3

Plants Under Stress

Key Findings

The key findings of this chapter are presented in the bullet points below.

- There is little experimental or real-world evidence to support the suggestion C_3 plants may out-compete C_4 plants and thereby replace them in a high-CO_2 environment. (A C_3 plant is one in which CO_2 is fixed into a compound containing three carbon atoms before entering the Calvin cycle of photosynthesis. A C_4 plant fixes CO_2 into a compound containing four carbon atoms.)

- N-fixing legumes are not likely to out-compete non-N-fixing plants in various ecosystems.

- Future increases in the air's CO_2 content may increase the competitiveness of *non*-weeds over weeds.

- Atmospheric CO_2 enrichment asserts its greatest positive influence on diseased as opposed to healthy plants; it has the ability to significantly ameliorate the deleterious effects of stresses imposed on plants by numerous pathogenic invaders.

- Increases in the air's CO_2 content improve plants' ability to withstand the deleterious effects of heavy metals that may be present in soils at ordinarily toxic levels.

- Rising atmospheric CO_2 concentrations may reduce the frequency and severity of pest outbreaks detrimental to agriculture, while not seriously impacting herbivorous organisms found in natural ecosystems.

- Specific genetic alterations to crops may enable them to better withstand the assaults of insects pests, better bear the consequences of possible future increases in seasonal maximum air temperatures, and take advantage of the positive effects of atmospheric CO_2 enrichment on various plant properties and processes, while elevated CO_2 simultaneously reduces the severity of possible negative effects that could arise from the escape of transplanted genes into the natural environment.

- Data obtained from open experimental systems suggest herbivore damage to trees may decrease in a CO_2-enriched environment. If herbivore damage were to increase, other evidence suggests air of higher CO_2 concentration makes Earth's trees more capable of surviving severe defoliation.

- Higher CO_2 concentrations tend to reduce fluctuating asymmetry in plant leaves, leading to more symmetrical leaves that are less susceptible to attacks by herbivores, because they are under less stress of both genetic and environmental origin than leaves growing in less-CO_2-enriched air.

- Atmospheric CO_2 enrichment can stimulate biomass production in both iron-sufficient and iron-deficient plants, while it increases internal iron (Fe) use efficiency, stimulates root growth, and increases root exudation of Fe-mobilizing phytosiderophores in sub-apical root zones, thereby increasing the competitiveness of plants with rhizosphere microorganisms such as barley in their quest for this trace element.

- Whether light intensity is high or low, or leaves are sunlit or shaded, when the CO_2 content of the air is increased, so are the various biological processes that lead to plant robustness. Less than optimal light intensities, therefore, do not negate the beneficial effects of atmospheric CO_2 enrichment. In fact, under low light conditions, the benefits of atmospheric CO_2 enrichment on plant growth are often relatively greater than when light conditions are ideal.

- The maximum benefits of elevated levels of atmospheric CO_2 for the growth and grain production of rice and wheat cannot be realized in soils that are highly deficient in nitrogen, but increasing nitrogen concentrations above what is considered adequate may not result in proportional gains in CO_2-induced growth and yield enhancement. Although there are significant exceptions to the rule, many agricultural crops experience increases in net photosynthesis and biomass production even when soil nitrogen concentrations are a limiting factor to growth.

- CO_2-induced stimulations of percent root infection by various fungi are generally greater under lower, rather than higher, soil nitrogen concentrations. This tendency implies elevated CO_2 will enhance fungal-plant interactions to a greater extent when soil nutrition is less-than-optimal for plant growth, which is the common state of most ecosystems not subjected to the fertilization practices typical of intensive agriculture.

- Atmospheric CO_2 enrichment stimulates photosynthesis and biomass production in grasses and grassland species when soil nitrogen avail-ability is high and/or moderate. Where nitrogen availability is low, grasslands given enough time still have the ability to overcome soil nitrogen limitations and produce positive CO_2-induced growth responses.

- Generally speaking, the degree of soil nitrogen availability positively impacts the aerial fertilization effect of atmospheric CO_2 enrichment on the growth of young aspen, pine, spruce, and other young tree species by promoting a greater CO_2-induced growth enhancement in soils of adequate, as opposed to insufficient, nitrogen content.

- Atmospheric CO_2 enrichment typically reduces—and more often than not completely overrides—the negative effects of ozone pollution on the photosynthesis, growth, and yield of essentially all agricultural crops that have been experimentally evaluated.

- Earth's trees, like much of the rest of the biosphere, are better equipped to live long and productive lives in CO_2-enriched air, even when experiencing the generally negative influence of atmospheric ozone pollution.

- Although labeled by the United Nations and the U.S. Environmental Protection Agency as a dangerous air pollutant, not only is CO_2 not a "pollutant," it is actually an anti-pollutant that helps plants overcome the negative effects of real air and soil pollutants and better enables their removal from polluted areas.

- Plants growing in CO_2-enriched air typically respond by increasing their biomass production, even under conditions of low soil phosphorus content, and this effect is especially strong among plants that possess the ability to increase root phosphatase activity.

- Contrary to the claim that low concentrations of soil nitrogen will curtail the ability of the productivity-enhancing effect of rising atmospheric CO_2 concentration to maintain increased plant growth and ecosystem carbon sequestration rates over the long term, real-world data from several multiyear experiments indicate additional CO_2-induced carbon input to the soil stimulates microbial decomposition and thus leads to more available soil nitrogen.

- Extensive experimentation on loblolly pine trees (plus several understory species) at the Duke Forest long-term free-air CO_2 enrichment (FACE) site has conclusively demonstrated the progressive nitrogen limitation hypothesis has been disproven, suggesting the growth-enhancing benefits of atmospheric CO_2 enrichment should continue as the air's CO_2 content rises.

- The buildup of soil salinity from repeated irrigations can produce growth stresses in agricultural plants, but these stresses can be overcome by the rise in the air's CO_2 concentration.

- As the atmosphere's CO_2 content rises, nearly all agricultural crops, grassland plants, and trees will exhibit enhanced rates of photosynthesis and biomass production that will not be diminished by any global warming that might accompany it. If ambient air temperatures rise concurrently, the growth-promoting effects of atmospheric CO_2 enrichment likely will rise even more as Earth gets "greener."

- The rise in the air's CO_2 content is a powerful antidote for the deleterious biological impacts that might be caused by an increase in the flux of UV-B radiation at the surface of Earth due to depletion of the planet's stratospheric ozone layer.

- The rise in the atmosphere's CO_2 content likely will lead to substantial increases in the photosynthetic rates and biomass production of the world's plants, even under stressful conditions imposed by less-than-optimum soil moisture conditions.

- Non-parasitic weeds likely will be no more competitive in high-CO_2 conditions than they are today, and many of them could be a little less competitive. Atmospheric CO_2 enrichment may provide non-weeds with greater protection against weed-induced decreases in productivity, thereby increasing the competitiveness of non-weeds over weeds. And although atmospheric CO_2 enrichment increases the growth of many weeds, the fraction helped is likely not as large as among non-weeds.

- The rising CO_2 content of the air appears to reduce the negative effects of parasitic weed infection, so that infected host plants continue to exhibit positive (but somewhat reduced) growth responses to elevated CO_2.

Introduction

As was discussed in Chapters 1 and 2, the aerial fertilization effect of Earth's rising atmospheric CO_2

concentration is conferring multiple benefits on terrestrial plants and soils. Such benefits are almost universally acknowledged to occur when growing conditions are ideal, but some have countered that under predicted future CO_2-induced global warming, growing conditions for many plants will be less than ideal. Such counteracting forces to growth, they claim, might negate the benefits of atmospheric CO_2 enrichment. The focus of the current chapter, therefore, is to investigate such claims by examining the responses of plants under various stresses to atmospheric CO_2 enrichment.

As demonstrated in the many sections and subsections below, atmospheric CO_2 enrichment has been shown to ameliorate the negative effects of a number of environmental stresses. The growth enhancement produced by an increase in the air's CO_2 concentration is generally greater under stressful and resource-limited conditions than when growing conditions are ideal.

The physical and environmental stresses addressed below include competition from weeds, diseases, herbivory, nitrogen insufficiency, ozone pollution, phosphorus and nitrogen insufficiency, salinity, higher temperatures, drought, and weeds. IPCC predicts many of these stresses can be expected to increase in a warmer world, but (a) this is not what is revealed by the record of the twentieth century, which IPCC claims experienced "unprecedented" global warming, and (b) in nearly every case, CO_2 enrichment is shown experimentally to immunize plants from these stresses or mitigate their consequences. For example, atmospheric CO_2 enrichment typically reduces—and more often than not completely overrides—the negative effects of ozone pollution on the photosynthesis, growth, and yield of essentially all agricultural crops that have been experimentally evaluated. And the buildup of soil salinity from repeated irrigations can produce growth stresses in agricultural plants, but these stresses can be overcome by the rise in the air's CO_2 concentration.

This chapter contains good news for those concerned about mankind's ability to feed a growing population in coming years, an issue addressed in depth in the following chapter. Importantly, none of the models used to forecast the impact of global warming on crops makes any provision for these positive effects of CO_2 enrichment. One can only conclude that this invalidates their overly pessimistic predictions.

3.1 Competition

One of the concerns about rising concentrations of atmospheric CO_2 is that some plants might benefit more than others, resulting in competitive advantages and ecological changes that could be judged as "bad" because of their effects on wildlife or plants that are beneficial to mankind. This section addresses this issue by surveying research on the different effects of atmospheric CO_2 enrichment on C_3 and C_4 plants, nitrogen-fixers and non-nitrogen-fixers, and weeds and crops.

3.1.1 C_3 vs. C_4 Plants

- There is little experimental or real-world evidence from natural systems to support the suggestion C_3 plants may out-compete C_4 plants and thereby replace them in a high-CO_2 environment. (A C_3 plant is one in which CO_2 is fixed into a compound containing three carbon atoms before entering the Calvin cycle of photosynthesis. A C_4 plant fixes CO_2 into a compound containing four carbon atoms.)

C_3 plants typically respond better to atmospheric CO_2 enrichment than do C_4 plants in increasing their rates of photosynthesis and biomass production. Thus it has been suggested rising atmospheric CO_2 concentrations may lead to C_3 plants out-competing C_4 plants and displacing them, thereby decreasing the biodiversity of certain ecosystems. The story is much more complex than suggested by this simple scenario.

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

BassiriRad *et al.* (1998) report elevated CO_2 enhanced the ability of the perennial C_4 grass *Bouteloua eriopoda* to increase its uptake of NO_3^- and PO_4^{3-} considerably more than the perennial C_3 shrubs *Larrea tridentata* and *Prosopis glandulosa*. And in an eight-year study of the effects of twice-ambient atmospheric CO_2 concentrations on a pristine tallgrass prairie in Kansas, Owensby *et al.* (1999) found the elevated CO_2 concentration did not affect the basal coverage of its C_4 species or their relative contribution to the composition of the ecosystem.

The anti-transpirant effect of atmospheric CO_2 enrichment discussed by Pospisilova and Catsky 1999) is also often more strongly expressed in C_4 plants than in C_3 plants, and it typically allows C_4 plants to better cope with water stress. In a study of the C_3 dicot *Abutilon theophrasti* and the C_4 dicot *Amaranthus retroflexus*, for example, Ward *et al.* (1999) found *Amaranthus retroflexus* exhibited a greater relative recovery from drought than did the C_3 species. This suggests, they write, “the C_4 species would continue to be more competitive than the C_3 species in regions receiving more frequent and severe droughts.”

Morgan *et al.* (2001) published the results of an open-top chamber study of a native shortgrass steppe ecosystem in Colorado (USA), where they exposed the enclosed ecosystems to atmospheric CO_2 concentrations of 360 and 720 ppm for two six-month growing seasons. In spite of an average air temperature increase of 2.6°C caused by the presence of the open-top chambers, the elevated CO_2 increased above-ground biomass production by an average of 38% in both years of the study, and when 50% of the standing green plant biomass was defoliated to simulate grazing halfway through the growing season, atmospheric CO_2 enrichment still increased aboveground biomass by 36%. The communities enriched with CO_2 also tended to have greater amounts of moisture in their soils than communities exposed to ambient air. This phenomenon likely contributed to the less negative and, therefore, less stressful plant water potentials measured in the CO_2-enriched plants. The elevated CO_2 did not preferentially stimulate the growth of C_3 species over C_4 species in these communities, nor did it significantly alter the percentage composition of C_3 and C_4 species in the shortgrass steppe ecosystem.

This result was very similar to what Wand *et al.* (1999) found in an extensive review of the scientific literature published between 1980 and 1997. Analyzing nearly 120 individual responses of C_3 and C_4 grasses to elevated CO_2, they found average photosynthetic enhancements of 33 and 25%, respectively, for C_3 and C_4 plants, along with biomass enhancements of 44 and 33%, respectively, for a doubling of the air’s CO_2 concentration. These larger growth responses in the C_4 species suggest “it may be premature to predict that C_4 grass species will lose their competitive advantage over C_3 grass species in elevated CO_2.”

Campbell *et al.* (2000) provided support for that conclusion. They reviewed research conducted between 1994 and 1999 by a worldwide network of 83 scientists associated with the Global Change and Terrestrial Ecosystems (GCTE) Pastures and Rangelands Core Research Project 1, published in more than 165 peer-reviewed scientific journal articles. After analyzing this body of research, the 17 scientists conclude the “growth of C_4 species is about as responsive to CO_2 concentration as [is that of] C_3 species when water supply restricts growth, as is usual in grasslands containing C_4 species.” Thus this group of scientists provided no evidence for the suggestion C_3 plants may out-compete C_4 plants and thereby replace them in high-CO_2 conditions.

Derner *et al.* (2003) studied the effects of atmospheric CO_2 enrichment to 200 ppm above ambient in a FACE experiment conducted in the field at Maricopa, Arizona (USA) in which they evaluated the growth of C_3 cotton (*Gossypium hirsutum* L.) and C_4 sorghum (*Sorghum bicolor* (L.) Moench) in monocultures and low- and high-density mixtures under both optimum and less than optimum soil water conditions. They found no significant CO_2-soil water interactions, and the 14 researchers thus report the plant growth responses to atmospheric CO_2 enrichment as averages of the wet and dry treatment results.

When grown in monoculture for two months, the aboveground biomass of cotton was 85% greater in the CO_2-enriched treatment than in the ambient-air treatment, and the aboveground biomass of sorghum was 2% lower in the CO_2-enriched air than in the ambient air. In the low-density plant mixture, these responses were exacerbated: the aboveground biomass of sorghum was reduced by 14% in the CO_2-enriched air, and cotton was increased by 154%. In the high-density mixture, this trend continued: sorghum biomass was reduced by 16% in the CO_2-enriched air, and cotton was increased by 276%.

When grown in monoculture, C_3 cotton was significantly stimulated by atmospheric CO_2 enrichment, and C_4 sorghum experienced a small growth reduction. When grown in competition with each other, these positive and negative tendencies were both amplified, and more so when the crowding of the plants was greater.

This study merits careful attention. Importantly, soil water status did not impact the growth response of either species to atmospheric CO_2 enrichment, in contradiction of what had been observed in many earlier experiments (Idso and Idso, 1994). In addition, the negative response of sorghum to elevated CO_2 clashes with the results of several other studies of C_4 plants, where double-digit percentage increases in growth had been the rule (Poorter, 1993; Wand *et al*., 1999). Thus it is necessary to consider still other experimental results.

Zeng *et al*. (2011) note, "among the 18 most harmful weeds in the world, 14 are C_4," and "by contrast, of the 86 plant species that supply most of the world's food, only 5 are C_4 (Patterson and Flint, 1995)." In addition, "studies comparing C_3 crops with C_4 weeds (Wary and Strain, 1987; Patterson *et al*., 1984; Patterson, 1986; Patterson and Flint, 1990, 1995; Alberto *et al*., 1996; Fround-Williams, 1996; Ziska, 2000) ... have demonstrated that elevated CO_2 favors the growth and development of C_3 over C_4 species."

Zeng *et al*. grew rice (*Oryza sativa* L., a C_3 crop) in competition with barnyard grass (*Echinochloa crusgalli* L., a C_4 weed) in a standard paddy-field experiment conducted in ambient air and in air enriched with an extra 200 ppm of CO_2 via FACE technology at Xiaoji Village, Yangzhou City in Eastern China over a period of 120 days. The eight Chinese scientists and their Norwegian colleague found the elevated CO_2 significantly enhanced rice biomass (straw +27.3%, ears +37.6%), tillers (+20%), leaf area index (+11.7%), and net assimilation rate (+50.1%), but they note it reduced all but the last of these characteristics of barnyard grass: biomass (straw -43.6%, ears -47.9%), tillers (-46.1%), leaf area index (-27.3%), and net assimilation rate (+14.1%, the only positive result, but much less than the +50.1% of the rice). In addition, "the absolute uptake of C, N, P, K by rice was increased while those of barnyard grass decreased." Zeng *et al*. write, "rising atmospheric CO_2 concentration could alter the competition between rice and barnyard grass in paddy fields in favor of rice."

These studies show there is little experimental or real-world evidence to support the suggestion C_3 plants may out-compete C_4 plants and thereby replace them in a high-CO_2 environment.

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3.1.2 N-Fixers vs. Non-N-Fixers

- N-fixing legumes are not likely to out-compete non-N-fixing plants in various ecosystems.

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

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

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

The few studies of this question that have been conducted to date do not suggest N-fixing legumes will out-compete non-N-fixing plants in a world with higher CO_2 concentrations in the air.

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3.1.3 Weeds vs. Non-Weeds

- Future increases in the air's CO_2 content may increase the competitiveness of non-weeds over weeds.

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

Dukes (2002) grew model serpentine grasslands common to California (USA) in competition with the invasive forb *Centaurea solstitiali*s at atmospheric CO_2 concentrations of 350 and 700 ppm for one year. They found elevated CO_2 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 C_3 and C_4 weeds at atmospheric CO_2 concentrations of 260 and 660 ppm, finding elevated CO_2 increased pine biomass by 22% while eliciting no response from either type of weed.

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

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

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

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

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

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

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3.2 Disease

3.2.1 Legumes

- Atmospheric CO_2 enrichment can ameliorate the deleterious effects of various stresses imposed on legumes by numerous pathogenic invaders, providing reason to conclude plants will gain the advantage as the air's CO_2 content rises in the future, enabling them to deal successfully with pathogenic organisms and the damage they inflict.

As the atmosphere's CO_2 content rises, nearly all plants should continue to exhibit increasing rates of photosynthesis and, as a result, increased biomass production. This section investigates whether such benefits are exhibited in legumes suffering from pathogenic diseases.

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

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

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

In light of the opposing changes in pathogen behavior induced by the elevated level of atmospheric CO_2 in this experiment—reduced aggressiveness but increased fecundity—it was difficult to determine the ultimate impact of atmospheric CO_2 enrichment on the pathogen-host relationship of this particular plant. One year later, however, the publication of new research provided more insight.

Pangga *et al*. (2004) grew well-watered and well-fertilized seedlings of the Fitzroy cultivar of *Stylosanthes scabra* in a controlled-environment facility maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm, where they inoculated six-, nine- and 12-week-old plants with *C. gloeosporioides*. Ten days after inoculation, they counted the anthracnose lesions on the plants and classified them as either resistant or susceptible.

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

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

Lau *et al*. (2008) measured the amounts of pathogen damage done to the common prairie plant *Lespedeza capitata* growing in ambient and elevated (560 ppm) CO_2 treatments in the seventh and eighth years (2004 and 2005) of the BioCON study (Reich *et al*., 2001) conducted at the Cedar Creek Natural History Area in Minnesota (USA), where the CO_2 treatments were applied during the daylight hours of each growing season.

Lau *et al*. write, disease incidence "was lower in the elevated CO_2 environment, although this difference [10% less in 2004 and 53% less in 2005] was statistically significant only in 2005 ($P < 0.01$)." They point out, "because disease caused major reductions in reproductive output, the effects of CO_2 on disease incidence may be important for *L. capitata* evolution and population dynamics." In addition, they note, Strengbom and Reich (2006), "working in the same experimental site ... also found that elevated CO_2 ... reduced disease incidence on *Solidago rigida*."

