *all* leaf damage categories among *all* species: chewing (-48%), mines (-37%), eye spot gall (-45%), leaf tier (-52%), leaf mite (-23%) and leaf gall (-16%). Hall *et al.* thus concluded that the changes they observed in leaf chemical constituents and herbivore damage "suggest that damage to plants may decline as atmospheric CO₂ levels continue to rise."

Last of all, 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 CO₂ 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 CO₂ 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 CO₂ regardless of species, herbivore damage, or growing season," rising by 11% in 2000, 18% in 2001 and 41% in 2002 as a result of atmospheric CO₂ enrichment, as best we can determine from the researchers' bar graphs. Also, the five scientists report that "lepidopteran larvae can exhibit slower growth rates when feeding on elevated CO₂ plants (Fajer *et al.*, 1991) and become more susceptible to pathogens, parasitoids, and predators (Lindroth, 1996; Stiling *et al.*, 1999)," noting further that at their field site, "which hosts the longest continuous study of the effects of elevated CO₂ on insects, herbivore populations decline markedly under elevated CO₂ (Stiling *et al.*, 1999, 2002, 2003; Hall *et al.*, 2005b)."

In conclusion, it would appear that the large and continuous enhancement of condensed tannin concentrations in oak tree foliage produced in CO₂-enriched air is a good omen for people worried about greenhouse gas-induced global warming, because methane emissions from ruminants feeding on foliage rich in condensed tannins tend to be lower than methane

emissions from ruminants feeding on foliage of lower tannin concentration. In addition, the marked tannin-induced declines in herbivore populations observed in CO₂-enriched open-top-chamber studies bodes well for the ability of earth's vegetation to better resist herbivore attacks as the air's CO₂ content continues to climb.

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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6.7.10. Worms

Perhaps the best known worm in the world is the common earthworm. How will it be affected as the air's CO₂ content continues to climb, and how will its various responses affect the biosphere? What about other worms? How will they fare in a CO₂-enriched world of the future, and what will be the results of their responses? Last of all -- which question we shall address first of all -- why do we even care?

"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), for example, "by ingestion and digestion of plant residue and subsequent egestion of cast material, earthworms can redistribute nutrients in a soil and enhance enzyme activity, thereby increasing plant availability of both soil and plant residue nutrients," as others have also demonstrated (Bertsch *et al.*, 1988; McCabe *et al.*, 1988; Zachmann and Molina, 1988). Likewise, 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) additionally report that the presence of earthworms appears to mitigate the deleterious effects of certain soil toxins; while Logsdon and Lindon (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 care about what happens to earthworms as the air's CO₂ content rises because of the many important services they provide for earth's plant life.

So how might rising atmospheric CO₂ concentrations impact earthworms? Edwards (1988) says that "the most important factor in maintaining good earthworm *populations* [our italics] in agricultural soils is that there be adequate availability of organic matter," while Hendrix *et al.*

(1988) and Kladvikó (1988) report that greater levels of plant productivity promote greater levels of earthworm *activity*. Consequently, since the most ubiquitous and powerful effect of atmospheric CO₂ enrichment is its stimulation of plant productivity, 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 CO₂ content should significantly increase earthworm populations and amplify the many beneficial services they provide for plants.

Then there's the second most significant and common impact of atmospheric CO₂ enrichment on plants: its *antitranspirant effect*, whereby elevated levels of atmospheric CO₂ reduce leaf stomatal apertures and slow the rate of evaporative water loss from the vast bulk of earth's vegetation. 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 is also something earthworms seem to love, i.e., plenty of soil moisture.

In light of these many proven facts, it should not have been surprising that when Zaller and Arnone (1997) fumigated open-top and -bottom chambers they established in a calcareous grassland near Basal, Switzerland with air of either 350 or 600 ppm CO₂ for an entire growing season, they found that the mean annual soil moisture content in the CO₂-enriched chambers was 10% 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% greater in the CO₂-enriched chambers than in the control chambers. In addition, because earthworm casts are rich in organic carbon and nitrogen, the cumulative amount of these important nutrients on a per-land-area basis was found to be 28% greater in the CO₂-enriched chambers than it was in the ambient-air chambers. And 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. What is more, they found that the CO₂-induced *growth stimulation* experienced by the various grasses was also greater for those plants growing nearer the earthworm casts.