Eastburn *et al*. (2010) note, "globally, soybean is the most widely planted dicot crop and has economic significance due to its wide variety of uses, ranging from food and health products to printing inks and biodiesel [fuels]," but "little to no work has evaluated the influence of future atmospheric conditions on soybean diseases," even though "worldwide yield losses to all soybean diseases combined are about 11% (Wrather *et al*., 1997), which is equivalent to more than 24 million metric tons based on current production."

Eastburn *et al*. evaluated the individual and combined effects of elevated carbon dioxide (CO_2, 550 ppm) and ozone (O_3, 1.2 times ambient) on three economically important soybean diseases—downy mildew, *Septoria* brown spot, and sudden death syndrome (SDS)—over the three-year period 2005–2007 under natural field conditions at the soybean free-air CO_2-enrichment (SoyFACE) facility on the campus of the University of Illinois (USA). The five researchers found "elevated CO_2 alone or in combination with O_3 significantly reduced downy mildew disease severity by 39–66% across the three years of the study." They also report "elevated CO_2 alone or in combination with O_3 significantly increased brown spot severity in all three years," but "the increase was small in magnitude." Finally, "the atmospheric treatments had no effect on the incidence of SDS."

Braga *et al*. (2006) examined the effects of atmospheric CO_2 enrichment on another soybean pathogen in three independent experiments. They grew well-watered soybean (*Glycine max* (L.) Merr) plants of two cultivars (IAC-14, susceptible to stem canker disease, and IAC-18, resistant to stem canker disease) from seed through the cotyledon stage in 5-liter pots placed in open-top chambers maintained at atmospheric CO_2 concentrations of either 360 or 720 ppm in a glasshouse. They measured various plant properties and processes, concentrating on the production of glyceollins (the major phytoalexins, or anti-microbial compounds, produced in soybeans) in response to the application of ß-glucan elicitor (derived from mycelial walls of *Phythophthora sojae*) to carefully created and replicated wounds in the surfaces of several soybean cotyledons.

The IAC-14 cultivar did not exhibit a CO_2-induced change in glyceollin production in response to elicitation—as Braga *et al*. had hypothesized would be the case, since this cultivar is susceptible to stem canker disease. But the IAC-18 cultivar, which has the potential to resist the disease to varying degrees, experienced a 100% CO_2-induced increase in the amount of glyceollins produced after elicitation, a response the researchers describe as remarkable. Braga *et al*. say the CO_2-induced response they observed "may increase the potential of the soybean defense since infection at early stages of plant development, followed by a long incubation period before symptoms appear, [as] is characteristic of the stem canker disease cycle caused by Dpm [*Diaporthe phaseolorum* (Cooke & Ellis) Sacc. f. sp. *Meridionalis* Morgan-Jones]." The response they observed "indicates that raised CO_2 levels forecasted for next decades may have a real impact on the defensive chemistry of the cultivars."

Kretzschmar *et al*. (2009) noted "isoflavonoids constitute a group of natural products derived from the phenylpropanoid pathway, which is abundant in soybeans," and "the inducible accumulation of low molecular weight antimicrobial pterocarpan phytoalexins, the glyceollins, is one of the major defense mechanisms implicated in soybean resistance." The authors evaluated "the effect of an elevated CO_2 atmosphere on the production of soybean defensive secondary chemicals induced by nitric oxide and a fungal elicitor." They grew soybeans from seed for nine days in a glasshouse in large, well-watered pots placed in open-top chambers maintained at atmospheric CO_2 concentrations of either 380 or 760 ppm, examining changes in the production of phytoalexins and some of their precursors in the activity of three enzymes related to their biosynthetic pathways.

Kretzschmar *et al*. report "elevated CO_2 combined with nitric oxide resulted in an increase of intermediates and diverted end products (daidzein—127%, coumestrol—93%, genistein—93%, luteolin—89% and apigenin—238%) with a concomitant increase of 1.5–3.0 times in the activity of enzymes related to their biosynthetic routes." These findings, the four Brazilian researchers write, are evidence of "changes in the pool of defense-related flavonoids in soybeans due to increased carbon availability, which may differentially alter the responsiveness of soybean plants to pathogens in CO_2 atmospheric concentrations such as those predicted for future decades."

The studies reviewed here show elevated CO_2 can significantly ameliorate the deleterious effects of various stresses imposed on legume plants by numerous pathogenic invaders, but there remains a need to clarify some issues through further research. Nevertheless, the large number of ways in which elevated CO_2 has been demonstrated to increase plant resistance to pathogen attack gives reason to conclude plants will gain the advantage as the air's CO_2 content climbs, enabling them to deal successfully with pathogenic organisms and the damage they inflict.

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3.2.2 Other Agricultural Plants

- Atmospheric CO_2 enrichment asserts its greatest positive influence on infected as opposed to healthy plants because it can significantly ameliorate the deleterious effects of various stresses imposed on plants by pathogenic invaders.

As the air's CO_2 content rises, nearly all plants should continue to exhibit increasing rates of photosynthesis and increased biomass production. This section examines whether such benefits occur in plants that are suffering from various pathogen-induced diseases, specifically non-legume agricultural plants.

Plessl *et al.* (2007) write, "potato late blight caused by the oomycete *Phytophthora infestans* (Mont.) de Bary is the most devastating disease of potato worldwide," and "infection occurs through leaves and tubers followed by a rapid spread of the pathogen finally causing destructive necrosis." The five researchers grew individual well-watered and fertilized plants of the potato cultivar Indira in controlled-environment chambers maintained at atmospheric CO_2 concentrations of either 400 or 700 ppm. Four weeks after the start of the experiment, researchers cut the first three fully developed pinnate leaves from the plants and inoculated them with zoospores of *P. infestans* in Petri dishes containing water-agar. They evaluated the leaves' symptoms daily via comparison with control leaves similarly treated but unexposed to the pathogen.

The German scientists report the 400- to 700-ppm increase in CO_2 "dramatically reduced symptom development," including extent of necrosis (down by 44% four days after inoculation and 65% five days after inoculation), area of sporulation (down by 100% four days after inoculation and 61% five days after inoculation), and sporulation intensity (down by 73% four days after inoculation and 17% five days after inoculation). These findings, Plessl *et al.* write, "clearly demonstrated that the potato cultivar Indira, which under normal conditions shows a high susceptibility to *P. infestans*, develops resistance against this pathogen after exposure to 700 ppm CO_2," and "this finding agrees with results from Jwa *et al*. (1995), who reported an increased tolerance of tomato plants to *Phytophthora* root rot when grown at elevated CO_2."

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

Malmstrom and Field (1997) grew individual oat plants for two months in pots placed in phytocells maintained at atmospheric CO_2 concentrations of 350 and 700 ppm, and they infected one-third of the plants with the barley yellow dwarf virus (BYDV), which affects more than 150 plant species worldwide, including all major cereal crops. They found elevated CO_2 stimulated rates of net photosynthesis in all plants, regardless of pathogen infection. However, the greatest percentage increase occurred in diseased specimens (48% vs. 34%). Moreover, atmospheric CO_2 enrichment decreased stomatal conductance by 50% in infected plants but by only 34% in healthy ones, which led to a CO_2-induced doubling of the instantaneous water-use efficiency of the healthy plants but a 2.7-fold increase in the diseased plants.

After 60 days of growth under these conditions, the researchers determined the extra CO_2 increased total plant biomass by 36% in infected plants but 12% in healthy plants. In addition, whereas elevated CO_2 had little effect on root growth in the healthy plants, it increased root biomass in the infected plants by up to 60%. Malmstrom and Field conclude CO_2 enrichment "may reduce losses of infected plants to drought" and "may enable diseased plants to compete better with healthy neighbors."

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

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

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

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

Strengbom and Reich note the "indirect effects from elevated CO_2, i.e., lower disease incidence, had a stronger effect on realized photosynthetic rate than the direct effect of higher CO_2." They conclude, "it may be necessary to consider potential changes in susceptibility to foliar diseases to correctly estimate the effects on plant photosynthetic rates of elevated CO_2." In addition, they found the plants grown in CO_2-enriched air had lower leaf nitrogen concentrations than those grown in ambient air, as is often observed in studies of this type. They say their results "are, thus, also in accordance with other studies that have found reduced pathogen performance following reduced nitrogen concentration in plants grown under elevated CO_2 (Thompson and Drake, 1994)." In addition, they write, their results are "also in accordance with studies that have found increased [disease] susceptibility following increased nitrogen concentration of host plants (Huber and Watson, 1974; Nordin *et al*., 1998; Strengbom *et al*., 2002)."

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

Al-Kayssi (2009) notes soil solarization "is a method of heating the soil by using polyethylene sheets as mulching over moistened soil, to retain solar radiation during the hot season," so "soil-borne pathogens may be killed by lethal heat (>40°C) and weakened by sub-lethal heat (<38–40°C) to the extent that they are unable to cause damage to plants or they are more susceptible to chemical toxicants." This technique "has been successfully used to control soil-borne pathogens and weeds (Katan *et al*., 1976; Mahrer, 1979; Grinstein *et al*., 1979; Katan, 1981; Mahrer *et al*., 1984; Avissar *et al*., 1986; Al-Karaghouli *et al*., 1990; Al-Kayssi and Al-Karaghouli, 1991)."

Al-Kayssi conducted a laboratory experiment where "clay soil samples infested with *Verticillium dahliae* were exposed to different CO_2 concentrations (350, 700, 1050, 1400, 1750 ppm air) and incubated in hot water baths at 35, 40, 45, 50 and 55°C," while "field plots were exposed to the same CO_2 levels during soil solarization in three periods (1st of July to 30th of September, 1st of August to 30th of September, and 1st to 30th of September)."

The Iraqi researcher found higher than normal CO_2 contents in the soil increased maximum soil temperatures while reducing the length of time required to kill 90% of the propagules of *V. dahliae* in natural field soil with moisture content at field capacity. He notes this killing time parameter in soil heated to 35°C was reduced from 24 days at the normal ambient CO_2 concentration to 15 days at 1,750 ppm CO_2, and sub-lethal soil temperatures were raised to lethal levels as the soil's CO_2 content was raised. This finding suggests a high-CO_2 environment could make soil solarization a more important method of controlling soil-borne pathogens and weeds than it is today.

These studies indicate atmospheric CO_2 enrichment asserts a relatively greater positive influence on infected as opposed to healthy plants. Moreover, they suggest elevated CO_2 can significantly ameliorate the deleterious effects of various stresses imposed on plants by pathogenic invaders. Consequently, as the atmosphere's CO_2 concentration continues its upward climb, Earth's vegetation should be increasingly better equipped to deal with pathogenic organisms and the damage they do.

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3.2.3 Trees

- The balance of evidence obtained to date demonstrates trees are better able to withstand pathogen attacks in CO_2-enriched air as opposed to ambient-CO_2 air.

Plant pathogens reduce growth in agricultural and natural ecosystems worldwide; estimates of financial loss due to such reductions amount to more than $33 billion annually in the United States alone (Pimentel *et al*., 2000). It is thus natural to wonder—and important to determine—how rising atmospheric CO_2 will affect plant-pathogen interactions. This section examines what researchers have learned about these phenomena from experiments conducted on various types of trees.

Leaf spot disease, which is characterized by chlorotic to necrotic localized leaf lesions, is caused by the *Cercospora* (a large genus of ascomycete fungi) that affect, in the words of McElrone *et al.* (2010), "numerous economically important plant species around the world, including grapes, cereals, soybeans, peanuts, orchids, coffee, alfalfa and potatoes (Sinclair *et al*., 1987)," as well as redbud (*Cercis canadensis*) and sweetgum (*Liquidambar styraciflua*) trees, such as those growing at the Duke Forest FACE facility in Orange County, North Carolina (USA), where McElrone *et al.* studied the disease throughout the growing seasons of five years (2000–2003 and 2005).

The six scientists assessed how elevated CO_2 (to 200 ppm above the ambient air's CO_2 concentration) and natural interannual climatic variability affected the incidence and severity of leaf spot disease among the sweetgum and redbud trees growing in the several FACE rings at the Duke Forest site. In order "to determine how photosynthetic capacity surrounding pathogen damage was affected by CO_2 exposure, the spatial pattern of photosystem II operating efficiency was quantified on *C. canadensis* leaves still attached to plants with an imaging chlorophyll fluorometer," they write.

McElrone *et al.* determined "disease incidence and severity for both species were greater in years with above average rainfall," and "in years with above average temperatures, disease incidence for *Liquidambar styraciflua* was decreased significantly." They also note elevated CO_2 increased disease incidence and severity "in some years." However, they write, the "chlorophyll fluorescence imaging of leaves revealed that any visible increase in disease severity induced by elevated CO_2 was mitigated by higher photosynthetic efficiency in the remaining undamaged leaf tissue and in a halo surrounding lesions." Although atmospheric CO_2 enrichment was sometimes observed to increase the incidence and severity of leaf spot disease, the photosynthesis-enhancing effect of the extra CO_2 compensated for the photosynthetic productivity lost to the disease by enhancing productivity in healthy portions of diseased leaves and in leaves without lesions, with no net ill effect.

Fleischmann *et al.* (2010) grew well-watered European Beech (*Fagus sylvatica* L.) trees from seed for four years in growth chambers maintained at either 400 or 700 ppm CO_2 in a greenhouse. During this period, they gave the trees an adequate supply of all essential nutrients, but in the case of nitrogen (N), there were low N and high N treatments, where they gave the high-N treatment twice as much nitrogen as the low-N treatment. In addition, half of the seedlings were infected with *Phytophthora citricola*—a root pathogen known to infest the roots and trunks of European Beech trees—in the early summer of the third year of the study, and half of the trees in each treatment were harvested and examined at the ends of the third and fourth years of the experiment.

The three German researchers write, "chronic elevation of atmospheric CO_2 increased the susceptibility of beech seedlings towards the root pathogen *P. citricola*, while additional nitrogen supply reduced susceptibility." They found 27% of the infected plants in the low-N high-CO_2 treatment had been killed by the pathogen by the end of their study, and only 9% of the infected plants in the high-N high-CO_2 treatment had died. Surviving beech seedlings of the low-N high-CO_2 treatment "managed to tolerate the root infection by (a) increasing their carbon gain, (b) improving their fine root functionality and (c) changing their allometric relation between below-ground and above-ground biomass."

Fleischmann *et al.* conclude infected beech seedlings in the low-N high-CO_2 treatment responded to the pernicious pathogen and "enhanced [their] primary production rates in the second year of the experiment and increased above-ground biomass significantly as compared to control trees."

Percy *et al.* (2002) grew the most widely distributed North American tree species—trembling aspen—in 12 30-m-diameter FACE rings near Rhinelander, Wisconsin (USA) in air maintained at ambient CO_2 and O_3 concentrations, ambient O_3 and elevated CO_2 (560 ppm during daylight hours), ambient CO_2 and elevated O_3 (46.4–55.5 ppb during daylight hours), and elevated CO_2 and O_3 over the period of each growing season from 1998 through 2001. Throughout the experiment they assessed several of the young trees' growth characteristics, as well as their responses to poplar leaf rust (*Melampsora medusae*), which they note "is common on aspen and belongs to the most widely occurring group of foliage diseases." They found elevated CO_2 alone did not alter rust occurrence, but elevated O_3 alone increased it by nearly fourfold. When applied together, the elevated CO_2 reduced the enhancement of rust development caused by elevated O_3 from nearly fourfold to just over twofold.

Parsons *et al.* (2003) grew two-year-old saplings of paper birch and three-year-old saplings of sugar maple in well-watered and -fertilized pots from early May until late August in glasshouse rooms maintained at either 400 or 700 ppm CO_2. They found the whole-plant biomass of paper birch was increased by 55% in the CO_2-enriched portions of the glasshouse, and sugar maple was increased by 30%. In addition, concentrations of condensed tannins were increased by 27% in the paper birch (but not the sugar maple) saplings grown in the CO_2-enriched air. Parsons *et al*. conclude "the higher condensed tannin concentrations present in the birch fine roots may offer these tissues greater protection against soil-borne pathogens and herbivores." Parsons *et al*. report CO_2-induced increases in fine root concentrations of total phenolics and condensed tannins also have been observed in warm temperate conifers by King *et al*. (1997), Entry *et al*. (1998), Gebauer *et al*. (1998), and Runion *et al*. (1999), and in cotton by Booker (2000).

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

Hypothesizing these consequences could have resulted from a direct deleterious effect of elevated CO_2 on the fungal pathogen, McElrone *et al*. performed other experiments in controlled-environment chambers. These experiments revealed the elevated CO_2 benefited the fungal pathogen as well as the red maple saplings, as the authors report "exponential growth rates of *P. minima* were 17% greater under elevated CO_2." They obtained similar results when they repeated the *in vitro* growth analysis two additional times in different growth chambers.

When "scanning electron micrographs verified that conidia germ tubes of *P. minima* infect *A. rubrum* leaves by entering through the stomata," the researchers turned their attention to the pathogen's mode of entry into the saplings' foliage. In this investigation they report both stomatal size and density were unaffected by atmospheric CO_2 enrichment, but "stomatal conductance was reduced by 21–36% under elevated CO_2, providing smaller openings for infecting germ tubes." They conclude the reduced disease severity under elevated CO_2 was also likely due to altered leaf chemistry, as elevated CO_2 increased total leaf phenolic concentrations by 15% and tannin concentrations by 14%.

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

Runion *et al*. (2010) write, obligate pathogens "have a more intimate relationship with their host and must have the host to survive," whereas facultative pathogens "live saprophytically and generally result in disease (or tend to be more severe) under conditions of plant stress such as low nutrition or water." They grew well-watered and well-fertilized seedlings of loblolly pine (*Pinus taeda*) and northern red oak (*Quercus rubra*) out-of-doors in open-top chambers constructed in large soil bins located at the USDA-ARS National Soil Dynamics Laboratory in Auburn, Alabama (USA), where they exposed the plants to atmospheric CO_2 concentrations of either 360 or 720 ppm with or without infecting them with the fusiform rust fungus (the obligate pathogen *Cronartium quercuum* f.sp. *fusiforme*), and with or without infecting them with the pitch canker fungus (the facultative pathogen *Fusarium circinatum*) for various lengths of time ranging from weeks to a year, with each of the three experiments being conducted twice.

With respect to the pine *Fusarium* rust study, Runion *et al*. state "percent infection was not significantly affected by CO_2 concentration," yet "the percentage of loblolly pine seedlings which died as a result of rust infection was generally significantly lower under elevated CO_2 in both runs of the experiment." With respect to the oak *Fusarium* rust study, they report "the percent of oak seedlings with uredia was consistently lower for seedlings exposed to elevated CO_2 in both runs," and "the percent of oak seedlings with telia was significantly lower for seedlings exposed to elevated CO_2 at the 16 and 19 days evaluations in both runs of the experiment." With respect to the pine pitch canker study, the four researchers say "the percent of loblolly pine seedlings which developed cankers following inoculation with the pitch canker fungus was consistently lower for seedlings grown under elevated CO_2 in both runs of the experiment ... with infection in elevated CO_2-grown seedlings remaining about half that of ambient-grown seedlings."

Runion *et al.* conclude "disease incidence—regardless of pathogen type—may be reduced as atmospheric CO_2 concentration continues to rise," which should significantly benefit the two species of trees in the high-CO_2 environment.

The balance of evidence obtained to date demonstrates an enhanced ability of trees to withstand pathogen attacks in CO_2-enriched as opposed to ambient-CO_2 air. As the atmosphere's CO_2 concentration rises, Earth's vegetation should fare better against the ravages inflicted on it by myriad debilitating plant diseases.

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3.3 Heavy Metal Toxicity

- Increases in the air's CO_2 content improve plants' ability to withstand the deleterious effects of heavy metals that may be present in soils at ordinarily toxic levels.