The upshot of these various observations is that atmospheric CO₂ enrichment sets in motion a self-enhancing cycle of positive biological phenomena, whereby increases in the air's CO₂ content (1) stimulate plant productivity and (2) reduce plant evaporative water loss, which results in (1) more organic matter entering the soil and (2) a longer soil moisture retention time and/or greater soil water contents, all of which factors lead to the development of larger and more active earthworm populations, which enhance many important soil properties, including fertility, structure, aeration and drainage, which improved properties further enhance the growth of the plants whose CO₂-induced increase in productivity was the factor that started the whole series of processes on the road to a higher level of activity in the first place, and so on.

But the good news doesn't end there. 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)." Hence, on the basis of these studies and their own

micro-morphological investigation of structural development and organic matter distribution in two calcareous marine loam soils on which pear trees had been grown for 45 years (one of 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 CO₂ enrichment that stimulates the activity of earthworms also leads to more -- and more *secure* -- sequestration of carbon in earth's soils, thereby reducing the potential for CO₂-induced global warming.

Two additional studies have further demonstrated the active role worms play in helping earth's soils store and preserve carbon. 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 ¹⁴C 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."

Lastly, Bossuyt *et al.* (2007) conducted a pair of experiments designed to investigate "at what scale and how quickly earthworms manage to protect SOM." In the first experiment, soil aggregate size distribution together with total C and ¹³C were measured in three treatments - control soil, soil + ¹³C-labeled sorghum leaf residue, and soil + ¹³C-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 ¹³C 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.

But there's still *more* to the story of CO₂ and worms. In an intriguing research paper published in *Soil Biology & Biochemistry*, 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 CO₂ in blanket peat environments."

Ten seedlings of an indigenous grass of blanket peat were then transplanted into each of the microcosms, while 100 enchytraeid worms were added to each of half of the mini-ecosystems. These procedures resulted in the creation of four experimental treatments: ambient temperature, ambient temperature + enchytraeid worms, elevated temperature, and elevated temperature + enchytraeid worms. The resulting 48 microcosms - sufficient to destructively harvest three replicates of each treatment four 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 of all, 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%, while at the elevated temperature expected for a doubling of the air's CO₂ content, the worms had *no effect at all* on DOC. In addition, Cole *et al.* note 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 CO₂ content, just as was suggested by the results of the study of Jongmans *et al.*

In concluding this summary of research results related to the direct and indirect effects of atmospheric CO₂ enrichment on various types of worms and their subsequent activities that (1) amplify the positive effects of CO₂ on plants and (2) reduce the negative effects of CO₂ on climate, we briefly recount the findings of Yeates *et al.* (2003), who report a number of interesting results they obtained 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 CO₂ concentration of 360 ppm and three others at a concentration of 475 ppm (a CO₂ enhancement of only 32%) for a period of four to five years. The pasture contained about twenty species of plants, including C₃ and C₄ grasses, legumes and forbs; but the scientists' attention was focused more on what happened to the microfauna inhabiting the soil in which the plants grew than on the plants themselves.

Nematode populations increased significantly in response to the 32% increase in the air's CO₂ concentration. Of the various feeding groups studied, Yeates *et al.* report 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, however, were recorded among omnivores (97%) and predators (105%). Most dramatic of all, root-feeding populations of the *Longidorus* nematode taxon rose by a whopping 330%. Also increasing in abundance were earthworms: *Aporrectodea caliginosa* by 25% and *Lumbricus rubellus* by 58%. Enchytraeids, on the other hand, *decreased* in abundance, by approximately 30%.

What are the ramifications of these observations? 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 obviously helps pasture plants to grow better. Hence, the CO₂-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 CO₂-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, it would appear that the lowly earthworm and still lowlier soil nematodes respond to increases in the air's CO₂ content, via a number of plant-mediated phenomena, in ways that further enhance the positive effects of atmospheric CO₂ enrichment on plant growth and development, while at the same time helping to sequester more carbon more securely in the soil and thereby reducing the potential for CO₂-induced global warming.

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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6.8. Greening of the Earth

Over two decades ago, Idso (1986) published a small item in *Nature* advancing the idea that the aerial fertilization effect of the CO₂ that is liberated by the burning of coal, gas and oil was destined to dramatically enhance the productivity of earth's vegetation. In fact, in a little book he had published four years earlier (Idso, 1982), he had predicted that "CO₂ effects on both the managed and unmanaged biosphere will be overwhelmingly positive," if not "mind-boggling." And in a monograph based on a lecture he gave nine years later (Idso, 1995), he said that "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." Consequently, and in light of the fact that Idso's worldview is nearly the exact *opposite* of the apocalyptic vision promulgated by climate alarmists, it is instructive to see what real-world observations reveal about the matter; and in this section we do so for various regions of the world, and for the globe as a whole.