Noting copper (Cu) is "an essential micronutrient [that] plays a vital role in maintaining normal metabolism in higher plants," but "is toxic to plant cells at higher concentrations and causes the inhibition of plant growth or even death," Jia *et al.* (2007) grew a Japonica rice cultivar in control and Cu-contaminated soil for one full growing season at ambient and elevated atmospheric CO_2 concentrations (370 and 570 ppm), measuring leaf Cu concentrations at the tillering, jointing, heading, and ripening stages.

At the tillering stage of the plants' progression, leaf Cu concentrations in the plants growing in the Cu-contaminated soil of both CO_2 treatments were about 90% greater than those in the plants growing in the uncontaminated soil of both CO_2 treatments. By the time the plants had reached the jointing stage, the mean leaf Cu concentration in the plants growing in the Cu-contaminated soil in the CO_2-enriched air had dropped to the same level as the plants growing in uncontaminated soil in ambient air, and this equivalence was maintained throughout the plants' subsequent heading and ripening stages.

For the plants growing in contaminated soil in ambient air, leaf Cu concentrations remained 50% greater than those of the plants growing in contaminated soil in CO_2-enriched air at the end of the experiment. Thus the negative effect of a more-than-five-fold increase in soil Cu concentration, which increased leaf Cu concentration by approximately 90% at the crop tillering stage, was completely ameliorated throughout the rest of the crop's development by a 54% increase in the atmosphere's CO_2 concentration.

Jia *et al*. (2011a) note "mining and smelting, disposal of sewage sludge and use of cadmium (Cd) rich phosphate fertilizers have contaminated large areas throughout the world, causing an increase in the Cd content of the soil (Liu *et al*., 2007)." This is, they note, an unfortunate development, because "cadmium is a non-essential element that negatively affects plant growth and development processes, such as respiration and photosynthesis (Vega *et al*., 2006), water and mineral uptake (Singh and Tewari, 2003), cell division (Fojtova *et al*., 2002) and cellular redox homoeostasis (Romero-Puertas *et al*., 2004)."

Jia *et al*. studied the interactive effects of Cd contamination and atmospheric CO_2 enrichment on a perennial ryegrass (*Lolium perenne*), growing it from seed hydroponically in half-strength Hoagland solution for three days, followed by growth in full-strength Hoagland solution for five and 20 days and at a range of Cd concentrations ranging from 0 to 160 µmol/liter. Regardless of Cd treatment, the five researchers found "the Cd concentration was much lower under elevated CO_2 than under ambient CO_2," most likely due to the "fast growth triggered by elevated CO_2," such that in their experiment "the dry biomass increased by 81.2% for shoots and 55.2% for roots under non-Cd stress, and an average of 99.1% for shoots and 68.5% for roots under Cd stress, respectively." The five Chinese scientists conclude, "under elevated CO_2, *L. perenne* may be better protected against Cd stress with higher biomass, lower Cd concentration and better detoxification by phytochelatins." In addition, "lower Cd concentration in plants under elevated CO_2 may relieve the Cd toxicity to plants and reduce the risk of Cd transport in the food chain."

Jia *et al*. (2011b) obtained similar results when they hydroponically grew two important forage crops (*Lolium perenne* and *Lolium multiflorum*) at three different Cd (0, 4, and 16 mg/L) and two different atmospheric CO_2 (360 or 1,000 ppm) concentrations in individual pots in controlled-environment chambers for three weeks. They found "root morphological parameters, including root length, surface area, volume, tip number, and fine roots, all decreased under Cd exposure," whereas "by contrast, elevated levels of CO_2 significantly increased all those parameters in the presence of Cd, compared to the CO_2 control, suggesting that elevated levels of CO_2 had an ameliorating effect on Cd-induced stress." The extra 640 ppm of CO_2 also increased the shoot dry weight of *L. multiflorum* by 68%, 92%, and 90% and *L. perenne* by 65%, 61%, and 67% at low, medium, and high (0, 4, and 16 mg/L) cadmium concentrations. It increased the root dry weight of *L. multiflorum* by 65%, 54%, and 50% and *L. perenne* by 47%, 67%, and 10%. The researchers note, "total Cd uptake per pot, calculated on the basis of biomass, was significantly greater under elevated levels of CO_2 than under ambient CO_2," increasing by 42–73% in plant shoots. Meanwhile, elevated CO_2 resulted in a reduction of Cd concentration in the plants' tissues.

The seven scientists note the high Cd uptake under CO_2-enriched conditions for the two *Lolium* species indicate great potential for use in the phytoremediation of Cd-contaminated soils in a CO_2-enriched environment. Also, because of much greater biomass production, the reduction of Cd concentrations in the forage crops' tissues suggests the rise in the air's CO_2 content could improve the safety of these crops, as was demonstrated by Guo *et al*. (2006), who according to Jia *et al*. (2011b), "reported decreased Cd accumulation in leaves, stems, roots and grains of rice at elevated CO_2"; by Zheng *et al*. (2008), who "showed that *Pteridium revolutum* and *Pteridium aquilinum* grown on Cu-contaminated soils accumulated less Cu in plant tissues at elevated levels of CO_2 than at ambient CO_2", and by Li *et al*. (2010), who also "found that elevated levels of CO_2 diluted [rice] grain Cd concentration."

Tukaj *et al*. (2007) note cadmium has been demonstrated to cause "inhibition or inactivation of many enzymes, thereby disturbing the growth, respiration, or photosynthesis in plant cells and algae (Tukendorf and Baszynski, 1991; Sanita di Toppi and Gabbrielli, 1999; Prasad *et al*., 2001; Faller *et al*., 2005)." The four Polish scientists grew the unicellular green alga *Scenedesmus armatus* for periods of one, two, and three days in batch cultures that contained a 93μM concentration of cadmium and were continuously bubbled with air of either 0.1% or 2% (v/v) CO_2—equivalent to approximately 1,000 and 20,000 ppm CO_2, respectively—while making a number of measurements of algal properties and physiological processes.

The researchers found the density of the cultures grown for three days at 2% CO_2 "was markedly higher in comparison to cultures grown at 0.1% CO_2 concentration mainly due to the growth rate acceleration during the first day of culture." After 24 hours of cadmium exposure, for example, "growth was inhibited to about 49% at 0.1% CO_2, whereas at 2% CO_2 only to about 74% of the controls." In addition, "cadmium inhibited the rate of oxygen evolution (70% of control) of cells cultured at 0.1% CO_2 [but] had no effect on the rate of oxygen evolution of cells cultured at 2% CO_2."

The researchers state their results suggest the protective mechanism(s) directed against cadmium was (were) "more efficient in algae cultured under elevated CO_2 than algae cultured under low level of CO_2." They also note "the main detoxifying strategy of plants contaminated by heavy metals is the production of phytochelatins (PCs)," as described by Cobbett (2000), and they report "cells grown at 2% CO_2—after 24 hours of exposure—produced much more PCs than cells cultured at 0.1% CO_2." Their data indicate the CO_2-induced phytochelatin enhancement of their study was more than tenfold. They conclude, "algae living in conditions of elevated CO_2 are better protected against cadmium than those at ordinary CO_2 level."

Taken together, the studies reviewed here bode well for the ability of plants in a CO_2-enriched environment to better deal with the problem of heavy metal soil toxicity.

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3.4 Herbivory

By itself, a rising atmospheric CO_2 concentration may reduce the frequency and severity of pest outbreaks detrimental to agriculture, without seriously affecting herbivorous organisms found in natural ecosystems.

In addition, specific genetic alterations to crop plants may increase their resistance to assaults of insect pests, allow them to better bear the consequences of possible future increases in seasonal maximum air temperatures, and help them take advantage of the positive effects of atmospheric CO_2 enrichment on various plant properties and processes. At the same time, the elevated CO_2 would reduce the severity of possible negative effects that could arise from the escape of transplanted genes into the natural environment.

3.4.1 Herbaceous Plants

- Rising atmospheric CO_2 concentrations may reduce the frequency and severity of pest outbreaks detrimental to agriculture, without seriously impacting herbivorous organisms found in natural ecosystems.

Kerslake *et al*. (1998) grew five-year-old heather (*Calluna vulgaris*) plants collected from a Scottish moor in open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 600 ppm. Twice during the study, they allowed larvae of the destructive winter moth *Operophtera brumata*—whose outbreaks periodically cause extensive damage to heather moorland—to feed on current-year shoots. Feeding on the high-CO_2-grown foliage did not affect larval growth rates, development, or final pupal weights; nor was moth survivorship significantly altered. The three researchers conclude their study provides "no evidence that increasing atmospheric CO_2 concentrations will affect the potential for outbreak of *Operophtera brumata* on this host."

Newman *et al*. (1999) inoculated tall fescue (*Festuca arundinacea*) plants growing in open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm with bird cherry-oat aphids (*Rhopalosiphum padi*). After nine weeks, the plants growing in the CO_2-enriched air had experienced a 37% increase in productivity and were covered with far fewer aphids than the plants growing in ambient air. The result was a "win" for the favored plants and a "loss" for the destructive insects.

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

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

Joutei *et al*. (2000) grew bean (*Phaseolus vulgaris*) plants in controlled environments kept at atmospheric CO_2 concentrations of 350 and 700 ppm, into which they introduced the destructive agricultural mite *Tetranychus urticae*. They found female mites produced 34% and 49% fewer offspring in the CO_2-enriched chambers in their first and second generations, respectively. These reductions in the reproductive success of this mite, which attacks more than 150 crop species worldwide, has important agricultural implications in terms of crop production.

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

Coviella and Trumble (2000) determined toxins produced by *Bacillus thuringiensis* (Bt)—which are applied to crop plants by spraying as a means of combating various crop pests—were "more efficacious" in cotton grown in an elevated CO_2 environment than in ambient air, an important benefit for modern agriculture. In addition, Coviella *et al*. (2000) write, "elevated CO_2 appears to eliminate differences between transgenic [Bt-containing] and nontransgenic plants for some key insect developmental/fitness variables including length of the larval stage and pupal weight," which could prove significant for nature in the event of inadvertent Bt gene transference to wild relatives of transgenic crop lines.

Barbehenn *et al*. (2004b) note increases in the air's CO_2 content typically lead to greater decreases in the concentrations of nitrogen and, therefore, protein in the foliage of C_3 as compared to C_4 grasses, citing Wand *et al*. (1999). Barbehenn *et al*. write, "it has been predicted that insect herbivores will increase their feeding damage on C_3 plants to a greater extent than on C_4 plants (Lincoln *et al*., 1984, 1986; Lambers, 1993)." The three researchers grew *Lolium multiflorum* Lam. (Italian ryegrass, a common C_3 pasture grass) and *Bouteloua curtipendula* (Michx.) Torr. (sideoats gramma, a native C_4 rangeland grass) in chambers maintained at either the ambient atmospheric CO_2 concentration of 370 ppm or 740 ppm for two months. They allowed newly molted sixth instar larvae of *Pseudaletia unipuncta* (a grass-specialist noctuid) and *Spodoptera frugiperda* (a generalist noctuid) to feed on the grasses' foliage.

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

Barbehenn *et al*. conclude "there will not be a single pattern that characterizes all grass feeders" with respect to their feeding preferences and developmental responses under conditions where certain C_3 plants may experience foliar protein concentrations lower than those they exhibit today, nor will the changes that may occur necessarily impede herbivore development or damage the health and vigor of their host plants.

Barbehenn *et al*. (2004a) fed some of the identical foliage of the same experiment to grasshopper (*Melanoplus sanguinipes*) nymphs reared to the fourth instar stage. They note "*M. sanguinipes* did not significantly increase its consumption rate when feeding on the C_3 grass grown under elevated CO_2," which they say implies "post-ingestive mechanisms enable these grasshoppers to compensate for variable nutritional quality in their host plants." They further suggest some of these post-ingestive responses may include "changes in gut size, food residence time, digestive enzyme levels, and nutrient metabolism (Simpson and Simpson, 1990; Bernays and Simpson, 1990; Hinks *et al*., 1991; Zanotto *et al*., 1993; Yang and Joern, 1994a,b)." If anything, *M. sanguinipes* growth rates were increased, perhaps by as much as 12%, when they fed on the C_3 foliage produced in the CO_2-enriched, as compared to the ambient-air treatment.

Therefore, just as was found in Barbehenn *et al*.

(2004b), the CO_2-induced decrease in leaf protein concentration observed in this study did not induce an increase in consumption in the C_3 plant studied, nor did it reduce the growth rate of the herbivore studied. Therefore, the scientists state, "although compensatory feeding was commonly observed in early studies [of this subject], the absence of compensatory feeding on C_3 plants grown under elevated CO_2 has since been observed frequently among herbivorous insects (Bezemer and Jones, 1998)."

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

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

Ayres *et al.* (2008) reported the responses of belowground nematode herbivores to atmospheric CO_2 enrichment to approximately 350 ppm above ambient in experiments conducted on three grassland ecosystems in Colorado and California (USA) and Montpellier, France. They note "soil moisture increased in response to elevated CO_2 in the California, Colorado, and French stud[ies] (Hungate *et al*., 1997; Nijs *et al*., 2000; Morgan *et al*., 2004)." They also found "elevated CO_2 increased root biomass by approximately 3–32% in the first 5 years of the Coloradoan study (Pendall *et al*., 2004), by 23% after 6 years in the Californian study (Rillig *et al*., 1999), and by 31% after 6 months in the French study (Dhillion *et al*., 1996)." Regarding nematodes, they add, "CO_2 enrichment did not significantly affect the family richness, diversity, or PPI [plant parasitic nematode index] of herbivorous nematodes in the Colorado, California, or French study," noting "in each experiment, neutral effects were the most frequent response to CO_2 enrichment." The seven scientists conclude, "one consequence of increased root production, without changes in belowground herbivore populations, might be greater plant inputs to soil," which "may lead to greater soil organic matter pools in grassland ecosystems, potentially enhancing soil carbon sequestration."

Lau *et al.* (2008) measured the amounts of herbivore and pathogen damage done to the common prairie legume *Lespedeza capitata* growing in ambient and elevated (560 ppm) CO_2 treatments in the seventh and eighth years (2004 and 2005) of the BioCON study (Reich *et al*., 2001) conducted at the Cedar Creek Natural History Area in Minnesota (USA), where the CO_2 treatments were applied during the daylight hours of each growing season. In this setting, three types of pests inflicted herbivore damage—generalist chewers (primarily grasshoppers), *Pachyschelus laevigatus* (Coleoptera: *Buprestidae*), and *Tortriedon* sp. (Lepidoptera)—and pathogen damage was caused by *Pythium* or *Fusarium* spp.

Lau *et al.* say they detected "no evidence that the CO_2 treatments affected herbivore damage." As to pathogen damage, they found disease incidence "was lower in the elevated CO_2 environment, although this difference [10% less in 2004 and 53% less in 2005] was statistically significant only in 2005 ($P < 0.01$)." Therefore, and because "disease caused major reductions in reproductive output," the five researchers write, "the effects of CO_2 on disease incidence may be important for *L. capitata* evolution and population dynamics," and this phenomenon should significantly benefit this species in a high-CO_2 environment. In addition, they note Strengbom and Reich (2006), "working in the same experimental site ... also found that elevated CO_2 ... reduced disease incidence on *Solidago rigida*."

Coll and Hughes (2008) describe their work as "the first study that measured the effect of global atmospheric change on an omnivorous consumer," exploring the impacts of elevated atmospheric CO_2 on the behavior and performance of an omnivorous bug (*Oechalia schellenbergii*, Heteroptera: Pentatomidae) and its prey, a polyphagous chewing herbivorous pest (*Helicoverpa armigera*; Lepidoptera: Noctuidae), feeding on pea (*Pisum sativum*) foliage grown in controlled-environment cabinets maintained at atmospheric CO_2 concentrations of either 360 or 700 ppm. They found the *H. armigera* pests that fed on the elevated CO_2-grown pea plants were significantly smaller than those that fed on the ambient CO_2-grown pea plants, and the bigger *O. schellenbergii* bugs that fed on them "performed best when fed larvae from the elevated-CO_2 treatment," because the prey of that treatment "were smaller and thus easier to subdue." Only 13.3% of the predation attempts made on the larvae fed ambient-CO_2-grown foliage were successful, as compared to 78.2% for the larvae fed elevated-CO_2-grown foliage.

The two researchers conclude "elevated CO_2 may benefit generalist predators through increased prey vulnerability, which would put pest species under higher risk of predation." Consequently, and "since omnivory is widespread in agroecosystems," they argue "yield loss to most pest species will be lower under elevated atmospheric CO_2 levels, compared to the current condition."

The majority of evidence to date suggests rising atmospheric CO_2 concentrations may reduce the frequency and severity of pest outbreaks detrimental to agriculture, without seriously impacting herbivorous organisms found in natural ecosystems.

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3.4.2 Transgenic Plants

- Specific genetic alterations to crop plants may improve their ability to withstand the assaults of insects pests, bear the consequences of possible future increases in seasonal maximum air temperatures, and take advantage of the positive effects of atmospheric CO_2 enrichment on various plant properties and processes. Meanwhile, elevated CO_2 reduces the severity of possible negative effects that could arise from the escape of transplanted genes into the natural environment.

Toxins produced by *Bacillus thuringiensis* (Bt) supplied to crops via foliar application have been used as a means of combating crop pests for well over half a century. The effectiveness of this management technique depends primarily on the amount of Bt-produced toxins ingested by targeted insects. This section examines how atmospheric CO_2 enrichment might impact this phenomenon.

If atmospheric CO_2 concentrations are high but soil nitrogen levels are low, foliar concentrations of nitrogen are generally reduced from what they are at ambient CO_2 concentrations, suggesting insects would have to eat more foliage to get their normal requirement of nitrogen for proper growth and development in CO_2-enriched air. By consuming more foliage, the insects also would ingest more Bt-produced toxins, and would thus be more severely impacted by those substances.

To test this hypothesis, Coviella and Trumble (2000) grew cotton plants in each of six Teflon-film chambers in a temperature-controlled greenhouse, where three of the chambers were maintained at an atmospheric CO_2 concentration of 370 ppm and three were maintained at 900 ppm CO_2. In addition, half of the plants in each chamber were given high levels of nitrogen (N) fertilization, and half received low levels (30 vs. 130 mg N/kg soil/week). After 45 days of growth under these conditions, the researchers removed leaves from the plants and dipped them in a Bt solution, after which known amounts of treated leaf material were fed to *Spodoptera exigua* larvae and the responses measured and analyzed.

The two researchers determined the plants grown in the elevated CO_2 chambers did indeed have significantly lower foliar nitrogen concentrations than those grown in the ambient CO_2 chambers under the low N fertilization regime, but this was not the case under the high N regime. They also discovered older larvae fed with foliage grown in elevated CO_2 with low N fertilization consumed significantly more plant material than insects fed with foliage grown in ambient CO_2; but again, they found no differences with high N fertilization. Finally, and "consistent with the effect of higher Bt toxin intake due to enhanced consumption," they found "insects fed on low N plants had significantly higher mortality in elevated CO_2." They identified no such effect in the high N treatment. Consequently, with respect to pest management using Bt-produced toxins supplied to crops via foliar application, Coviella and Trumble conclude "increasing atmospheric CO_2 is making the foliar applications more efficacious."

Coviella *et al.* (2000) addressed what happens to transgenic plants into which the Bt gene for producing the toxin has been artificially inserted. They grew cotton plants in 12 Teflon-film chambers in a temperature-controlled greenhouse, where six chambers were maintained at an atmospheric CO_2 concentration of 370 ppm and six were maintained at 900 ppm CO_2. Half of the cotton plants in each of these chambers were of a transgenic line containing the Bt gene for the production of the Cry1Ac toxin, which is mildly toxic for *Spodoptera exigua*, and the other half were of a near isogenic line without the Bt gene. Half of the plants in each chamber received low and high levels of N fertilization. Between 40 and 45 days after leaves emerged, researchers removed leaves from the plants and fed them to the *S. exigua* larvae, measuring and analyzing a number of larval responses and various leaf properties.