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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6.8.1. Africa

In an article by Fred Pearce that was posted on the website of *New Scientist* magazine on 16 September 2002 entitled "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% of the continent was experiencing severe desertification. The world of nature, however, told a vastly different story. Pearce began his eye-opening article by stating that "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."

And 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." What is more, 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 percent 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) actually detected a steady *rise* in rainfall use efficiency, suggesting that plant productivity and coverage of the desert had actually *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 20th century; and 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 stunning 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* entitled "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) also report finding "a consistent trend of increasing vegetation greenness in much of the region," which they describe as "remarkable." And they say that increasing rainfall over the last few years "is certainly one reason" for the greening phenomenon. However, they find that 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% and 35%, 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 CO₂ 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. Be that as it may, and *whatever* was the reason for the greening of the Sahel over the past quarter-century, it is clear that in spite of what the world's climate alarmists claim were *unprecedented increases* in the "twin evils" of anthropogenic CO₂ emissions and global warming, the Sahel experienced an increase in vegetative prowess 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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6.8.2. 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 CO₂-induced climate change that yielded a mean countrywide temperature increase of 3.0°C and a mean precipitation increase of 3.9% for the 50-year period ending in AD 2050. In doing so, they determined that "*all of China* [our italics] would *benefit* [our italics] from climate change in most scenarios." In addition, they state that "the effects of CO₂ fertilization should [also] be included, for some studies indicate that this may produce a significant increase in yield," an increase that is *extremely* well established.

The great 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." As one example of this fact, 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)." Acting together, therefore, it is clear that the increases in China's agricultural production estimated to result from the direct effects of increased anthropogenic CO₂ emissions *plus* the increases due to the changes in temperature and precipitation typically predicted to result from these emissions could well prove the deciding factor in determining whether China's population *will* or *will not* be able to adequately feed itself at the midpoint of the current century, which could well spell the difference between whether the world of that day will be peaceful or embroiled in conflict.

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 CO₂ 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 CO₂ content would raise the forest's NPP by 14.0%, that a concomitant temperature increase of 2°C would boost the NPP increase to 15.7%, and that adding a 20% increase in precipitation would push the NPP increase all the way to 25.7%. Last of all, they calculated that a 20% increase in precipitation and a 4°C increase in temperature would also boost the forest's NPP by 25.7%.

In contrast to typical climate-alarmist contentions, therefore, it is clear that many projections of Asian ecosystem responses to potential increases in atmospheric CO₂ and temperature are *not* catastrophically negative, even when the projected increases in air temperature are as large as the 4°C rise investigated by Su *et al.* In fact, as in the case of their analysis, many of the responses are *positive*, and strongly so. One of the reasons for this discrepancy between real-world *fact* and climate-alarmist *fiction* is that climate-alarmists typically disregard the many beneficial effects of concomitant atmospheric CO₂ enrichment, including the ability of elevated levels of atmospheric CO₂ to significantly increase plant growth and water use efficiency, as well as their tendency to alter the physiology of plants to where they actually *prefer* warmer temperatures, which phenomenon is expressed as a CO₂-induced increase in the temperature at which plants photosynthesize most effectively.

Related evidence for the reality of these phenomena is presented in the work of Grunzweig *et al.* (2003), who tell the tale of the Yatir forest (a 2800-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 CO₂, water vapor and energy between terrestrial ecosystems and the atmosphere (Baldocchi *et al.*, 2001), the forest's annual net ecosystem CO₂ exchange was just as high as that of many high-latitude boreal forests and actually higher than that of most temperate forests.

How could this possibly be?