They found the low-N plants in the elevated CO_2 treatment had lower foliar N concentrations than the low-N plants in the ambient CO_2 treatment, and the transgenic plants from the low-N, high CO_2 treatment produced lower levels of Bt toxin than the transgenic plants from the low-N, ambient CO_2 treatment. The high level of N fertilization only partially compensated for the latter high-CO_2 effect, and in the ambient CO_2 treatment there was also a significant increase in days to pupation for insects fed transgenic plants.

This difference was not evident in elevated CO_2. Pupal weight in ambient CO_2 was significantly higher in non-transgenic plants, and again, this difference was not observed in elevated CO_2.

The three researchers write, "these results support the hypothesis that the lower N content per unit of plant tissue caused by the elevated CO_2 will result in lower toxin production by transgenic plants when nitrogen supply to the plants is a limiting factor." They also note "elevated CO_2 appears to eliminate differences between transgenic and non-transgenic plants for some key insect developmental/fitness variables including length of the larval stage and pupal weight."

These findings suggest, in the case of inadvertent Bt gene transference to wild relatives of transgenic crop lines, elevated levels of atmospheric CO_2 will tend to negate certain of the negative effects the wayward genes might otherwise inflict. The rise in the air's CO_2 content could therefore constitute a buffer against this potential outcome.

Coviella *et al.*'s results also suggest transgenic crops designed to produce Bt-type toxins may become less effective in carrying out the objectives of their design as the air's CO_2 content rises. Coupling this possibility with the fact the foliar application of *Bacillus thuringiensis* to crops should become even more effective in a higher-CO_2 world, as Coviella and Trumble found, it can be argued the implantation of toxin-producing genes in crops is not viable in the face of the rise in the air's CO_2 content, which reduces that technique's effectiveness at the same time it increases the effectiveness of direct foliar applications.

Although it is difficult to predict the future of genetic modification of crops for pesticidal purposes, it is useful to know the rise in the atmosphere's CO_2 concentration will help both nature and agriculture, whatever the outcome of the current debate.

In a study of three different types of rice—a wild type (WT) and two transgenic varieties, one with 65% wild-type rubisco (AS-77) and one with 40% wild-type rubisco (AS-71)—Makino *et al.* (2000) grew plants from seed for 70 days in growth chambers maintained at 360 and 1,000 ppm CO_2. They harvested the plants and determined their biomass, finding the mean dry weights of the WT, AS-77, and AS-71 varieties grown in air of 360 ppm were, respectively, 5.75, 3.02, and 0.83 g. In air of 1,000 ppm CO_2, corresponding mean dry weights were 7.90, 7.40, and 5.65 g. Consequently, although the growth rates of the genetically engineered rice plants were far inferior to the wild type when grown in normal air of 360 ppm CO_2 (with AS-71 producing less than 15% as much biomass as the wild type), when grown in air of 1,000 ppm CO_2 they experienced far greater CO_2-induced increases in growth: a 145% increase in the case of AS-77 and a 581% increase for AS-71. Thus, whereas the transgenic plants were highly disadvantaged in normal air of 360 ppm CO_2, they were found to be pretty much on an equal footing in highly CO_2-enriched air..

Chen *et al.* (2005) grew well-watered and well-fertilized plants of two varieties of cotton—one expressing Cry1A (c) genes from *Bacillus thuringiensis* and a non-transgenic cultivar from the same recurrent parent—in pots placed in open-top chambers maintained at either 375 or 750 ppm CO_2 in Sanhe County, Hebei Province, China, from planting in mid-May to harvest in October. During this period, they collected several immature bolls and analyzed them for various chemical characteristics, and they refrigerated others for later feeding to cotton bollworm larvae, whose growth characteristics they closely monitored. The five researchers found the elevated CO_2 treatment increased immature boll concentrations of condensed tannins by approximately 22% and 26% in transgenic and non-transgenic cotton, respectively. In addition, elevated CO_2 slightly decreased the body biomass of the cotton bollworms and reduced moth fecundity. The Bt treatment was even more effective in this regard, and the negative cotton bollworm responses were expressed most strongly in the combined Bt-high-CO_2 treatment. Chen *et al.* conclude the expected higher atmospheric CO_2 concentrations of the future will "either not change or only slightly enhance the efficacy of Bt technology against cotton bollworms."

Chen *et al.* (2007) report growing the same two cotton cultivars under the same conditions from the time of planting on 10 May 2004 until the plants were harvested in October, after which egg masses of the cotton bollworms were reared in a growth chamber under ambient-CO_2 conditions. They fed three successive generations of bollworms either transgenic or non-transgenic cotton bolls from plants grown in either ambient or twice-ambient atmospheric CO_2 concentrations, assessing a number of physiological characteristics of the bollworms. Chen *et al.* report "both elevated CO_2 and transgenic Bt cotton increased larval lifespan," but they decreased "pupal weight, survival rate, fecundity, frass output, relative and mean relative growth rates, and the efficiency of conversion of ingested and digested food." They write, “transgenic Bt cotton significantly decreased the population-trend index compared to non-transgenic cotton for the three successive bollworm generations, especially at elevated CO_2.”

The four researchers conclude the negative effects of elevated CO_2 on cotton bollworm physiology and population dynamics “may intensify through successive generations,” in agreement with the findings of Brooks and Whittaker (1998, 1999) and Wu *et al*. (2006). They conclude “both elevated CO_2 and transgenic Bt cotton are adverse environmental factors for cotton bollworm long-term population growth.”

Fu *et al*. (2008) note “heat stress is a major constraint to wheat production and negatively impacts grain quality, causing tremendous economic losses, and may become a more troublesome factor due to global warming.” They “introduced into wheat the maize gene coding for plastidal EF-Tu [protein synthesis elongation factor]” to assess “the expression of the transgene, and its effect on thermal aggregation of leaf proteins in transgenic plants,” and “the heat stability of photosynthetic membranes (thylakoids) and the rate of CO_2 fixation in young transgenic plants following exposure to heat stress.” They found “improved protection of leaf proteins against thermal aggregation, reduced damage to thylakoid membranes and enhanced photosynthetic capability following exposure to heat stress,” and these results “support the concept that EF-Tu ameliorates negative effects of heat stress by acting as a molecular chaperone.”

Fu *et al*. describe their work as “the first demonstration that a gene other than HSP [heat shock protein] gene can be used for improvement of heat tolerance,” noting it also indicates “the improvement is possible in a species that has a complex genome,” such as hexaploid wheat. They conclude their results “strongly suggest that heat tolerance of wheat, and possibly other crop plants, can be improved by modulating expression of plastidal EF-Tu and/or by selection of genotypes with increased endogenous levels of this protein.”

It appears specific genetic alterations to crop plants may improve their ability to withstand the assaults of insects pests, bear the consequences of possible future increases in seasonal maximum air temperatures, and take advantage of the positive effects of atmospheric CO_2 enrichment on various plant properties and processes. Elevated CO_2 reduces the severity of any negative effects that could arise from the escape of transplanted genes into the natural environment.

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3.4.3 Woody Plants

Data obtained from open experimental systems in the field suggest herbivore damage to trees may decrease in a CO_2-enriched environment. However, if the opposite circumstances were to occur, other evidence suggests air of higher CO_2 concentration would make trees more capable of surviving severe defoliation events. In addition, higher CO_2 concentrations tend to reduce fluctuating asymmetry in plant leaves, leading to more symmetrical leaves that are less susceptible to attacks by herbivores, because they are under less stress of both genetic and environmental origin than leaves growing in less-CO_2-enriched air.

3.4.3.1 Maple

- In contrast to the view herbivores will do more damage to trees, including maples, in CO_2-enriched air as a result of enhanced feeding on lower-quality foliage, data from open experimental systems suggest such damage may decrease in a CO_2-enriched environment. Evidence also suggests sugar maple may be more capable of surviving severe defoliation events that in the past have been implicated in the widespread decline of maples.

Insect pests have greatly affected trees in the past and likely will continue to do so in the future. The rise in the atmosphere's CO_2 concentration may affect this phenomenon. Here we review studies that have addressed this subject as it applies to three maple tree species.

Williams *et al.* (2003) studied *Acer rubrum* saplings beginning their fourth year of growth in open-top chambers maintained at four atmospheric CO_2/temperature combinations: ambient temperature, ambient CO_2; ambient temperature, elevated CO_2 (ambient + 300 ppm); elevated temperature (ambient + 3.5°C), ambient CO_2; and elevated temperature, elevated CO_2. They collected first instar gypsy moth larvae on various branches of the trees and observed their behavior. They report, "larvae feeding on CO_2-enriched foliage ate a comparably poorer food source than those feeding on ambient CO_2-grown plants, irrespective of temperature." Nevertheless, the "CO_2-induced reductions in foliage quality (e.g. nitrogen and water) were unrelated to insect mortality, development rate and pupal weight," and these and any other phytochemical changes that may have occurred "resulted in no negative effects on gypsy moth performance." They also write, "irrespective of CO_2 concentration, on average, male larvae pupated 7.5 days earlier and female larvae 8 days earlier at elevated temperature." They conclude the observed temperature-induced hastening of the insects' development would likely expose the trees to less predation and parasitism risk.

Hamilton *et al.* (2004) note many single-species investigations suggest increases in atmospheric CO_2 will increase herbivory (Bezemer and Jones, 1998; Cannon, 1998; Coviella and Trumble, 1999; Hunter, 2001; Lincoln *et al.*, 1993; Whittaker, 1999). However, because there are so many feedbacks and complex interactions among the numerous components of real-world ecosystems, they warn one ought not put too much faith in these predictions until relevant real-world ecosystem-level experiments have been completed.

Hamilton *et al.* "measured the amount of leaf tissue damaged by insects and other herbivorous arthropods during two growing seasons in a deciduous forest understory continuously exposed to ambient (360 ppm) and elevated (560 ppm) CO_2 conditions." This forest, at the Duke Forest FACE facility near Chapel Hill, North Carolina (USA), was dominated by loblolly pine trees that accounted for fully 92% of the ecosystem's total woody biomass. It contained 48 species of other woody plants (trees, shrubs, and vines) that had naturally established themselves in the forest's understory. Hamilton *et al.* quantified the loss of foliage due to herbivory experienced by three deciduous tree species, one of which was *Acer rubrum*. They report, "we found that elevated CO_2 led to a trend toward reduced herbivory in [the] deciduous understory in a situation that included the full complement of naturally occurring plant and insect species." In 1999, for example, they determined "elevated CO_2 reduced overall herbivory by more than 40%," and in 2000 they say they observed "the same pattern and magnitude of reduction."

Hamilton *et al.* say they "found no evidence for significant changes in leaf nitrogen, C/N ratio, sugar, starch or total leaf phenolics in either year of [the] study." They note these findings agree with those of "another study performed at the Duke Forest FACE site that also found no effect of elevated CO_2 on the chemical composition of leaves of understory trees (Finzi and Schlesinger, 2002)."

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

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

Knepp *et al*. (2005) quantified leaf damage caused by insects chewing on saplings of seven species (including *Acer rubrum*) in 2001, 2002, and 2003, and five additional species (including *Acer barbatum*) in 2001 and 2003, also at the Duke Forest FACE site. They found, “across the seven species measured in each of the three years, elevated CO_2 caused a reduction in the percentage of leaf area removed by chewing insects,” such that “the percentage of leaf tissue damaged by insect herbivores was 3.8% per leaf under ambient CO_2 and 3.3% per leaf under elevated CO_2.” The greatest effects occurred in 2001, when “across 12 species the average damage per leaf under ambient CO_2 was 3.1% compared with 1.7% for plants under elevated CO_2,” which is “indicative of a 46% decrease in the total area and total mass of leaf tissue damaged by chewing insects in the elevated CO_2 plots.”

Knepp *et al*. write, “given the consistent reduction in herbivory under high CO_2 across species in 2001, it appears that some universal feature of chemistry or structure that affected leaf suitability was altered by the treatment.” They also note “forest herbivory may decrease under elevated CO_2 because of a decline in the abundance of chewing insects,” citing Stiling *et al*. (2003) and noting “slower rates of development under elevated CO_2 prolongs the time that insect herbivores are susceptible to natural enemies, which may be abundant in open-top chambers and FACE experiments but absent from greenhouse experiments.” In addition, they suggest “decreased foliar quality and increased per capita consumption under elevated CO_2 may increase exposure to toxins and insect mortality,” also noting “CO_2-induced changes in host plant quality directly decrease insect fecundity,” citing Coviella and Trumble (1999) and Awmack and Leather (2002).

Knepp *et al*. conclude, “in contrast to the view that herbivore damage will increase under elevated CO_2 as a result of compensatory feeding on lower quality foliage, our results and those of Stiling *et al*. (2003) and Hamilton *et al*. (2004) in open experimental systems suggest that damage to trees may decrease.”

Kruger *et al*. (1998) explored the consequences of an *increase* in herbivore-induced damage in a future CO_2-enriched world, although that is unlikely to occur. They grew well-watered and well-fertilized one-year-old *Acer saccharum* saplings in glasshouses maintained at atmospheric CO_2 concentrations of either 356 or 645 ppm for 70 days, to determine the effects of elevated CO_2 on photosynthesis and growth. On the 49th day of differential CO_2 exposure, they removed 50% of the saplings’ leaf area from half of the trees in order to study the impact of concomitant simulated herbivory. They found the 70-day CO_2 enrichment treatment increased the total dry weight of the non-defoliated seedlings by about 10%. When the trees were stressed by simulated herbivory, the CO_2-enriched maples produced 28% more dry weight over the final phase of the study than the maples in the ambient-air treatment did. Kruger *et al*. conclude that in a high-CO_2 environment “sugar maple might be more capable of tolerating severe defoliation events which in the past have been implicated in widespread maple declines.”

These studies indicate maple trees—and probably many, if not most, other trees—may fare much better against the periodic assaults of leaf-damaging herbivores as the air’s CO_2 content continues to rise.

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3.4.3.2 Oak

- Research suggests various insect pests will do decreasing amounts of damage to oak trees as the air's CO_2 concentration rises.

In order to determine whether the ongoing rise in the air's CO_2 content will exacerbate or ameliorate herbivore damage to oak trees, Dury *et al*. (1998) grew four-year-old *Quercus robur* seedlings in pots in greenhouses maintained at ambient and twice-ambient atmospheric CO_2 concentrations in combination with ambient and elevated (ambient plus 3°C) air temperatures for approximately one year, to study the interactive effects of elevated CO_2 and temperature on leaf nutritional quality. The researchers determined the elevated temperature treatment significantly reduced leaf palatability, and leaf toughness increased as a consequence of temperature-induced increases in condensed tannin concentrations. In addition, the imposition of higher temperatures significantly reduced leaf nitrogen content, as did elevated CO_2.

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

They discovered total leaf miner densities were 38% less on the foliage of trees growing in CO_2-enriched air than on that of trees growing in ambient air. Atmospheric CO_2 enrichment consistently reduced the absolute numbers of the study's six leaf miner species. At the same time, the elevated CO_2 treatment increased the leaf area consumed by the less-abundant herbivore miners by approximately 40% relative to the areas mined by the more-abundant herbivores present on the foliage exposed to ambient air. Despite this increase in feeding, the leaf miners in the CO_2-enriched chambers experienced significantly greater mortality than those in the ambient-air chambers. And although CO_2-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 CO_2-enriched foliage.

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

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

The researchers write, "both the abundance of the guild of leafmining lepidopterans and damage caused by leaf chewing insects attacking myrtle oak were depressed in elevated CO_2." Leafminer abundance was 44% lower ($P = 0.096$) in the CO_2-enriched chambers compared to the ambient-air chambers, and the abundance of leaves suffering chewing damage was 37% lower ($P = 0.072$) in the CO_2-enriched air. Myrtle oak trees growing in their natural habitat likely will suffer far less damage from both leaf miners and leaf chewers as the air's CO_2 concentration rises in the years ahead.

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

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

In one final study of the Florida scrub-oak ecosystem, Hall *et al.* (2005a) examined the effects of an extra 350 ppm of CO_2 on litter quality, herbivore activity, and their interactions. Over the three years of this experiment (2000, 2001, 2002), they determined "changes in litter chemistry from year to year were far larger than the effects of CO_2 or insect damage, suggesting that these may have only minor effects on litter decomposition." The one exception to this finding, they write, was "condensed tannin concentrations[, which] increased under elevated CO_2 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 CO_2 enrichment, as best as can be determined from their bar graphs.

The five researchers also report "lepidopteran larvae can exhibit slower growth rates when feeding on elevated CO_2 plants (Fajer *et al.*, 1991) and become more susceptible to pathogens, parasitoids, and predators (Lindroth, 1996; Stiling *et al.*, 1999)," noting further that at their field site, "which hosts the longest continuous study of the effects of elevated CO_2 on insects, herbivore populations decline[d] markedly under elevated CO_2 (Stiling *et al.*, 1999, 2002, 2003; Hall *et al.*, 2005b)."

The evidence accumulated to date with respect to herbivory in oak trees indicates various insect pests will do decreasing amounts of damage to such trees as the air's CO_2 concentration climbs ever-higher.

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3.4.3.3 Miscellaneous

- Numerous studies of numerous insect pests of numerous species of trees indicate atmospheric CO_2 enrichment may contribute to reduced herbivory in forest ecosystems.

Insect pests have had enormous impacts on Earth's trees and shrubs in the past. Will the anticipated increase in the atmosphere's CO_2 concentration exacerbate or ameliorate their effects? This section describes and discusses the results of several studies that address this question.

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

Gleadow *et al*. (1998) grew eucalyptus seedlings in glasshouses maintained at 400 and 800 ppm CO_2 for six months, observing biomass increases of 98% and 134% in high and low nitrogen treatments, respectively. They also studied a sugar-based compound called prunasin, which produces cyanide in response to tissue damage caused by foraging herbivores. Although elevated CO_2 caused no significant change in leaf prunasin content, the proportion of nitrogen allocated to prunasin increased by approximately 20% in the CO_2-enriched saplings, suggesting a potential for increased prunasin had the eucalyptus saplings been under attack by herbivores.

In a study of simulated herbivory, Kruger *et al*. (1998) grew seedlings of one-year-old maple (*Acer saccharum*) and two-year-old aspen (*Populus tremuloides*) trees in glasshouses with atmospheric CO_2 concentrations of 356 and 645 ppm for 70 days. At the 49-day point of the experiment, half of the leaf area on half of the trees in each treatment was removed, and this defoliation caused the final dry weights of both species growing in ambient air to decline. In the CO_2-enriched glasshouse, on the other hand, the defoliated maple trees ended up weighing just as much as the non-defoliated maple trees. The defoliated aspen trees ended up weighing a little less, but not significantly less, than their non-defoliated counterparts. Thus, atmospheric CO_2 enrichment improved both species' ability to recover from the debilitating effect of leaf removal, suggesting a future world of higher atmospheric CO_2 concentration may make these trees better able to deal with physical damage inflicted on them by herbivores.

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

Hattenschwiler and Schafellner (1999) grew seven-year-old spruce (*Picea abies*) trees at atmospheric CO_2 concentrations of 280, 420, and 560 ppm and various nitrogen deposition treatments for three years, allowing nun moth larvae to feed on current-year needles for 12 days. Larvae placed on the CO_2-enriched foliage consumed less needle biomass than those placed on the ambient-grown foliage, regardless of nitrogen treatment. The larvae feeding on needles produced by the CO_2-enriched trees attained an average final biomass only two-thirds of that attained by the larvae that fed on needles produced at 280 ppm CO_2. The nun moth is a powerful defoliator that resides in most parts of Europe and East Asia between 40 and 60°N latitude; the results of this study suggest the rise in the air's CO_2 content likely will lead to significant reductions in damage to spruce and other coniferous trees by this insect pest.

Parsons *et al*. (2003) grew two-year-old saplings of paper birch (*Betula papyrifera* Marsh.) and three-year-old saplings of sugar maple (*Acer saccharum* Marsh.) in well-watered and -fertilized 16-L pots from early May until late August in glasshouse rooms maintained at either 400 or 700 ppm CO_2. The whole-plant biomass of paper birch was increased by 55% in the CO_2-enriched rooms, and the biomass of sugar maple was increased by 30%. Condensed tannins were unaltered in sugar maple but increased by 27% in paper birch in the CO_2-enriched treatment. The three researchers note, "the higher condensed tannin concentrations present in the birch fine roots may offer these tissues greater protection against soil-borne pathogens and herbivores." CO_2-induced increases in fine root concentrations of total phenolics and condensed tannins also have been observed in warm temperate conifers by King *et al*. (1997), Entry *et al*. (1998), Gebauer *et al*. (1998), and Runion *et al*. (1999), as well as in cotton by Booker (2000).

Holton *et al*. (2003) reared parasitized and non-parasitized forest tent caterpillars (*Malacosoma disstria*) on two quaking aspen (*Populus tremuloides*) genotypes (216, which is O_3-tolerant, and 259, which is O_3-sensitive) alone and in combination at the Aspen FACE site in northern Wisconsin (USA), in plots exposed to ambient air; ambient air + 200 ppm extra CO_2; ambient air + 50% extra ozone; and ambient air + 200 ppm extra CO_2 and 50% extra O_3. The researchers found "elevated CO_2 had little effect on both primary and secondary metabolites of aspen" and "had few biologically significant effects on forest tent caterpillar performance." Elevated O_3 altered foliar composition much more than did elevated CO_2, and it improved tent caterpillar performance under ambient CO_2 conditions, but not in CO_2-enriched air. The extra CO_2 of this study totally thwarted the positive impact of the extra O_3 on caterpillar performance, thus possibly eliminating a major negative consequence for the trees.

Kuokkanen *et al*. (2003) grew two-year-old birch (*Betula pendula* Roth) seedlings in ambient air of 350 ppm CO_2 or air enriched to a CO_2 concentration of 700 ppm under conditions of either ambient temperature or ambient temperature plus 3°C for one full growing season in the field in closed-top chambers at the Mekrijarvi Research Station of the University of Joensuu in eastern Finland. During the middle of the summer, when carbon-based secondary compounds of birch leaves are fairly stable, they picked several leaves from each tree and determined their condensed tannin concentrations, along with the concentrations of other physiologically important substances.

The concentration of total phenolics, condensed tannins, and their derivatives significantly increased in the birch leaves produced in the CO_2-enriched air, as also was observed by Lavola and Julkunen-Titto (1994), Williams *et al*. (1994), Kinney *et al*. (1997), Bezemer and Jones (1998), and Kuokkanen *et al*. (2001). The extra 350 ppm of CO_2 nearly tripled condensed tannin concentrations in the ambient-temperature air, and it increased their concentrations in the elevated-temperature air by a factor greater than 3.5. The presence of condensed tannins in leaves tends to greatly reduce methane emissions from ruminants that feed on them, which in turn reduces the supposed global warming impact.

Mattson *et al*. (2004) write, "although there have been many studies on the effects of elevated CO_2 on the interaction between plants and their insect herbivores (see Bezemer and Jones, 1998; Hunter, 2001), comparable studies on mammalian herbivores are lacking altogether, even though mammals play important roles in dynamics of many ecosystems (McNaughton and Sabuni, 1988; Pastor and Naiman, 1992)." Mattson *et al*. grew one-year-old seedlings of silver birch (*Betula pendula*) in closed-top chambers for one summer and autumn in pots containing an unfertilized commercial peat maintained at three different soil nitrogen (N) levels (low = 0 kg N ha^{-1}, medium = 150 kg N ha^{-1}, high = 500 kg N ha^{-1}) and two temperature (T) levels (ambient and ambient + 3°C) in air of either 362 or 700 ppm CO_2 concentration. They carried out feeding trials with caged Eurasian hares (*Lepus timidus*) and performed chemical analyses of the tops of the seedlings and the basal parts of their stems.

In a second experiment, they grew paper birch (*Betula papyrifera*) from seed for two 140-day growing seasons in well-watered and well-fertilized pots placed in FACE rings maintained at atmospheric CO_2 concentrations of either 362 or 562 ppm, after which (in an unplanned aspect of the study) North American eastern cottontail rabbits (*Sylvilagus floridanus*) fed *ad libitum*, consuming bark tissue down to the wood and scoring it, on the basal third of the seedlings. These tissues were tested for the presence of various herbivore-deterring chemical constituents.

"As expected," the six scientists write, "elevated CO_2 substantially increased the above-ground woody biomass growth of both paper birch (63%) and silver birch (21%)." In addition, noting "numerous studies have shown that elevated atmospheric CO_2 often, but not always, elicits increases in carbon partitioning to carbon-based secondary plant compounds," which often act as deterrents to herbivory, they say their findings "confirm this general pattern in silver and paper birch." Finally, they report high CO_2 reduced hare feeding on silver birch shoots by as much as 48%, and it reduced rabbit feeding on paper birch stems by about 51%. Neither temperature nor severe early season defoliation (another treatment) affected tree resistance against these mammalian herbivores.

Calling the anti-herbivory effect of elevated CO_2 "remarkably strong," and noting rabbits "overwhelmingly preferred ambient CO_2 plants," Mattson *et al.* say their data "clearly suggest that the defensive biochemistry of paper birch twigs as well as the main stem were [positively] altered as the result of elevated CO_2."

Noting the "detrimental effects of ozone on plants are well known," and "carbon dioxide generally affects trees in opposite ways to ozone," Valcama *et al.* (2007) conducted a literature review they describe as "the first quantitative analysis of the interactive effects of elevated O_3 and elevated CO_2 on tree chemistry and herbivore performance," based on the results of "63 studies conducted on 22 tree species and 10 insect herbivore species and published between 1990 and 2005."

With respect to ways elevated O_3 may benefit insect herbivores that tend to damage trees, Valkama *et al.* say they determined "elevated O_3 significantly shortened development time of insect herbivores [when they are exposed and vulnerable to attack by various enemies] and increased their pupal mass in the overall dataset." In addition, they report the "relative growth rate of chewers was significantly increased by 3.5% under elevated O_3." However, "these effects were counteracted by elevated CO_2," such that "elevated O_3 in combination with CO_2 had no effect on herbivore performance"—except when elevated CO_2 was added to the O_3-enriched air, it not only counteracted the O_3-induced increase in pupal biomass, it actually reduced it by 7% below ambient air.

Valkama *et al.*'s analysis of much of the pertinent experimental data obtained prior to 2006 suggests in the interactions between insect herbivores and trees, the rise in the air's CO_2 content likely plays an important role in negating, and in some cases even more than negating, the damage otherwise capable of being done to Earth's forests by insect pests. Subsequent research has continued to demonstrate these effects.

Huttunen *et al.* (2007) grew silver birch (*Betula pendula* Roth) seedlings in pots filled with peat at three levels of nitrogen (N) fertility—no N, moderate N (130 kg N ha^{-1}) and high N (270 kg N ha^{-1})—in climate-controlled closed-top chambers from mid-June to October 2002 at the Mekrijarvi Research Station of the University of Joensuu, Finland. The chambers were maintained at atmospheric CO_2 concentrations of either 360 or 720 ppm and at either ambient air temperatures or elevated air temperatures 2°C above ambient from June to August and 4°C above ambient for the remainder of the growing season. The researchers mimicked larval and adult leaf-feeding patterns exhibited during real-world defoliation by manually damaging the leaves of the seedlings by tearing off the apical halves of either 25% or 50% of all leaves greater than 1 cm in length on 1 July (mid-season) and again on 29 July (late-season). They determined total plant shoot and root biomass once the plants had gone dormant in October.

As best as can be determined from the six scientists' bar graphs of their results, and averaged over all three defoliation treatments, the elevated CO_2 treatment increased the biomass of the seedlings in the moderate and high-N fertility treatments much more than it increased the biomass of the seedlings in the no-N fertility treatment (29 and 30%, respectively, vs. 13%). The same was also true of the combined elevated CO_2 and elevated temperature treatment, where the corresponding treatment-induced biomass increases were 34 and 36% vs. 20%, suggesting the heightened temperatures tended to augment the beneficial effects of the elevated CO_2 treatment, with the greatest amplification being manifest in the no-N fertility treatment (54% vs. 17 and 20% in the moderate- and high-N treatments, respectively).

Averaged over all three N fertility treatments, the effect of the elevated CO_2 was to increase the plant biomass of the undefoliated seedlings by approximately 25%, the 25%-defoliated seedlings by 24%, and the 50%-defoliated seedlings by 22%. The effect of the combined elevated CO_2 and elevated temperature treatment was to increase the plant biomass of the same three categories of seedlings by approximately 31%, 30%, and 29%, respectively. Huttunen *et al*. conclude, "climatic change"—which they specifically defined to mean elevated atmospheric temperature and CO_2—"will have a positive impact on the compensatory ability of defoliated silver birch seedlings."

In another study conducted with the same trees under the same conditions, Huttunen *et al*. (2008) studied leaf palatability to adult blue alder leaf beetles (*Agelastica alni*). They periodically measured a host of seedling parameters related to plant chemical and morphological defense properties. The researchers' findings were varied and complex, but their most basic finding was that the blue alder leaf beetle's "total leaf consumption was higher under the ambient climatic conditions than under elevated temperature, elevated CO_2, or the combination of elevated temperature and CO_2."

Nabity *et al*. (2012) write, "arthropod herbivory can reduce plant productivity by removing photosynthetic leaf area," noting Zangerl *et al*. (2002), Aldea *et al*. (2005, 2006), and Patankar *et al*. (2011) indicate, in some cases, "damage to leaf surfaces causes a reduction in the quantum efficiency of photosystem II fluorescence, which is highly correlated with the rate of carbon assimilation." Working at the Aspen FACE site in north-central Wisconsin (USA), the four researchers studied how different types of herbivore damage (leaf-chewing, gall-forming, and leaf-folding) altered component processes of photosynthesis under both ambient and elevated (ambient + 200 ppm) atmospheric CO_2 concentrations in aspen (*Populus tremuloides*, genotype 216) trees, as well as how the damage caused by leaf-chewing insects impacted photosynthesis in birch (*Betula papyrifera*) trees.

The four researchers found "growth under elevated CO_2 reduced the distance that herbivore-induced reductions in photosynthesis propagated away from the point of damage in aspen and birch," leading them to conclude, "at least for these species," elevated CO_2 "may reduce the impact of herbivory on photosynthesis," a very positive development.

Hamilton *et al*. (2012) noted "the response of complex plant and animal communities to global change is highly variable (Tylianakis *et al*., 2008)," but "recent studies have documented that loss of foliage to arthropod herbivores decreases under elevated CO_2 in woody communities (Hamilton *et al*., 2004; Knepp *et al*., 2005; Stiling and Cornelissen, 2007)." They also note the fitness and in some cases population size of herbivorous insects may decline in communities exposed to elevated CO_2 (Hillstrom and Lindroth, 2008; Hillstrom *et al*., 2010)," although the "effects of elevated CO_2 on naturally-occurring arthropod assemblages have not yet been widely characterized."

Working at the Duke Forest FACE facility in the Piedmont region of North Carolina (USA)—where three 30-meter-diameter plots of an expansive stand of loblolly pine had their atmospheric CO_2 concentrations boosted by about 200 ppm, and where three other such plots were maintained at the normal ambient CO_2 concentration—Hamilton *et al*. counted the numbers of arthropods found in each of the six plots every two weeks throughout June and July of 2005, assigning them to different feeding guilds. In addition, they analyzed stable isotope data for spiders collected in the ambient and elevated CO_2 plots in order to determine the extent herbivorous prey species moved into and out of the elevated CO_2 plots.

The seven U.S. scientists write their isotopic data "gave no indication that the treatment plots represented a 'boundary' to the movement of insects." In addition, they determined there was no detectable effect of elevated CO_2 on the total number of individual arthropods in the two sets of treatment plots. However, they write, "there was an increase in the numbers of individuals collected in primarily predaceous orders (Araneae and Hymenoptera; from 60% to more than 150%) under elevated CO_2 and a decrease in the numbers in primarily herbivorous orders (Lepidoptera and Coleoptera; from -30 to -45%)." Hamilton *et al*. conclude "decreases in herbivorous arthropods and increases in predaceous arthropods may contribute to reduced herbivory under elevated CO_2 in forest systems."

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3.4.3.4 Fluctuating Asymmetry

- Higher concentrations of atmospheric CO_2 tend to reduce fluctuating asymmetry in plant leaves, leading to more symmetrical leaves that appear to be less susceptible to attacks by herbivores.

Fluctuating asymmetry (FA) is the term used to describe small variations from perfect symmetry in otherwise bilaterally symmetrical characters in an organism (Moller and Swaddle, 1997). It is thought to arise in consequence of developmental instability experienced during ontogeny that is caused by various stresses, including both genetic and environmental factors (Martel *et al*., 1999; Cornelissen and Stiling, 2005). It has been studied extensively in animals but less so in plants (Moller and Shykoff, 1999).

In the first study to address the effects of atmospheric CO_2 enrichment on leaf asymmetry and herbivore response, Cornelissen *et al*. (2004) studied native scrub-oak community at the Kennedy Space Center, Titusville, Florida (USA), which is dominated by myrtle oak (*Quercus myrtifolia*) and sand live oak (*Quercus geminata*), under atmospheric CO_2 concentrations of either 370 or 700 ppm. Based on measurements of distances from the leaf midrib to the left and right edges of the leaf at its widest point and leaf areas on the left and right sides of the leaf midrib, Cornelissen *et al*. determined "asymmetric leaves were less frequent in elevated CO_2, and, when encountered, they were less asymmetric than leaves growing under ambient CO_2." In addition, "*Q. myrtifolia* leaves under elevated CO_2 were 15.0% larger than in ambient CO_2 and *Q. geminata* leaves were 38.0% larger in elevated CO_2 conditions." They also report "elevated CO_2 significantly increased tannin concentration for both *Q. myrtifolia* and *Q. geminata* leaves," and "asymmetric leaves contained significantly lower concentrations of tannins than symmetric leaves for both *Q. geminata* and *Q. myrtifolia*."

Cornelissen *et al*. write, "a possible explanation for [reduced asymmetry in leaves under elevated CO_2] is the fact that, in contrast to other environmental stresses, which can cause negative effects on plant growth, the predominant effect of elevated CO_2 on plants is to promote growth with consequent reallocation of resources (Docherty *et al.*, 1996).” Another possibility, they say, “is the fact that CO_2 acts as a plant fertilizer,” and, as a result, “elevated CO_2 ameliorates plant stress compared with ambient levels of CO_2,” which is one of the well-documented biological benefits of atmospheric CO_2 enrichment documented by Idso and Idso (1994).

As to the ancillary finding of CO_2-induced increases in tannin concentrations in the leaves of both oaks (a mean increase of approximately 35% for *Q. myrtifolia* and 43% for *Q. geminata*), it should be noted this phenomenon may provide both species with greater protection against herbivores, and part of that protection may be associated with the observed CO_2-induced reductions in the amount and degree of asymmetry in the leaves of the CO_2-enriched trees. Consistent with this hypothesis, Stiling *et al.* (1999, 2003) found higher abundances of leaf miners in the leaves of the trees in the ambient CO_2 chambers, where asymmetric leaves were more abundant, and in the current study it was determined leaf miners attacked asymmetric leaves more frequently than would be expected by chance alone in both CO_2 treatments.

In further support of this CO_2-induced benefit, Cornelissen and Stiling (2005) evaluated patterns of asymmetry in 40 leaves from each of 30 trees of each of two species of oak—sand live oak (*Quercus geminata*) and turkey oak (*Q. laevis*)—at the University of South Florida Botanical Garden in Tampa, Florida (USA), well before any herbivores had begun to attack the trees that growing season. They examined patterns of leaf asymmetry, leaf quality, and herbivory for 30 individual trees of each of the two oak species from March to October of the same year.

The “before and after” measurements indicate differential herbivory patterns neither caused nor affected patterns of leaf FA. The authors write, “herbivores may use asymmetry as a cue to plant quality and suitable oviposition sites,” as plants with a higher percentage of asymmetric leaves were attacked more frequently by various leaf miners, as were leaves on the same plant more asymmetric. Cornelissen and Stiling report, “asymmetric leaves of both plant species exhibited better nutritional quality for herbivores than symmetric leaves,” with asymmetric leaves possessing “significantly lower concentrations of tannins [-22% for *Q. geminata* and -36% for *Q. laevis*] and higher nitrogen content [+8% for both species].”

Kaligaric *et al.* (2008) measured the degree of FA in “undamaged (not grazed, not visibly attacked by herbivores or pathogens) fully developed leaves” of the Mediterranean shrub *Myrtus communis* L. growing along an atmospheric CO_2 gradient (570, 530, 490, 450, 410, and 370 ppm) moving away from a natural CO_2 spring, “I Borboi,” near Lajatico (Pisa, Tuscany, Italy) at distances of 2, 18, 34, 50, 66, and 82 m, respectively, from the CO_2 source.

The four researchers report they found “a significant and negative correlation between CO_2 concentration and leaf FA,” such that “with increased CO_2 concentration the leaf FA decreased.” This result, they write, “confirms what was obtained by Cornelissen *et al.* (2004) on *Quercus myrtifolia* and *Quercus geminata* (in a short-term experiment).” In addition, they note “*Myrtus communis*, grown under elevated CO_2 concentration at ‘I Borboi,’ showed a reduction in xylem embolism and an increase in hydraulic efficiency (Tognetti *et al.*, 2001),” stating “improved water relations could represent a good explanation for the observed reduction in leaf FA [as the air’s CO_2 content increased].”

Kaligaric *et al.* conclude “adaptation and selection could explain the tendency towards decreased leaf FA in plants from the CO_2 spring relative to ambient conditions,” since “the more symmetrical leaves under long-term elevated CO_2 concentration were more developmentally stable in these conditions.”

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3.5 Iron Stress

- Atmospheric CO_2 enrichment can stimulate biomass production in both iron-sufficient and iron-deficient plants, and it increases internal iron (Fe) use efficiency, stimulates root growth, and increases root exudation of Fe-mobilizing phytosiderophores in sub-apical root zones, thereby increasing the competitiveness of plants with rhizosphere microorganisms in their quest for this trace element.

Little is known about the interaction of CO_2 and iron stress on the growth of plants; few researchers have investigated this topic. In one study, Haase *et al.* (2008) grew barley (*Hordeum vulgare* L. cv. Europa) plants from seed for four weeks—both hydroponically in nutrient solution having adequate or less-than-adequate iron (Fe) concentrations (+Fe and -Fe, respectively), as well as in rhizobox microcosms filled with soil under the same two conditions of iron availability—in controlled-environment chambers maintained at atmospheric CO_2 concentrations of either ambient CO_2 (400 ppm) or elevated CO_2 (800 ppm). They found the elevated atmospheric CO_2 treatment stimulated biomass production in both the Fe-sufficient and Fe-deficient barley plants, in both hydroponics and soil culture. They also discovered three CO_2-induced modifications in plant activity: "(i) increased internal Fe use efficiency, (ii) stimulation of root growth, and (iii) increased root exudation of Fe-mobilizing phytosiderophores in the sub-apical root zones."

Since phytosiderophores act as metal chelators that mobilize sparingly soluble inorganic forms of iron and zinc and make them more readily available to plants, the eight researchers suggest atmospheric CO_2 enrichment increases the competitiveness of plants such as barley with rhizosphere microorganisms in their quest for these often difficult-to-obtain trace elements, which helps to explain the strong growth response of barley to atmospheric CO_2 enrichment they observed, even when iron availability was low.