Grunzweig *et al.* note that the increase in atmospheric CO₂ concentration that has occurred since pre-industrial times should have improved water use efficiency (WUE) in most plants by increasing the ratio of CO₂ fixed to water lost via evapotranspiration. That this hypothesis is indeed correct has been demonstrated by Leavitt *et al.* (2003) within the context of the long-term atmospheric CO₂ enrichment experiment of Idso and Kimball (2001) on sour orange trees. It has also been confirmed in nature by Feng (1999), who obtained identical (to the study of Leavitt *et al.*) CO₂-induced WUE responses for 23 groups of naturally-occurring trees scattered across western North America over the period 1800-1985, which response, Feng concludes, "would have caused natural trees in arid environments to grow more rapidly, acting as a carbon sink for anthropogenic CO₂," which is exactly what Grunzweig *et al.* found to be happening in the Yatir forest on the edge of the Negev Desert. In addition, the latter researchers 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."

In light of these several observations, it is only natural to expect that as atmospheric CO₂ concentrations and air temperatures rise hand-in-hand, both natural and agro-ecosystems would exhibit ever-increasing rates of net primary production ... *and so they do*, as has been demonstrated by a number of data-driven studies.

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% over a broad contiguous swath of Asia stretching from Europe through Siberia to the Aldan plateau, where almost 58% 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 also 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% in the *area* of Russian forests. In addition, the team of US, Austrian and Russian scientists reported that "within the range of 50-65° of latitude [the range of 90% of Russian forests], the relationship between biomass density and the area-averaged NDVI is very close to a linear function, with a slope of ~1," citing 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* [our italics] 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 that are *not* mentioned are the aerial fertilization effect and the transpiration-reducing effect of the increase in the air's CO₂ concentration that was experienced over the study period. Applied together, the sum of these several 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.

Also working in an area not expected to show a positive response to the "twin evils" of rising air temperatures and atmospheric CO₂ concentrations, 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% of total arid regions and for 88.2% of total semiarid regions, such that the area of arid regions decreased by 6.9% and the area of semiarid regions decreased by 7.9%. 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." Interestingly, in this regard, they report 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)." Hence, it would appear that the dreaded climatic change claimed to have been experienced by the globe over the latter part of the 20th century was either (1) not so dreaded after all or (2) *totally 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.

Continuing in much the same vein, 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%. 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 in response to (1) the ongoing recovery of the planet from the growth-inhibiting chill of the Little Ice Age, which was likely *the coldest period of the current interglacial*, plus (2) the aerial fertilization effect of the historical and still-ongoing rise in the atmosphere's CO₂ concentration, as well as (3) the growth-promoting effect of anthropogenic nitrogen deposition.

Applying the same techniques, Fang *et al.* (2003) looked at the whole of China, finding that its terrestrial NPP increased by 18.7% 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 CO₂, and also greater than expected from climate, based on broad geographic patterns."

But is this really so?

From 1982 to 1999, the atmosphere's CO₂ concentration rose by approximately 27.4 ppm. Based on the procedures and reasoning described in a *CO₂ Science* Editorial of [18 Sep 2002](#), the aerial fertilization effect of this CO₂ increase could be expected to have increased the NPP of the conglomerate of forest types found in China by about 7.3%. 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%. 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%/day x 5 days = 8.0%, which brings the total CO₂-induced plus warming-induced increase in NPP to 15.3%.

Last of all, we note there is a well-documented positive synergism between increasing air temperature and CO₂ 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 CO₂-induced 7.3% NPP enhancement to the 10.7% enhancement that when combined with the 8.0% enhancement caused by the warming-induced increase in growing season length would produce the 18.7% increase in NPP 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 CO₂ concentration that occurred between 1982 and 1999 in China: a dramatically stimulated terrestrial biosphere that is growing ever more productive with each passing year. This is the *true observed consequence* of the "twin evils" of the radical climate-alarmist movement (rising CO₂ and temperature); and it is about as opposite and far removed as one can get from the horror stories this group promulgates, i.e., that the increases in these two factors are greater threats to the well-being of the biosphere, including humanity, than either *nuclear warfare* or *world terrorism*.

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 CO₂ concentration (Keeling *et al.*, 1996)," the former of which phenomena they further suggest "was probably due to the rise in atmospheric CO₂ 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 ultra-enhancement of early spring growth that is provided by the ongoing rise in the air's CO₂ concentration.

Citing a total of 20 scientific papers at various places in the following quote from their research report, Piao *et al.* conclude that "results from observed atmospheric CO₂ and O₂

concentrations, inventory data, remote sensing data, and carbon process models have all suggested that terrestrial vegetation NPP of the Northern Hemisphere has increased over the past 2 decades and, as a result, the northern terrestrial ecosystems have become important sinks for atmospheric CO₂." Again, we agree, and again we wonder what there is about these very impressive positive observations that inspire radical environmentalists to classify the *twin evils* of rising atmospheric CO₂ and temperature as *worse than nuclear warfare and global terrorism*.