Jin *et al.* (2009) grew 20-day-old plants for an additional seven days in controlled-environment chambers maintained at atmospheric CO_2 concentrations of either 350 or 800 ppm in an iron (Fe)-sufficient medium with a soluble Fe source or under Fe-limited conditions in a medium containing the sparingly soluble hydrous Fe(III)-oxide. They found the elevated CO_2 increased plant growth in both the Fe-sufficient and Fe-limited media, with shoot fresh weight increasing by 22% and 44%, respectively, and root fresh weight increasing by 43% and 97%, respectively. Jin *et al*. report, "the elevated CO_2 under Fe-limited conditions enhance[d] root growth, root hair development, proton release, root FCR [ferric chelate reductase] activity, and expressions of LeFR01 and LeIRT1 genes [which respectively encode FCR and the Fe(II) transporter in tomato], all of which enable plants to access and accumulate more Fe." Also, as would be expected, "the associated increase in Fe concentrations in the shoots and roots alleviated Fe-deficiency-induced chlorosis."

Jin *et al.* state the bioavailability of iron to terrestrial plants "is often limited (Guerinot and Yi, 1994), particularly in calcareous soils, which represent 30% of the Earth's [land] surface (Imsande, 1998)." They conclude "Fe nutrition in plants is likely to be affected by the continued elevation of atmospheric CO_2, which, in turn, will affect crop production." As their work strongly suggests, those important effects should be highly beneficial, and Sasaki *et al*. (1998) suggest even wider biospheric benefits, demonstrating elevated CO_2 concentrations significantly enhanced both the ferric reductase activity and Fe uptake capacity of the marine alga *Chlorococcum littorale* cultured in Fe-limited media.

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3.6 Light Stress

- Whether light intensity is high or low, or leaves are sunlit or shaded, an increase in the CO_2 content of the air increases the biological processes that lead to plant robustness. Less than optimal light intensities do not negate the beneficial effects of atmospheric CO_2 enrichment. In fact, under low light conditions, the benefits of atmospheric CO_2 enrichment on plant growth are often relatively greater than when light conditions are ideal.

Granados and Korner (2002) grew three tropical understory vines (*Gonolobus cteniophorus*, *Ceratophytum tetragonolobum*, and *Thinouia tomocarpa*) for seven months in controlled-environment chambers maintained at atmospheric CO_2 concentrations of 280, 420, 560, and 700 ppm in combination with low and high light intensities, to study the interactive effects of the two parameters on the vines' growth. Plant biomass was found to be 61% greater at high light than at low light. However, the greatest relative CO_2-induced growth response in each species occurred in the low light environment. Increasing the atmospheric CO_2 concentration from 280 to 420 ppm, for example, increased *Gonolobus* biomass by 86 and 32% in low and high light environments, respectively, *Ceratophytum* biomass by 249 and 24% in low and high light environments, respectively, and *Thinouia* biomass by 65% in low light.

Harnos *et al*. (2002) grew winter wheat (*Triticum aestivum* L. cv. Emma) in open-top chambers maintained at atmospheric CO_2 concentrations of 365 and 700 ppm. Among other things, they too report elevated CO_2 stimulated photosynthetic rates to a greater extent under light-limiting than under non-light-limiting conditions. Twice-ambient CO_2 concentrations increased net photosynthesis rates by approximately 100% in upper-canopy leaves and by about 770% further down in the canopy, where light intensity was 60% less than in the upper canopy. This indicates increasing atmospheric CO_2 concentrations likely will lead to enhanced photosynthesis rates by winter wheat plants, even in leaves deep in their canopies, where irradiance is severely reduced due to shading by upper-canopy leaves.

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

Leakey *et al*. (2002) grew seedlings of *Shorea leprosula* (an under-story rainforest tree) in controlled environments maintained at atmospheric CO_2 concentrations of 376 and 711 ppm in combination with low irradiance treatments delivered in either a uniform or intermittent (sunfleck) manner for about seven months, to study the effects of elevated CO_2 and low light intensity on photosynthesis and growth in this species. They found the initial steady-state rates of photosynthesis measured in the shade in CO_2-enriched leaves were approximately 109% greater than those observed in ambient-grown leaves. In addition, seedlings in the sunfleck treatment grown in elevated CO_2 displayed post-irradiance rates of photosynthesis 14% greater than those observed in control seedlings. Taken together, these increases in photosynthesis led to CO_2-induced increases in carbon uptake 59 and 89% greater than those observed in control seedlings subjected to uniform and sunfleck light treatments, respectively. The seedlings subjected to uniform irradiance produced more biomass than those exposed to sunfleck irradiance, but the CO_2-induced percentage increase in biomass was greater under the sunfleck irradiance regime (60%) than under the uniform irradiance regime (25%).

Rasineni *et al*. (2011) write, "excess light limits photosynthesis by photoinhibition, resulting in reduced carbon gain and also causing photo-damage (Oquist and Huner, 1993; Pastenes *et al*., 2003; Allakhverdiev and Murata, 2004; Nishiyama *et al*., 2006)," and thus "plants grown in tropical climates usually experience significantly high irradiance leading to the strong midday depression of photosynthesis (Hymus *et al*., 2001)." They utilized two open-top chambers in the Botanical Gardens of the University of Hyderabad, India—each of which contained four six-month-old specimens of the fast-growing tropical *Gmelina arborea* tree, which they maintained at optimum moisture and nutrient levels—to measure several plant physiological properties and processes related to leaf photosynthesis and photosystem II (PSII) photochemistry and photo-inhibition at both ambient and elevated CO_2 concentrations (360 and 460 ppm, respectively), working with "well-expanded and light-exposed leaves randomly chosen from the upper half of the plant canopy."

The three Indian scientists determined there were no significant differences in CO_2 assimilation rates between the ambient and elevated CO_2 grown plants during early morning hours, but thereafter "photo-synthesis typically maximized between 0900 hours and 1000 hours in both ambient and elevated CO_2-grown plants," which experienced net photosynthetic rates of 20 and 32.5 $\mu mol/m^2/s$, respectively, for a CO_2-induced enhancement of 62%, which for the more standard CO_2 enrichment of 300 ppm would be an enhancement of roughly 180%. Subsequently, during the midday period of 1100–1300 hours, the net photosynthesis rate was still significantly enhanced by about 37% (roughly equivalent to a 300-ppm induced increase of more than 100%) in the elevated CO_2 treatment. After that, the difference between the net photosynthetic rates of the two CO_2 treatments once again became insignificant.

Noting the "elevated CO_2 treatment mitigated PSII-photoinhibition through enhanced electron transport rates and through efficient biochemical reactions in leaves of *G. arborea*," Rasineni *et al*. conclude their data "demonstrate that future increases in atmospheric CO_2 may have positive effects on photochemical efficiency in fast growing tropical tree species," allowing them to take great advantage of the high-light midday period of potential maximum growth in Earth's tropical regions.

Kerstiens (1998) provided further evidence elevated atmospheric CO_2 helps to ameliorate the stress of low light intensities in trees, analyzing the results of 15 previously published studies of trees having differing degrees of shade tolerance. He found elevated CO_2 caused greater relative biomass increases in shade-tolerant species than in shade-intolerant or sun-loving species. In more than half the studies he analyzed, shade-tolerant species experienced CO_2-induced relative growth increases two to three times greater than those of less shade-tolerant species.

In an extended follow-up review analyzing 74 observations from 24 studies, Kerstiens (2001) reports twice-ambient CO_2 concentrations increased the relative growth response of shade-tolerant and shade-intolerant woody species by an average of 51 and 18%, respectively. Similar results were reported by Poorter and Perez-Soba (2001), who performed a detailed meta-analysis of research results pertaining to this topic, and subsequently by Kubiske *et al*. (2002), who measured photosynthetic acclimation in aspen and sugar maple trees. Low light intensity, therefore, is by no means a barrier to the benefits of an increase in the air's CO_2 content.

Herrick and Thomas (1999) found a 200 ppm increase in the air's CO_2 concentration enhanced the photosynthetic rates of sunlit and shaded leaves of sweetgum trees by 92 and 54%, respectively, at one time of year, and by 166 and 68% at another time. Naumburg and Ellsworth (2000) report a 200 ppm increase in the air's CO_2 content boosted steady-state photosynthetic rates in leaves of four hardwood understory species by an average of 60 and 40% under high and low light intensities, respectively. Even though these photosynthetic responses were significantly less in shaded leaves, they were still substantial, with mean increases ranging from 40 to 68% for a 60% increase in atmospheric CO_2 concentration.

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

Sefcik *et al.* (2006) grew seedlings of two shade-tolerant northern hardwood tree species—sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* J.F. Ehrh.)—as well as seedlings of two shade-intolerant northern hardwood tree species—black cherry (*Prunus serotina* J.F. Ehrh.) and paper birch (*Betula papyrifera* Marsh.)—for two full growing seasons inside open-top chambers maintained at either ambient (383 ppm) or elevated (658 ppm) atmospheric CO_2 concentrations in an overarching 90-year-old nitrogen-limited northern hardwood forest in Michigan (USA). They determined the seedlings' responses to atmospheric CO_2 enrichment in two contrasting degrees of shade: moderate shade (14.2 μmol photons m^{-2} s^{-1} = 5.6% full sun) and deep shade (6.5 μmol photons m^{-2} s^{-1} = 2.2% full sun). Sefcik *et al.* state "the magnitude of enhancement from exposure to elevated CO_2 was similar for both shade-tolerance groups," with the elevated CO_2 treatment increasing the mean light-saturated net photosynthetic rate by 63% in the shade-tolerant species and by 67% in the shade-intolerant species. More important, they write, "seedlings grown in deep shade, regardless of shade-tolerance group, showed a greater long-term photosynthetic enhancement to elevated CO_2 than those grown in moderate shade," with the mean long-term enhancement being 47% in moderate shade and a much larger 97% in deep shade.

Noting the same type of photosynthetic response "has also been found in a number of other studies, suggesting that the impact of a CO_2-enriched atmosphere increases as light becomes more limiting (Hattenschwiler, 2001; Granados and Korner, 2002; Leakey *et al.*, 2002)," Sefcik *et al.* conclude, "if long-term enhancement of photosynthesis in elevated CO_2 and deep shade translates into greater survival, especially for shade-intolerant species, this could have profound successional implications for nitrogen-limited northern hardwood forest composition in a future higher CO_2 atmosphere."

Elevated CO_2 often reduces a plant's light compensation point, which is the light intensity at which the amount of carbon fixed by photosynthesis is equal to that lost by respiration. Above that particular light intensity, net photosynthesis is positive. Below it, net photosynthesis is negative, and if prolonged, the plant will ultimately die. This phenomenon is especially beneficial to vegetation growing in deep shade beneath forest canopies that block out much of the incoming sunlight (Kubiske and Pregitzer, 1996; Osborne *et al*., 1997), and it also helps aquatic plants extend their life zones to greater depths (Zimmerman *et al*., 1997).

Whether light intensity is high or low, or leaves are shaded or sunlit, an increase in the CO_2 content of the air increases the various biological processes that lead to plant robustness. Less than optimal light intensities do not negate the beneficial effects of atmospheric CO_2 enrichment.

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3.7 Nitrogen Insufficiency

Numerous studies have investigated the effects of different soil nitrogen (N) concentrations on plant responses to increases in the air's CO_2 content, because some scientists have claimed a deficiency of soil nitrogen reduces the relative growth stimulation in plants that is typically provided by elevated concentrations of atmospheric CO_2. This section investigates that claim for various crops, fungi, grasses, and young trees.

The results of these experiments indicate some plants sometimes will not respond to atmospheric CO_2 enrichment at low levels of soil N, and others will. Some plants respond equally well to increases in the air's CO_2 content when growing in soils exhibiting a whole range of N concentrations. Most commonly, however, plants respond ever-better to rising atmospheric CO_2 concentrations as soil N concentrations rise. Interestingly, Earth's atmosphere and land surface are currently undergoing joint increases in CO_2 and N concentrations. Thus, the outlook is good for continually increasing terrestrial vegetative productivity as these trends continue.

3.7.1 Crops

The maximum benefits of elevated levels of atmospheric CO_2 for the growth and grain production of rice and wheat cannot be realized in soils that are highly deficient in nitrogen, but increasing nitrogen concentrations above what is considered adequate may not result in proportional gains in CO_2-induced growth and yield enhancement. Although there are significant exceptions to the rule, many agricultural crops experience increases in net photosynthesis and biomass production even when soil nitrogen concentrations are a limiting factor to growth.

3.7.1.1 Rice

- The maximum benefits of elevated levels of atmospheric CO_2 for the growth and grain production of rice cannot be realized in soils that are highly deficient in nitrogen, but increasing nitrogen concentrations above what is considered adequate may not result in proportional gains in CO_2-induced growth and yield enhancement.

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

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

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

These observations indicate the maximum benefits of elevated levels of atmospheric CO_2 for the growth and grain production of rice cannot be realized in soils highly deficient in nitrogen, but increasing nitrogen concentrations above what is considered adequate may not result in proportional gains in CO_2-induced growth and yield enhancement.

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3.7.1.2 Wheat

- The maximum benefits of elevated levels of atmospheric CO_2 for the growth and grain production of wheat cannot be realized in soils that are highly deficient in nitrogen, but increasing nitrogen concentrations above what is considered adequate may not result in proportional gains in CO_2-induced growth and yield enhancement.

Smart *et al*. (1998) grew wheat from seed for 23 days in controlled-environment chambers maintained at atmospheric CO_2 concentrations of 360 and 1,000 ppm and two concentrations of soil nitrate, finding the extra CO_2 increased average plant biomass by approximately 15 percent, irrespective of soil nitrogen content. In a more realistic FACE experiment, however, Brooks *et al*. (2000) grew spring wheat for two seasons at atmospheric CO_2 concentrations of 370 and 570 ppm at both high and low levels of nitrogen fertility, obtaining twice the yield enhancement (16 percent vs. 8 percent) in the high nitrogen treatment.

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

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

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

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3.7.1.3 Other Crops

- Agricultural crops generally experience greater

> CO_2-induced percentage increases in net photosynthesis and biomass production even when soil nitrogen concentrations are a limiting factor, although there are some significant exceptions to the rule.

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

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

Newman *et al.* (2003) investigated the effects of two levels of nitrogen fertilization and an approximate doubling of the air's CO_2 concentration on the growth of tall fescue, an important forage crop. The plants were initially grown from seed in greenhouse flats, but after 16 weeks the researchers transplanted them into 19-liter pots filled with potting media given periodic applications of a slow-release fertilizer. Over the next two years of outdoor growth, the researchers periodically clipped, divided, and repotted the plants to ensure they did not become root-bound. At the end of that time, they placed the plants in 20 1.3-m-diameter open-top chambers, half of which were maintained at the ambient atmospheric CO_2 concentration and half of which received an approximately doubled CO_2 concentration of 700 ppm. In addition, half of the pots in each CO_2 treatment received 0.0673 kg N m^{-2} applied over a period of three consecutive days, and half received only one-tenth that amount. Researchers repeated the entire procedure three times during the 12-week study.

The researchers found the plants grown in the high-CO_2 air photosynthesized 15 percent more and produced 53 percent more dry matter (DM) under low N conditions and 61 percent more DM under high N conditions. The percent of organic matter (OM) was little changed, except under elevated CO_2 and high N, when %OM (as %DM) increased by 3 percent. In this study too, then, the greatest relative increase in productivity occurred under high soil N availability.

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

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

Fangmeier *et al*. (2000) grew barley plants in containers in open-top chambers maintained at atmospheric CO_2 concentrations of either 360 or 650 ppm and either a high or low nitrogen fertilization regime. Te elevated CO_2 had the greatest relative impact on yield when the plants were grown under the less-than-optimum low-nitrogen regime—a 48 percent increase vs. 31 percent under high-nitrogen conditions.

Kimball *et al*. (2002) summarized the findings of most FACE studies conducted on agricultural crops since the introduction of that technology in the late 1980s. In response to a 300 ppm increase in the air's CO_2 concentration, rates of net photosynthesis in several C_3 grasses were enhanced by an average of 46% under conditions of ample soil nitrogen supply and by 44% when nitrogen was limiting to growth. The differential for above-ground biomass production was much larger, with the C_3 grasses wheat, rice, and ryegrass showing an average increase of 18% at ample nitrogen but only 4% at low nitrogen. As to belowground biomass production, they experienced an average increase of 70% at ample nitrogen and 58% at low nitrogen. Similarly, clover experienced a 38% increase in belowground biomass production at ample soil nitrogen and a 32% increase at low soil nitrogen. Finally, with respect to agricultural yield—the true indicator of food and fiber production—wheat and ryegrass showed an average increase of 18% at ample nitrogen, and wheat saw only a 10% increase at low nitrogen.

These results indicate most agricultural crops generally experience greater CO_2-induced relative (percentage) increases in net photosynthesis and biomass production even when soil nitrogen concentrations are a limiting factor, although there are some exceptions to the rule.

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3.7.2 Fungi

- CO_2-induced stimulation of root infection by various fungi (which tends to benefit the plants) is generally greater under lower soil nitrogen concentrations. This implies elevated CO_2 will enhance fungal-plant interactions to a greater extent when soil nutrition is less than optimal for plant growth, which is the common state of most ecosystems not subjected to fertilization practices typical of intensive agriculture.

Nearly all plants establish intimate relationships with different fungal species at one point or another in their life cycles, and these fungi commonly aid plants in the acquisition of water and nutrients. In addition, fungal-plant interactions are often affected by variations in atmospheric CO_2 and soil nitrogen concentrations.

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

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

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

These observations suggest elevated CO_2 affects fungal-plant interactions in positive ways that may depend on soil nitrogen status. Typically, it appears CO_2-induced stimulations of percent root infection by various fungal components is greater under lower soil nitrogen concentrations. This tendency implies elevated CO_2 will enhance fungal-plant interactions to a greater extent when soil nutrition is less than optimal for plant growth, which is commonly the case for most ecosystems not subjected to cultural fertilization practices typical of intensive agricultural production.

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3.7.3 Grasses

- Atmospheric CO_2 enrichment stimulates photosynthesis and biomass production in grasses and grassland species when soil nitrogen availability is high or moderate. Where nitrogen availability is low, grasslands are able to overcome soil nitrogen limitations and produce positive CO_2-induced growth responses, given enough time.

Perennial ryegrass (*Lolium perenne* L.) has been used as a model species in many experiments to help elucidate grassland responses to atmospheric CO_2 enrichment and soil nitrogen availability. In the FACE study of Rogers *et al.* (1998), for example, ryegrass plants exposed to 600 ppm CO_2 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 CO_2, the CO_2-induced photosynthetic response was about 3-fold greater in a higher soil nitrogen regime (Casella and Soussana, 1997).

Similarly, in an open-top chamber study Davey *et al.* (1999) found an atmospheric CO_2 concentration of 700 ppm stimulated photosynthesis by 30% in this species when it was grown with moderate, but not low, soil nitrogen availability. Thus, CO_2-induced photosynthetic stimulations in perennial ryegrass can be influenced by soil nitrogen content, with greater positive responses typically occurring under higher, as opposed to lower, soil nitrogen availability.

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

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

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

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

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3.7.4 Trees

3.7.4.1 Aspen

- Typically, the aerial fertilization effect of atmospheric CO_2 enrichment stimulates the growth of young aspen trees in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting.

Does a deficiency of soil nitrogen lessen the relative growth stimulation of young quaking aspen (*Populus tremuloides* Michx) trees that is typically provided by elevated concentrations of atmospheric CO_2? Kubiske *et al.* (1998) grew cuttings of four quaking aspen genotypes for five months at CO_2 concentrations of 380 or 720 ppm and low or high soil nitrogen in open-top chambers in the field in Michigan (USA). Elevated CO_2 significantly increased net photosynthesis, regardless of soil nitrogen content, although there were no discernible increases in aboveground growth in the five-month study period. Belowground, elevated CO_2 significantly increased fine root production, but only in the high soil nitrogen treatment.

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

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

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

Taken together, these observations suggest the aerial fertilization effect of atmospheric CO_2 enrichment stimulates the growth of young aspen trees in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting.

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3.7.4.2 Pine

- Typically, the aerial fertilization effect of atmospheric CO_2 enrichment stimulates the growth of young pine trees in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting.