In conclusion, it would appear that rather than *devastating* the landscape, the historical increases in the atmosphere's CO₂ concentration and temperature have actually *fostered* a significant *greening of the earth*, including that observed throughout the length and breadth of Asia.

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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6.8.3. 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 thus 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. Thus, it is likely that future warming in this region may return it to a higher level of biological productivity than what it currently exhibits.

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 CO₂ 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 CO₂ 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% and leaf area index by 7%. These results, in their words, "indicate that the recent rise in atmospheric CO₂ may already have had significant impacts on productivity, structure and water relations of sclerophyllous shrub vegetation, which tended to offset the detrimental effects of climate change in the region."

How can we relate this observation to climate change predictions for the earth as a whole? For a nominal doubling of the air's CO₂ 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 CO₂. 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 CO₂ concentration rose by approximately 75 ppm, for an analogous climate response of exactly the same value: 0.01°C per ppm CO₂.

With respect to model-predicted changes in earth's *precipitation* regime, a doubling of the air's CO₂ 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 CO₂ content.

Cheddadi *et al.* (2001) employed a standard biogeochemical model (BIOME3) - which uses monthly temperature and precipitation data, certain soil characteristics, cloudiness, and atmospheric CO₂ concentration as inputs - to simulate the responses of various biomes in the region surrounding the Mediterranean Sea to changes in both climate (temperature and precipitation) and the air's CO₂ 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 CO₂, 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 CO₂ 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 CO₂ 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 [CO₂] conditions

than today," where [CO₂] is the abbreviation they use to represent "atmospheric CO₂ concentration."

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

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 [CO₂]." Likewise, they note that "under a high [CO₂] stomata will be much less open which will lead to a reduced evapotranspiration and lower water loss, both for C₃ and C₄ plants," adding 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 [CO₂], jointly with an increase of *ca.* 2°C in annual temperature would not lead to desertification on any part of the Mediterranean unless annual precipitation decreased drastically," where they define a *drastic* decrease as a decline of 30% or more. Equally important in this context is the fact that Hennessy *et al.* (1997) have indicated that a doubling of the air's CO₂ content would in all likelihood lead to a 5 to 10% *increase* in annual precipitation at Mediterranean latitudes, which is also what is predicted for most of the rest of the world. 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 20th 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 CO₂ and nitrogen deposition" are the primary determinants of changes in forest productivity.

In concluding this brief review of pertinent studies conducted in Europe, we note that within the context of today's obsession with the ongoing rise in the atmosphere's CO₂ content, as well as the many environmental catastrophes it has been predicted to produce, the overwhelmingly positive results that have been obtained are truly remarkable. This assessment is even *more* remarkable in light of the fact that the world's climate alarmists claim the warming of the past quarter-century was unprecedented over the last two millennia or more, and that this phenomenon is the greatest threat ever to be faced by the planet. Apparently the *plants* of Europe just don't understand the seriousness of the situation.

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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6.8.4. North America

In a paper entitled "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% 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.

After lying dormant for about a year, Zhou *et al.*'s attribution of this "greening" of the continent to concurrent 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 concurrent increase in the air's CO₂ concentration, and that fluctuations in temperature were primarily responsible for variations about the more steady upward trend defined by the increase in CO₂. In replying to this challenge, Kaufmann *et al.* (2002) claimed Ahlbeck was wrong and reaffirmed their initial take on the issue. In a further analysis of the question, in our editorial of [18 Sep 2002](#), *CO₂ Science* concluded that it was Ahlbeck who was "clearly the 'more correct' of the two camps." In fact, they came to the conclusion he was actually *totally* correct.