In a review of 11 papers dealing with both loblolly pine (*Pinus taeda* L.) and ponderosa pine (*Pinus ponderosa* Dougl.), Johnson *et al*. (1998) report when soil nitrogen levels were extremely deficient or so high as to be toxic, growth responses to atmospheric CO_2 enrichment in both species were negligible. For moderate soil nitrogen deficiencies, however, a doubling of the air's CO_2 content sometimes boosted growth by as much as 1,000%. In addition, atmospheric CO_2 enrichment mitigated the negative growth response of ponderosa pine to extremely high soil nitrogen concentrations.

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

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

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

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

Taken together, these observations indicate the aerial fertilization effect of atmospheric CO_2 enrichment stimulates the growth of young pine trees in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting. Evidence also suggests at some point the response to increasing soil nitrogen saturates, and beyond that point, higher N concentrations may reduce the growth response of young pine trees to elevated CO_2.

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3.7.4.3 Spruce

- Typically, the aerial fertilization effect of CO_2 enrichment stimulates the growth of young spruce trees in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting.

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

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

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

Typically, the aerial fertilization effect of atmospheric CO_2 enrichment stimulates the growth of young spruce trees in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting. Evidence also suggests at some point the response to increasing soil nitrogen saturates, and beyond that point, higher N concentrations may reduce the growth response of young spruce trees to elevated CO_2.

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3.7.4.4 Other

- Typically, the aerial fertilization effect of atmospheric CO_2 enrichment stimulates the growth of young tree species in soils of adequate and insufficient nitrogen content, although the stimulation is generally greater when nitrogen is not limiting.

Maillard *et al.* (2001) grew pedunculate oak seedlings for three to four months in greenhouses maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm under conditions of either low or high soil nitrogen concentration. The elevated CO_2 of their study stimulated belowground growth in the seedlings growing in the nitrogen-poor soil, significantly increasing their root-to-shoot ratios. It increased both the below- and above-ground biomass of seedlings growing in nitrogen-rich soil. The CO_2-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 CO_2 concentration of the air in their study enhanced total seedling biomass by approximately 30 and 140% under nitrogen-poor and nitrogen-rich soil conditions, respectively.

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

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

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

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

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3.8 Ozone Pollution

3.8.1 Agricultural Species

- Atmospheric CO_2 enrichment typically reduces—and more often than not completely overrides—the negative effects of ozone pollution on the photosynthesis, growth, and yield of essentially all agricultural crops that have been experimentally evaluated.

3.8.1.1 Soybean

- The high ozone concentrations that will exist in many parts of the world in the future will have severe negative consequences for soybean production, all else being equal. However, the higher CO_2 concentration predicted for the future will have an important ameliorative effect on the adverse impact of this major air pollutant. It may compensate, or even more than compensate, for the potential negative consequences of elevated O_3.

Air pollution-induced productivity losses to agriculture are serious, especially to soybeans (*Glycine max* L.). Some appreciation for the magnitude of this problem can be gained by considering East Asia, which has 25% of the world's population but produces only 21% of humanity's cereal needs. Wang and Mauzerall (2004) note air pollution, and especially that due to ozone (O_3), is an increasingly serious problem in this region, reducing agricultural productivity and exacerbating the problem of food security. The two researchers evaluates the impact of rising surface O_3 concentrations in East Asia on agricultural production in 1990 and its projected impact in 2020.

According to their "conservative estimates," the two scientists write, "due to O_3 concentrations in 1990, China, Japan and south Korea lost ... 23–27% of their yield of soybeans," and by 2020, the "loss due to increased levels of O_3 pollution is projected to increase to ... 28–35% for soybeans." As a result of these and other O_3-induced crop losses, Wang and Mauzerall conclude, "East Asian countries are presently on the cusp of substantial reductions in grain production," meaning they are also "on the cusp" of substantial reductions in food security.

Wahid *et al.* (2001) demonstrated the findings of Wang and Mauzerall are indeed "conservative." In a study of the effects of ozone pollution in the Punjab region of Pakistan, Wahid *et al.* periodically applied a powerful ozone protectant to soybeans growing in three locations near the city of Lahore—a suburban site, a remote rural site, and a rural roadside site—throughout two growing seasons (one immediately post-monsoon and one the following spring or pre-monsoon).

At the suburban site, application of the ozone protectant increased the weight of soybean seeds produced per plant by 47% in the post-monsoon season and by 113% in the pre-monsoon season. At the remote rural site, the corresponding yield increases were 94% and 182%, and at the rural roadside site, they were 170% and 285%. Averaged across all three sites and both seasons of the year, the mean increase in yield caused by countering the deleterious effects of this major air pollutant was nearly 150%, and because they found "the impacts of ozone on the yield of soybean are larger in the rural areas around Lahore than in suburban areas of the city," they conclude "there may be substantial impacts of oxidants on crop yield across large areas of the Punjab."

Clearly, whatever can be done to reduce O_3-induced crop losses—or eliminate them altogether—would be considered a benefit in areas where such pollution is commonplace. Rising atmospheric CO_2 concentrations can help to alleviate this problem.

Miller *et al.* (1998) grew soybeans for one season in pots in open-top chambers maintained at atmospheric CO_2 concentrations of 370, 482, 599, and 713 ppm in combination with atmospheric O_3 concentrations of 20, 50, and 79 ppb. By harvest time (113 days after planting), elevated CO_2 had significantly increased all biomass and growth variables measured, with the greatest enhancements occurring at the highest CO_2 and O_3 concentrations. Plants grown at 20 ppb O_3 and 713 ppm CO_2, for example, displayed total dry weights 48% greater than their ambient-air-grown counterparts, and plants grown at 79 ppb O_3 and 713 ppm CO_2 exhibited dry weights 53% greater than their ambient-air counterparts. Likewise, in the same experiment, Heagle *et al.* (1998) observed plants grown at 20 ppb O_3 and 713 ppm CO_2 displayed seed dry weights 20% greater than their ambient-air-grown counterparts, and plants grown at 79 ppb O_3 and 713 ppm CO_2 exhibited seed dry weights 74% greater.

Reid *et al.* (1998) grew soybeans in open-top chambers maintained at atmospheric CO_2 concentrations of 371 and 708 ppm and O_3 concentrations of 24 and 81 ppb. In the ambient-CO_2 air, the elevated O_3 exposure reduced the amount and activity of rubisco per unit leaf area, as well as leaf starch content. In the elevated-CO_2 air, elevated O_3 exposure had no effect on these three leaf parameters: the atmospheric CO_2 enrichment completely ameliorated potential O_3-induced damage.

Reid and Fiscus (1998) grew soybeans for a single season in pots placed in open-top chambers maintained at either ambient (365 ppm) or elevated (727 ppm) concentrations of atmospheric CO_2 and below-ambient (20 ppb) or 1.5 times ambient (74 ppb) levels of ozone. They found elevated CO_2 enhanced rates of photosynthesis regardless of the presence of ozone and typically ameliorated the negative effects of ozone on carbon assimilation.

In a literature review of O_3 and CO_2 effects on soybean photosynthesis, growth and yield, Morgan *et al.* (2003) write, "meta-analytic techniques were used to quantitatively summarize the response of soybean to an average, chronic ozone exposure of 70 ppb, from 53 peer-reviewed studies," after which they similarly derived the net effect of concurrently elevated O_3 and CO_2 (to unspecified concentrations described as being "above 400 ppm"). They found "when both O_3 and CO_2 are elevated, the mean decrease in photosynthesis is 7%," which "compares to a 20% loss for plants grown at elevated O_3 and the current ambient CO_2." The three researchers also report, "at maturity, the average shoot biomass was decreased 34% and seed yield was 24% lower" in response to elevated O_3 alone, but "seed yield decreases for plants grown in elevated O_3 and elevated CO_2 are only half of those for plants grown in current ambient CO_2 and elevated O_3."

They also found "significant ozone responses in several plant parameters at low daily average concentrations (less than 60 ppb)," which is less than current concentrations in many locations. In studies where the O_3 treatment average was less than 60 ppb, they report, "seed yield, shoot and root dry weight were all significantly decreased by about 10%," which suggests the atmospheric CO_2 enrichment employed in the joint O_3/CO_2 experiments likely would have completely eradicated the O_3-induced losses in plant production.

The findings of Booker *et al.* (2005a) suggest this conclusion is robust. They grew well-watered and well-fertilized soybeans from seeds sown either directly in the ground or in 15-liter pots out-of-doors in open-top chambers maintained at all combinations of low (24 ppb) or high (75 ppb) O_3 concentrations and ambient (373 ppm) or elevated (699 ppm) CO_2 concentrations in 1999, and in 21-liter pots maintained at all combinations of low (24 ppb) or high (75 ppb) O_3 concentrations and ambient (369 ppm) or elevated (717 ppm) CO_2 concentrations in 2000.

In 1999, in the pot-grown plants, the 212% increase in atmospheric O_3 concentration decreased net photosynthesis by approximately 21%. When the air's CO_2 concentration was simultaneously increased by 87%, the negative impact of the O_3 increase was more than ameliorated, as the plants exposed to elevated concentrations of both gases exhibited net photosynthesis rates 26% greater than the plants growing in low O_3 and CO_2 air. Likewise, in the ground-grown plants, the 212% increase in atmospheric O_3 concentration decreased net photosynthesis by approximately 14%, but when the air's CO_2 concentration was simultaneously increased by 87%, the negative impact of the O_3 increase was more than ameliorated, as the plants exposed to elevated concentrations of both gases exhibited net photosynthesis rates 40% greater than the plants growing in low O_3 and CO_2 air.

With respect to seed yield in 1999, in the pot-grown plants the 212% increase in atmospheric O_3 concentration decreased total seed biomass by approximately 27%, but when the air's CO_2 concentration was boosted by 87%, the negative impact of the O_3 increase was also more than ameliorated, as the plants exposed to elevated concentrations of both gases produced 15% more total seed biomass than those growing in low O_3 and CO_2 air. Likewise, in the ground-grown plants, the 212% increase in atmospheric O_3 concentration decreased total seed biomass by approximately 24%, but when the air's CO_2 concentration was boosted by 87%, the negative impact of the O_3 increase was more than ameliorated, as the plants exposed to elevated concentrations of both gases produced 15% more total seed biomass than those in low O_3 and CO_2 air.

With respect to seed yield in 2000, in the pot-grown plants the 212% increase in atmospheric O_3 concentration decreased total seed biomass by approximately 41%, but when the air's CO_2 concentration was simultaneously boosted by 94%, the negative impact of the O_3 increase was more than ameliorated, as the plants exposed to elevated concentrations of both gases produced 18% more total seed biomass than those in low O_3 and CO_2 air. Likewise, in the ground-grown plants, the 212% increase in atmospheric O_3 concentration decreased total seed biomass by approximately 39%, but when the air's CO_2 concentration was boosted by 94%, the negative impact of the O_3 increase was more than ameliorated, as the plants exposed to elevated concentrations of both gases produced 9% more total seed biomass than those in low O_3 and CO_2 air. In all of the many situations investigated by Booker *et al.*, slightly less than a doubling of the air's CO_2 concentration more than compensated for the deleterious effects of slightly more than a tripling of the atmosphere's O_3 concentration on both leaf net photosynthesis and total seed biomass production in soybeans.

In a similar two-year open-top chamber study of aboveground postharvest residue, Booker *et al.* (2005b) grew soybeans in reciprocal combinations of low and high atmospheric concentrations of O_3 (21 and 74 ppb, respectively) and CO_2 (370 and 714 ppm, respectively), finding residue mass input "is increased by elevated CO_2 and suppressed by O_3." They found elevated O_3 decreased aboveground postharvest residue by 15–46%, elevated CO_2 increased it by 28–56%, and in combination the CO_2 effect always predominated. In the case of leaves, for example, elevating the air's O_3 concentration dropped dry mass residue to only 54% of what it was under ambient conditions, and concurrently elevating the air's CO_2 concentration boosted it to 124% of what it was in ambient air. Corresponding results of 85% and 123% were obtained for petioles, 60% and 121% for stems, and 72% and 122% for husks. Consequently, as in the cases of net photosynthesis and seed yield investigated by Booker *et al.* (2005a), the results of this study demonstrated a slightly less than doubling of the air's CO_2 concentration more than compensated for the deleterious effects of slightly more than a tripling of the air's O_3 concentration on the production of aboveground postharvest residue in soybeans.

Booker and Fiscus (2005) grew well-watered and well-fertilized soybean plants for two years (1998 and 1999) out-of-doors in 21-liter pots in open-top chambers from emergence to maturity and exposed them to either charcoal-filtered air, charcoal-filtered air plus an extra 336 ppm CO_2, charcoal-filtered air plus 1.5 times normal ambient O_3, or charcoal-filtered air plus an extra 336 ppm CO_2 and 1.5 times normal ambient O_3. They found the imposition of elevated CO_2 alone increased soybean pod biomass by 23.0%, the imposition of elevated O_3 alone decreased pod biomass by 13.3%, and the imposition of elevated CO_2 and O_3 together increased pod biomass by 23.0%.

Today's high ozone concentrations and the even-higher concentrations of the future have and will continue to have severe negative consequences for soybean production, all else being equal. But the atmosphere's current high CO_2 concentration, plus the higher concentration it will have in the future, ameliorates the adverse impacts of this major air pollutant and will continue to do so in the years to come. The anticipated concentrations of CO_2 may more than compensate for the negative effects of elevated O_3.

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3.8.1.2 Wheat

- A number of studies conducted around the turn of the century demonstrate enriching the air with CO_2 substantially ameliorates a variety of negative influences of ozone pollution on the productivity of wheat plants.

Bender *et al.* (1999) analyzed the results of 13 open-top chamber studies in which spring wheat was grown at ambient and twice-ambient CO_2 concentrations in combination with ambient and elevated ozone (O_3) concentrations. They found the elevated O_3 treatment had little effect on growth and yield, suggesting either the O_3 concentrations employed in the studies were not high enough to elicit a negative response in the specific cultivar tested (Minaret) or the cultivar was highly tolerant of ozone. Consequently, elevated CO_2 was the primary variable influencing the growth and yield of the spring wheat. It proved very effective in this regard, increasing aboveground biomass by an average of 37% (with a range of 11 to 128%) and grain yield by an average of 35% (with a range of 11 to 121%).

Tiedemann and Firsching (2000) grew spring wheat from germination to maturity in controlled-environment chambers maintained at ambient (377 ppm) and enriched (612 ppm) atmospheric CO_2 concentrations and ambient (20 ppb) and enriched (61 ppb) atmospheric O_3 concentrations. The extra CO_2 increased mean photosynthetic rates at both O_3 concentrations, with the greatest absolute photosynthetic rates and the largest CO_2-induced percentage increases in photosynthesis being observed in the elevated CO_2/elevated O_3 treatment. Total grain yield was also greatest in the high CO_2/high O_3 treatment, with the elevated CO_2 increasing total grain yield at high O_3 by 38% relative to that observed at ambient CO_2 and elevated O_3. Moreover, the absolute value of total grain yield in the high CO_2/high O_3 treatment was not significantly different from that produced at ambient O_3, regardless of the atmospheric CO_2 concentration. Atmospheric CO_2 enrichment completely ameliorated the deleterious effects of ozone on photosynthesis and yield in this study.

Pleijel *et al.* (2000) grew spring wheat in open-top chambers maintained at atmospheric CO_2 concentrations of 340 and 680 ppm for three consecutive years. They exposed some plants in each CO_2 treatment to ambient, 1.5 x ambient, and 2 x ambient O_3 concentrations. These elevated O_3 concentrations negatively influenced wheat yield at both atmospheric CO_2 concentrations. Grain yield was always higher for the plants grown in the CO_2-enriched air, averaging 13% greater over the three years of the study and leading the scientists who conducted the work to conclude "the positive effect of elevated CO_2 could compensate for the yield losses due to O_3."

Vilhena-Cardoso and Barnes (2001) grew spring wheat for two months in environmental chambers fumigated with air containing atmospheric CO_2 concentrations of 350 and 700 ppm at ambient and elevated (75 ppb) O_3 concentrations in soils of low, medium, and high nitrogen content. The elevated O_3 treatment was shown to reduce photosynthetic rates in the ambient-CO_2-grown plants, but it had no effect on the CO_2-enriched plants, which maintained enhanced photosynthetic rates even in the high O_3 treatments. With respect to biomass production, elevated CO_2 increased total plant dry weight by 44, 29, and 12% at high, medium, and low soil nitrogen supply, respectively, and although elevated O_3 by itself reduced plant biomass, the simultaneous application of elevated CO_2 completely ameliorated this detrimental effect at all soil nitrogen concentrations.

Fangmeier and Bender (2002) analyzed mean grain yields of spring wheat derived from the ESPACE-Wheat project of the European Stress Physiology and Climate Experiment—Project 1, which was conducted for three growing seasons at eight experimental field sites across Europe that employed atmospheric CO_2 concentrations of 380, 540, and 680 ppm and O_3 concentrations of 32.5 and 60.3 ppb for half-day periods (Jager *et al.*, 1999). They found the high O_3 stress reduced wheat yields by an average of about 12% at the ambient CO_2 concentration. As the air's CO_2 concentration was increased to 540 and 680 ppm, there were no longer any significant reductions in yield due to the high O_3 stress. Whereas wheat yield in ambient-O_3 air increased by 34% over the entire CO_2 enrichment range investigated (380 to 680 ppm), it increased by 46% in the high-O_3 air, once again more than compensating for the O_3-alone-induced yield losses.

The results described above indicate enriching the air with CO_2 substantially ameliorates a variety of negative influences of ozone pollution on the productivity of wheat plants.

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3.8.1.3 Other Species

- Atmospheric CO_2 enrichment typically reduces, and more often than not completely counteracts, the negative effects of ozone pollution on the photosynthesis, growth, and yield of almost all agricultural crops that have been experimentally evaluated.

In addition to soybean and wheat, several studies have examined the effects of elevated CO_2 and ozone on photosynthesis and growth in other agricultural crops. The main findings of some of these studies are described below.

Cotton plants grown by Booker (2000) at elevated ozone concentrations exhibited 25 and 48 percent reductions in leaf mass per unit area and foliar starch concentration, respectively, relative to control plants grown in ambient air. When the cotton plants were simultaneously exposed to twice-ambient CO_2 concentrations, the reductions in these parameters were only 5 and 7 percent, respectively.

Wolf and van Oijen (2002) used a validated potato model to predict increases in European tuber production ranging from 1,000 to 3,000 kg of dry matter per hectare in spite of concomitant increases in ozone concentrations and air temperatures. In a field-based study, Vandermeiren *et al.* (2005) studied the impact of future increases in atmospheric ozone (O_3) and carbon dioxide (CO_2) concentrations on yield and tuber quality in potato (*Solanum tuberosum* L.). This research endeavor, they write, was "the first large-scale open-top chamber project to provide field-based data spanning a wide range of European climatic conditions and ozone concentrations for a widely used cultivar, cv. Bintje." After two years of intensive measurements made on potatoes growing throughout Europe—including Belgium, Finland, Germany, Ireland, Sweden, and the United Kingdom—they determined the relative yield losses expected to occur in response to O_3 concentrations projected to prevail in Europe at mid-century were a mere 5%. The four researchers also report "the prevailing conditions under climate scenarios for 2050 (including increases in temperature, solar radiation and CO_2 and O_3 concentrations) would increase the yield of irrigated potato crops by 2000–4000 kg ha^{-1} in most regions in Europe, primarily because of the beneficial influence of increased atmospheric CO_2," citing Wolf and Van Oijen (2003).

Plessl *et al.* (2005) grew well-watered and fertilized spring barley (*Hordeum vulgare* L. cv.