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% or more occurred across the continent from 1982 to 1998. During this period, the air's CO₂ concentration rose by 25.74 ppm, as calculated from the Mauna Loa data of Keeling and Whorf (1998), which amount is 8.58% of the 300 ppm increase that is often used as a reference for expressing plant growth responses to atmospheric CO₂ enrichment. Consequently, for herbaceous plants that display NPP increases of 30-40% in response to a 300-ppm increase in atmospheric CO₂ concentration, the CO₂-induced NPP increase experienced between 1982 and 1998 would be expected to have been 2.6-3.4%. Similarly, for woody plants that display NPP increases of 60-80% in response to a 300-ppm increase in atmospheric CO₂ (Saxe *et al.*, 1998; Idso and Kimball, 2001), the expected increase in productivity between 1982 and 1998 would have been 5.1-6.9%. Since both of these NPP increases are considerably less than the 30% or more observed by Hicke *et al.*, additional factors must have helped to stimulate NPP over this period, 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 CO₂ concentrations, increasingly intensive crop and forest management, increasing use of genetically improved plants, the regrowth of forests on abandoned cropland, and improvements in agricultural practices such as irrigation and fertilization. Whatever the mix might have been, one thing is clear: its ultimate effect was *overwhelming positive*.

In a vastly different type of study based on a 48-year record derived from an average of 17 measurements per year Raymond and Cole (2003) demonstrated that the export of *alkalinity*, in the form of bicarbonate ions, from the USA's Mississippi River to the Gulf of Mexico had increased by approximately 60% since 1953. "This increased export," 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% 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 CO₂, an increase [in] rainwater throughput, or an increase in plant and microbial production of CO₂ and organic acids in soils due to biological responses to increased rainfall and temperature." 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 CO₂ content, which also leads to "an increase in plant and microbial production of CO₂ and organic acids in soils." And as we note in our review of their paper, this phenomenon should have led to an increase in Mississippi River alkalinity equivalent to that which they had observed since 1953.

In a still-different type of 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 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 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ fertilization effect" of the type observed in "experimental manipulations of atmospheric CO₂ that report a stimulation of photosynthesis and above-ground productivity at high CO₂." 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 CO₂ could "increase minimum greenness by stimulating photosynthesis at the beginning of the growing season," citing the work of Idso *et al.* (2000), who discovered that although new spring branch growth of sour orange trees began on exactly the same day of the year in both ambient (400 ppm) and CO₂-enriched (700 ppm) open-top chambers, the *rate* of new-branch growth was initially *vastly* greater in the CO₂-enriched trees. Three weeks after branch growth began in the spring, for example, new branches on the CO₂-enriched trees were typically more than *four times* more massive than their counterparts on the ambient-treatment trees; while on a per-tree basis, over *six times* more new-branch biomass was produced on the CO₂-enriched trees, before declining to an approximate 80% stimulation typical of the bulk of the growing season. Consequently, by looking for a manifestation of the CO₂ fertilization effect at the time of year it is apt to be most strongly expressed, Lim *et al.* may well have found it. Between 1982 and 2001, for example, the air's CO₂ concentration rose by approximately 30 ppm. From Idso *et al.*'s findings of (1) more than a 300% initial increase in the biomass of new sour orange tree branches for a 300-ppm increase in the air's CO₂ concentration and (2) more than a 500% initial increase in *per-tree* new-branch biomass, we calculate that yearly minimum greenness should have increased by something between *something just over 30%* and *something just over 50%*, if other woody plants respond to atmospheric CO₂ enrichment as sour orange trees do; and when we calculate the mean 19-year increase in NDVI for the seven regions for which Lim *et al.* present data, we get an increase of *something just over 40%*, indicative of the fact that Lim *et al.*'s data are not only *qualitatively* consistent with their hypothesis, they are right on the mark *quantitatively* as well.

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," in the words of Xiao and Moody, "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," which once again spells good news for the biosphere.

Jumping a couple years closer to the present, 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 CO₂ 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 CO₂ 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." So what is the cause of the shrub expansion? ... and when did it begin?

Tape *et al.* are inclined to attribute it to large-scale pan-Arctic warming; and 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 CO₂ 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, as *the greening of the earth continues*.

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 CO₂ concentration that occurred after 1950. The two geographers say the sites they chose "fit several criteria designed to limit potential confounding influences associated with anthropogenic disturbance." 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 CO₂ levels, but where growth, particularly post-1950, has occurred under increasing and substantially higher atmospheric CO₂ concentrations." Utilizing meteorological evaluations of the Palmer Drought Severity Index, they 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 discovered 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 FACE studies (Ainsworth and Long, 2005)." Hence, they conclude their findings "suggest that elevated levels of atmospheric CO₂ are acting as a driving force for increased radial growth of ponderosa pine, but 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 CO₂ over the past 50 years, and that these effects would be most apparent during drought stress and on environmentally harsh sites," and in the following sentence they say their results "support these hypotheses." Hence, they conclude their paper by stating that "an atmospheric CO₂-driven growth-enhancement effect exists for ponderosa pine growing under specific natural

conditions within the interior Pacific Northwest," providing yet another important example of the ongoing CO₂-induced *greening of the earth*.

Last of all, and most recently, we come to the study of Wang *et al.* (2006), who 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 CO₂ concentration averaged 299 ppm; during the second it averaged 346 ppm. Also, the mean rate-of-rise of the atmosphere's CO₂ 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 CO₂ concentration was 15% greater and its rate-of-rise 285% 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 CO₂ concentration and the rate of atmospheric CO₂ increase were both relatively high," and they say that "these results are consistent with expectations for CO₂-fertilization effects." In fact, they say "the response of the studied young trees can be taken as strong circumstantial evidence for the atmospheric CO₂-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 CO₂ 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 CO₂ 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 tremendous benefits the historical increase in the air's CO₂ 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 thus paints a picture of the planet's terrestrial vegetation that is just the *opposite* of what is promulgated by the world's climate alarmists. Land-based plants are *not* "headed to hell in a hand basket." They

are *thriving*, thanks in large part to the ongoing rise in the atmosphere's CO₂ concentration - *as well as global warming!* - as ever more real-world observations continue to demonstrate.

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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6.8.5. Global

How have earth's terrestrial plants responded - on average and in their entirety - to the atmospheric temperature and CO₂ 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 that we reviewed on our website, Joos and Bruno (1998) used ice core and direct observations of atmospheric CO₂ and ¹³C to reconstruct the histories of terrestrial and oceanic uptake of anthropogenic carbon over the past two centuries. This project revealed, in their words, that "the biosphere acted on average as a source [of CO₂] during the last century and the first decades of this century ... Then, the biosphere turned into a [CO₂] sink," which implies a significant increase in global vegetative productivity over the last half of the 20th 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)." In following this procedure, they learned that over the last two decades of the 20th century, *when the heat was on*, "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 CO₂, to quantify changes in NPP, soil heterotrophic respiration (HR) and net ecosystem production (NEP) from 1981 to 1998. As an independent check on the NPP estimate of CEVSA, they also estimated 10-day NPP 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 CO₂ produced further increases in NPP and NEP." They also discovered that "the CO₂ 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 CO₂ is greater in warmer conditions, so the CO₂ 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 CO₂ fertilization and climatic variation accounted for 30% of the total terrestrial carbon sink implied by the atmospheric carbon budget (Schimel *et al.*, 2001), and the fraction changed from 13% in the 1980s to 49% in the 1990s," which indicates the growing importance of the CO₂ fertilization effect. Also, they say that "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 CO₂ 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 "CO₂ 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%, 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% (47.5-22.5°S), 7.4% (22.5°S-22.5°N), 3.7% (22.5-47.5°N), and 6.6% (47.5-90.0°N).

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 CO₂ concentrations *everywhere*.

With respect to the latter factor, which is featured prominently on our website, Nemani *et al.* say that "an increase in NPP of only 0.2% per 1-ppm increase in CO₂ could explain all of the estimated global NPP increase of 6.17% over 18 years *and is within the range of experimental evidence* [our italics]." However, they report that terrestrial NPP increased by more than 1% per year in Amazonia alone, noting that "this result cannot be explained solely by CO₂ fertilization." We tend to agree with Nemani *et al.* on this point, but also note that the aerial fertilization effect of atmospheric CO₂ enrichment is most pronounced at higher temperatures (see the previous section Growth Response to CO₂ with Other Variables - Temperature in this report), rising from next to nothing at a mean temperature of 10°C to a 0.33% NPP increase per 1-ppm increase in CO₂ at a mean temperature of 36°C for a mixture of plants comprised predominantly of herbaceous species (Idso and Idso, 1994). For woody plants, 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% to 1% NPP increase per 1-ppm increase in atmospheric CO₂, which would represent the lion's share of the growth stimulation observed by Nemani *et al.* in tropical Amazonia.

Be that as it may, the important take-home message of Nemani *et al.*'s study is that satellite-derived observations indicate that the planet's terrestrial vegetation significantly increased its productivity over the last two decades of the 20th century, in the face of a host of both real and imagined environmental stresses, chief among the latter of which was what climate alarmists routinely claim to be *unprecedented CO₂-induced global warming*, which they routinely represent as being anathema to life on earth. However, the doomsayers are 180 degrees out of phase with reality in this contention, as earth's vegetation has spoken *loud and clear* - by its ever-increasing growth rate - that it actually *loves* higher air temperatures and atmospheric CO₂ concentrations.

In another approach to the subject, Idso (1995) laid out the evidence for a worldwide increase in the growth rates of earth's forests that has been coeval with the progression of the Industrial Revolution and the rising CO₂ content of the atmosphere. The development of this concept *began* with the study of LaMarche *et al.* (1984), who analyzed annual growth rings of two species of pine tree growing near the timberline in California, Colorado, Nevada and New Mexico (USA), and who thereby discovered large increases in growth rate between 1859 and 1983, which rates exceeded what might have been expected from climatic trends but were consistent with the global trend of atmospheric CO₂. The developmental journey then *continued* with a study of ring-width measurements of Douglas fir trees in British Columbia, Canada, that also revealed a marked increase in growth in the trees' latter decades (Parker *et*

al., 1987), leading the principal investigator of the project to state that "environmental influences other than increased CO₂ have not been found that would explain this [phenomenon]." West (1988) reported much the same thing with respect to long-leaf pines in Georgia, i.e., that their annual growth increments had begun to rise at an unusual rate about 1920, increasing by approximately 30% by the mid-1980s; and he too stated that "the increased growth cannot be explained by trends in precipitation, temperature, or Palmer Drought Severity Index," leaving the rising CO₂ content of the atmosphere as the likely cause of the increase in productivity.

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

The next major development in the *continuing saga* was the finding of Graybill and Idso (1993) that very long ring-width chronologies (some stretching back nearly 1800 years) of high-altitude long-lived bristlecone, foxtail and limber pine trees in Arizona, California, Colorado and Nevada (USA) all developed an unprecedented upward growth trend somewhere in the 1850s that continued as far towards the present as the records extended. In this case, too, like the ones that preceded it, comparisons of the chronologies with temperature and precipitation records ruled out the possibility that either of these climatic variables played a significant role in enhancing the trees' growth rates, strongly implicating the historical rise in the air's CO₂ content as the factor responsible for their ever-increasing productivity over the prior century and a half.

Perhaps the most striking evidence of all for the significant 20th-century growth enhancement of earth's forests by the historical increase in the air's CO₂ 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 CO₂," 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 CO₂ 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) reported another impressive finding. Working with data on tree basal area (a surrogate for tropical forest biomass) for the period 1958-1996, which they obtained from *several hundred* plots of mature

tropical trees scattered about the world, they 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% of the missing terrestrial carbon sink of the entire globe. Hence, they suggested that "intact forests may be helping to buffer the rate of increase in atmospheric CO₂, thereby reducing the impacts of global climate change," as Idso (1991a,b) had earlier suggested, and they identified the aerial fertilization effect of the ongoing rise in the air's CO₂ 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; and 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 and less popular (i.e., ever more *politically incorrect*) to report positive biological consequences of the ongoing rise in the air's CO₂ concentration; and the conclusions of Phillips and company began to be repeatedly challenged (Sheil, 1995; Sheil and May, 1996; Condit, 1997; Clark, 2002; Clark *et al.*, 2003). In response to those challenges, *CO₂ Science* published an editorial rebuttal ([18 Jun 2003](#)), 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 20th 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 20th century is robust to the charge that this is an artifact due to the combination of data that vary in census interval (cf. Sheil, 1995)."

Lewis *et al.* (2005b) additionally noted that "Sheil's (1995) original critique of the evidence for increasing turnover over the late 20th century also suggests that the apparent increase could be explained by a single event, the 1982-83 El Niño Southern Oscillation (ENSO), as many of the recent data spanned this event." However, 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 CO₂ and climate promoted terrestrial GPP increases with a significant linear trend in all three tropical regions." In the Amazonian region, the rate of GPP increase was 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 "CO₂ 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 20th 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." Hence, and in spite of what climate alarmists routinely describe as *unprecedented increases* in the "twin evils" of rising atmospheric CO₂ concentrations and air temperatures (which some have described as being greater threats to the world than global terrorism or nuclear warfare), there has *in fact* been what Boisvenue and Running call a significant "greening of the biosphere," and the world's forests in particular.

Last of all, in one final satellite study of the globe, 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 CO₂ 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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