Scarlett) plants from seed for four weeks after emergence in containers located in controlled-environment chambers maintained at either ambient (400 ppm) or 1.75 x ambient (700 ppm) atmospheric CO_2 concentrations. They simultaneously exposed the plants to either ambient or 2 x ambient atmospheric O_3 concentrations, evaluating the individual and combined effects of the CO_2 and O_3 additions. The researchers report the "elevated CO_2 concentration significantly increased aboveground biomass [15%], root biomass [30%], and tiller number [41%], whereas double-ambient ozone significantly decreased these parameters." When applied together, the "ozone-induced reductions in growth parameters were strongly overridden by 700 ppm CO_2." In the doubled-ozone treatment, the 75% increase in the air's CO_2 content increased the barley's aboveground biomass by 42%, its root biomass by 75%, and its tiller number by 94%. Thus, a less than doubling of the air's CO_2 concentration more than compensated for a full doubling of the air's O_3 concentration, revealing the potential for the rise in the air's CO_2 content to more than overcome the negative growth effects of elevated O_3 concentrations on spring barley.

Yonekura *et al*. (2005) grew komatsuna (*Brassica campestris* cv. Rakuten) and radish (*Raphanus sativus* cv. Akamaru) plants from seed (one to a pot) in 1.4-L pots filled with "black soil" in controlled-climate chambers for 30 days in air of one of four different daylight O_3 concentrations—0–5 (charcoal-filtered), 60, 90, or 120 ppb—after which they destructively harvested the plants and determined their final dry weights. In the case of komatsuna (Japanese mustard spinach), where the edible portion of the vegetable is produced aboveground, the mean aboveground dry weights of the plants at the end of their 30-day growth cycle were 0.76, 0.63, 0.53, and 0.39 g in the 0–5, 60, 90, and 120 ppb O_3 treatments, respectively, when grown in ambient air of 380 ppm CO_2. When grown in air of 760 ppm CO_2, aboveground weights for the same set of O_3 concentrations were 1.19, 1.10, 0.98, and 0.85 g, representing CO_2-induced growth enhancements of 57%, 75%, 85%, and 118%. The doubling of the air's CO_2 concentration more than compensated for the negative impact caused by the highest of the four O_3 concentrations in ambient-CO_2 air, turning what would have been a 49% O_3-induced yield loss (from 0.76 to 0.39 g) into a 12% CO_2-induced yield gain (from 0.76 to 0.85 g).

In the case of radish, where the edible portion of the vegetable is produced belowground, the mean belowground dry weights of the plants at the end of their 30-day growth cycle were 0.63, 0.59, 0.39, and 0.36 g in the 0–5, 60, 90, and 120 ppb O_3 treatments, respectively, when grown in ambient air of 380 ppm CO_2. When grown in air of 760 ppm CO_2, however, belowground weights for the same set of O_3 concentrations were 1.45, 1.34, 1.15, and 0.88 g, which represent CO_2-induced growth enhancements of 132%, 127%, 195%, and 144%. Once again, the doubling of the air's CO_2 concentration more than compensated for the negative impact caused by the highest of the four O_3 concentrations in ambient-CO_2 air, turning what would have been a 43% O_3-induced yield loss (from 0.63 to 0.36 g) into a 40% CO_2-induced yield gain (from 0.63 to 0.88 g).

Burkey *et al*. (2007) grew peanuts (*Arachis hypogaea* L., cv NC-V11) in a field near Raleigh, North Carolina (USA) using standard agricultural practices for two years in open-top chambers maintained at all combinations of three CO_2 treatments (375, 548, and 730 ppm) and three O_3 treatments—charcoal-filtered air (CF, 22 ppb), non-filtered air (NF, 46 ppb), and O_3-enriched air (75 ppb)—after which they assessed peanut seed yields and qualities. They found "elevated CO_2 increased yield parameters 7 to 17% for plants grown in CF air and restored yield in NF air and elevated O_3 treatments to control or higher levels," while "market grade characteristics and seed protein and oil contents were not affected by elevated O_3 and CO_2."

The USDA Agricultural Research Service scientists conclude, in the case of peanuts, "the major impacts of rising atmospheric O_3 and CO_2 will be on productivity, not product quality," and as to productivity, their data indicate the positive effects of the rise in the air's CO_2 content should be able to compensate for concomitant future increases in tropospheric ozone concentrations. In fact, the continuing upward trend in atmospheric CO_2 concentration should more than compensate for any future increases in the air's O_3 content, because the latter will likely be relatively small due to the strong negative influence of elevated atmospheric CO_2 concentrations on vegetative isoprene emissions (Monson *et al*., 2007), which are responsible for increasing O_3 concentrations over land by perhaps 50% over what they would be in their absence (Poisson *et al*., 2000). Similarly, Arneth *et al*. (2007) calculated that when the effect of CO_2 on vegetative isoprene emissions is included, a properly forced model "maintains global isoprene emissions in ± 15% of present values," which should significantly temper the future rate-of-rise of the troposphere's ozone concentration.

Tu *et al.* (2009) grew *Arachis hypogaea* L. plants from seed to maturity out-of-doors near Raleigh, North Carolina (USA) in open-top chambers under adequately watered and fertilized conditions, exposing the plants to charcoal-filtered air, which was thus ozone-free, ambient air of unaltered ozone (O_3) concentration, and air containing 1.6 times the ambient O_3 concentration. All of these O_3 treatments were exposed to air of 376, 550, and 730 ppm CO_2. At the end of this period they harvested the crop and measured its final steam, leaf, and pod biomass.

They found "elevated CO_2 generally increased biomass production while O_3 suppressed it, and CO_2 ameliorated the O_3 effect." In terms of the season-long mean of midday net photosynthesis, for example, the 94% increase in the air's CO_2 concentration experienced in going from the lowest to the highest CO_2 treatment resulted in a 25% increase in net photosynthesis in the charcoal-filtered air, a 50% increase in the non-filtered air, and a 104% increase in the ozone-polluted air. As to the final aboveground biomass produced, the corresponding CO_2-induced increases were 10%, 41%, and 105%.

The four researchers also note "at mid-vegetative growth, elevated CO_2 significantly reduced leaf nitrogen concentrations by up to 44%," but "plant nitrogen concentrations only differed by 8% among CO_2 treatments at harvest while N_2 fixation was increased." They say their experiment suggests "symbiotic N_2 fixation is important for maintaining seed N concentrations and that CO_2 enhancement of symbiotic N_2 fixation may compensate for low soil N availability."

Tu *et al.* state a number of experiments, like theirs, "have shown that elevated CO_2 can offset the adverse effects of O_3 on crop biomass production and yield," citing Olszyk *et al.* (2000), Fuhrer (2003), and Fiscus *et al.* (2005). In addition, they note "the protective effect of elevated CO_2 against O_3 injury has been observed in a number of C_3 plant species, including cotton, peanut, rice, soybean, and wheat, due in large part to a reduction in O_3 uptake from reduced stomatal conductance and possibly from increases in photoassimilation rates and antioxidant metabolism," citing McKee *et al.* (2000), Booker and Fiscus (2005), Fiscus *et al.* (2005), and Booker *et al.* (2007).

Kumari *et al.* (2013) studied Palak (*Beta vulgaris* L. var Allgreen), "a cheap and popular leafy vegetable preferred mainly for iron content in the diet," which is "widely grown" and "suitable for all seasons in north India." Recognizing the global growth in both atmospheric CO_2 (an aerial fertilizer) and tropospheric ozone (O_3, an aerial pollutant) over the past two centuries, plus their anticipated future increases, Kumari *et al.* examined the interactive effects of these contrasting atmospheric molecules on the growth of palak. The three Indian researchers utilized open-top chambers at the botanical garden of Banaras Hindu University in the eastern Gangetic plains of India during December 2008 and January 2009, measuring morphological, biochemical, and yield responses of palak to ambient (A) and elevated (E) levels of CO_2 and O_3, alone and in combination. The atmospheric CO_2 concentrations employed in this study were ambient (normal air) and 570 ppm, and the O_3 concentrations utilized were ambient and ambient + 20 ppb, with the elevated values selected to match predicted concentrations at the end of the century under the A1B scenario of IPCC (2007).

Their analysis revealed elevated CO_2 enhanced various plant growth parameters in palak, including root length, shoot length, number of leaves, leaf area, root biomass, shoot biomass, total plant biomass, and yield (compare the ECO_2 values in Table 3.8.1.3.1 with the ACO_2 values), and elevated concentrations of ozone had a negative effect (compare the EO_3 values in Table 3.8.1.3.1 with the ACO_2 + AO_3 values). When enhanced ozone and enhanced carbon dioxide were tested together, the growth-enhancing effects of CO_2 were sufficient in every instance to overpower the growth-retarding effects of ozone for every plant parameter measured (compare the ECO_2 + EO_3 values in Table 3.8.1.3.1 with the ACO_2 + AO_3 values).

Kumari *et al.* conclude, for IPCC-predicted atmospheric concentrations of CO_2 and O_3 at the end of the century, "palak is going to be benefited as biomass enhancement was more under ECO_2 + EO_3 compared to ACO_2 + AO_3."

These studies indicate atmospheric CO_2 enrichment reduces, and more often than not completely overrides, the negative effects of ozone pollution on plant photosynthesis, growth, and yield.

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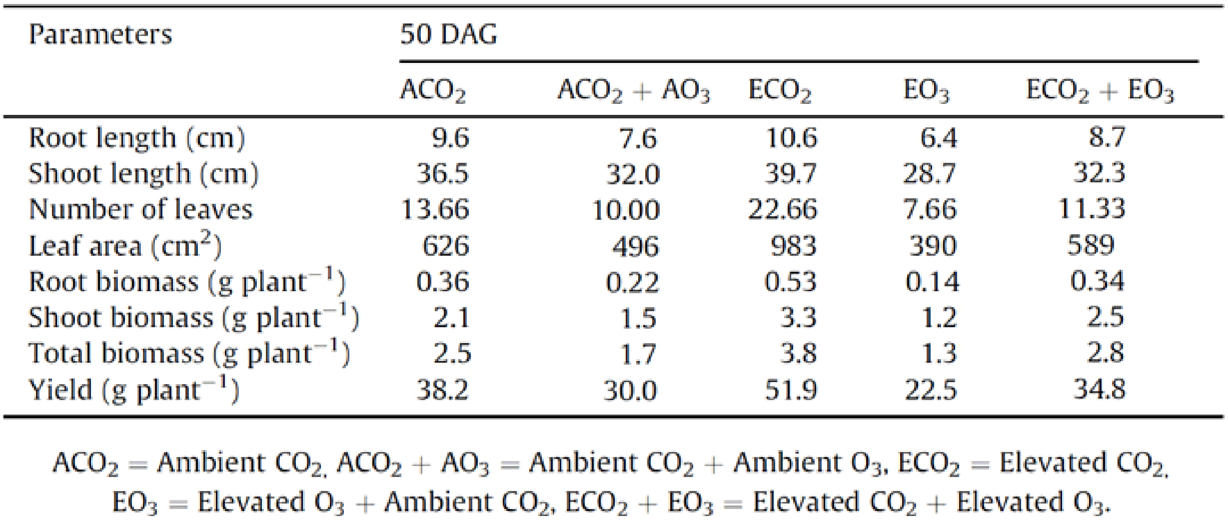

Parameters	50 DAG				
	ACO_2	$ACO_2 + AO_3$	ECO_2	EO_3	$ECO_2 + EO_3$
Root length (cm)	9.6	7.6	10.6	6.4	8.7
Shoot length (cm)	36.5	32.0	39.7	28.7	32.3
Number of leaves	13.66	10.00	22.66	7.66	11.33
Leaf area (cm^2)	626	496	983	390	589
Root biomass (g $plant^{-1}$)	0.36	0.22	0.53	0.14	0.34
Shoot biomass (g $plant^{-1}$)	2.1	1.5	3.3	1.2	2.5
Total biomass (g $plant^{-1}$)	2.5	1.7	3.8	1.3	2.8
Yield (g $plant^{-1}$)	38.2	30.0	51.9	22.5	34.8

ACO_2 = Ambient CO_2, $ACO_2 + AO_3$ = Ambient CO_2 + Ambient O_3, ECO_2 = Elevated CO_2, EO_3 = Elevated O_3 + Ambient CO_2, $ECO_2 + EO_3$ = Elevated CO_2 + Elevated O_3.

Table 3.8.1.3.1. Growth parameters of palak plants under different treatments of O_3 and CO_2, individually and in combination at 50 days after germination (DAG). Adapted from Kumari et al. (2013).

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3.8.2 Tree Species

3.8.2.1 Aspen

- Earth's aspen trees, like much of the rest of the biosphere, are better equipped to live long and productive lives in CO_2-enriched air, even when experiencing the generally negative influence of atmospheric ozone pollution.

Trees grown in CO_2-enriched air nearly always exhibit increased rates of photosynthesis and biomass production, and trees grown in ozone (O_3)-enriched air tend to experience the opposite effects. So what happens when both of these trace constituents of the atmosphere increase together? This question is explored below with respect to the most widely distributed tree species of North America: quaking aspen (*Populus tremuloides* Michx.).

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

King *et al*. (2001) studied the same young trees for two years, concentrating on belowground growth, where elevated O_3 alone had no effect on fine-root biomass. When the two aspen clones were simultaneously exposed to elevated CO_2 and O_3, there was an approximate 66% increase in the fine-root biomass of both. Wustman *et al*. (2001) found the aspen clones exposed to both elevated ozone and CO_2 had 40% fewer visible foliar injuries than clones exposed to elevated ozone and ambient CO_2.

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

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

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

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

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

Also studying the Aspen FACE site, Holton *et al.* (2003) raised parasitized and non-parasitized forest tent caterpillars on two quaking aspen genotypes (O_3-sensitive and O_3-tolerant) alone and in combination for one full growing season. They too found elevated O_3 improved tent caterpillar performance under ambient CO_2 conditions but not in CO_2-enriched air. Thus it is clear elevated ozone concentrations have significant negative impacts on the well-being of North America's most widely distributed tree species, and elevated carbon dioxide concentrations have significant positive impacts that often completely override the negative impacts of elevated O_3. Therefore, if the tropospheric O_3 concentration rises as expected (Percy *et al.* note "damaging O_3 concentrations currently occur over 29% of the world's temperate and subpolar forests but are predicted to affect fully 60% by 2100"), a concomitant rise in the air's CO_2 content will help to prevent damage to the planet's aspen trees.

Working at the same site, Oksanen *et al.* (2003) report they were able to "visualize and locate ozone-induced H_2O_2 [hydrogen peroxide] accumulation within leaf mesophyll cells, and relate oxidative stress with structural injuries in aspen." They discovered "H_2O_2 accumulation was found only in ozone-exposed leaves and not in the presence of elevated CO_2," leading them to conclude "CO_2 enrichment appears to alleviate chloroplastic oxidative stress."

King *et al.* (2005) evaluated the effect of CO_2 enrichment alone, O_3 enrichment alone, and the net effect of CO_2 and O_3 enrichment together after seven years of treatment at the Aspen FACE site. Relative to the ambient-air treatment, they found elevated CO_2 increased total biomass by 25%, whereas elevated O_3 decreased it by 23%. The combination of elevated CO_2 and O_3 resulted in a total biomass response of -7.8% relative to the control. King *et al.* thus conclude "exposure to even moderate levels of O_3 significantly reduces the capacity of net primary productivity to respond to elevated CO_2 in some forests." They suggest it makes sense to move forward with technologies that reduce anthropogenic precursors to photochemical O_3 formation, because their use would decrease an important constraint on the ability of forest ecosystems to benefit from the rise in the air's CO_2 concentration.

Kubiske *et al.* (2006) found individual tree and stand growth at the Aspen FACE site were significantly increased by the elevated CO_2 treatment but decreased by the elevated O_3 treatment, and the two effects essentially negated each other for no net change in the combined CO_2 plus O_3 treatment. They also state "growth in elevated CO_2 continued to increase each year but at a decreasing rate," such that "the annual growth increases under elevated CO_2 became smaller with each successive year." They examined several possible explanations for this phenomenon, including N limitations and water limitations.

The eight researchers write, "inter-annual variation in soil moisture did not modify the CO_2 or O_3 responses," and "N limitations on growth did not differ among treatments." In addition, they report "root-specific uptake of nitrate or ammonium was not affected by elevated CO_2 or O_3." The growth response to elevated CO_2 "paralleled decreasing July PPF [photosynthetic photon flux] from 2001 through 2004, and decreasing previous October temperatures from 2001 to 2003." Kubiske *et al.* conclude "a several-year trend of increasingly cloudy summers and cool autumns was responsible for the decrease in CO_2 growth response," explaining, "July PPF directly influences the amount of photosynthate available for stem volume growth," and "October temperature in the north-temperate latitudes is of major importance in the photosynthetic activity of trees before leaf senescence," the stored products of which are used "to support the determinate growth phase the following year."

Reporting the results of their study of the Wisconsin aspen trees during the eighth and ninth years of growing-season CO_2 enrichment, Riikonen *et al.* (2008) state elevated O_3 decreased net photosynthesis in aspen clone 42E by 30% and clone 271 by 13%, averaged over the growing season, and in aspen clone 216 by 42% in the late-season. Elevated CO_2 increased net photosynthesis in aspen clones 42E and 271 by 73 and 52%, respectively, averaged over the growing season, and in aspen clone 216, measured in the late-season only, elevated CO_2 enhanced net photosynthesis by 42%. They write, "elevated CO_2 delayed, and elevated O_3 tended to accelerate, leaf abscission in autumn." When both treatments were applied together, they report, "elevated CO_2 generally ameliorated the effects of elevated O_3," noting "leaf stomatal conductance was usually lowest in the combination treatment, which probably caused a reduction in O_3 uptake."

Kostiainen *et al.* (2008) studied interactive effects of elevated concentrations of CO_2 and O_3 on radial growth, wood chemistry, and structure of five 5-year-old trembling aspen clones at the Wisconsin FACE facility, where they had been exposed to four treatments—control, elevated CO_2 (560 ppm), elevated O_3 (1.5 x ambient), and their combination—for five full growing seasons. The researchers report, "elevated CO_2 in the presence of ambient O_3 tended to increase, and elevated O_3 in the presence of ambient CO_2 tended to decrease, stem radial growth," whereas "stem radial growth of trees in the combined elevated CO_2 + O_3 treatment did not differ from controls." None of the structural variables of the aspen wood was affected by the elevated CO_2 treatment, but elevated O_3 tended to decrease vessel lumen diameter.

Reporting on another aspect of the long-term aspen study at the Wisconsin FACE facility, Udling *et al.* (2008) investigated how a 40% increase above ambient values in CO_2 and O_3, alone and in combination, affected tree water use where "measurements of sap flux and canopy leaf area index (*L*) were made during two growing seasons, when steady-state *L* had been reached after more than 6 years of exposure to elevated CO_2 and O_3." The 40% increase in atmospheric CO_2 increased tree size and *L* by 40%, and the 40% increase in O_3 concentration decreased tree size and *L* by 22%. The combined effect of the two trace gas increases was an 18% increase in maximum stand-level sap flux. In addition, elevated O_3 predisposed aspen stands to drought-induced sap flux reductions, whereas increased tree water use in response to elevated CO_2 did not result in lower soil water content in the upper soil or decreasing sap flux relative to control values during dry periods.

Thus the negative effects of O_3 enrichment on tree growth and leaf development were more than compensated by the positive effects of an equal percentage increase in atmospheric CO_2 concentration. And although the net effect on sap flux was positive (so that the trees transferred more water to the atmosphere), when the aspen stands needed moisture most (during times of drought), the water was available to them, possibly because they "were growing in soil with CO_2-induced increases in litter build-up and water-holding capacity of the upper soil," as these latter two benefits and the extra water they could supply to the trees were lacking when the trees were exposed to elevated ozone.

Pregitzer *et al.* (2008) write, "all root biomass sampling previous to 2002 showed that O_3 exposure, alone or in combination with elevated CO_2, consistently resulted in lower coarse root biomass." In analyzing more recent data, they determined the elevated O_3 treatment significantly increased fine-root biomass in the aspen trees and, in combination with elevated CO_2, increased coarse root biomass in them as well. They conclude "the amount of carbon being allocated to aspen fine-root biomass under elevated O_3 is increasing over time relative to the control, especially in the elevated CO_2 and elevated O_3 treatment," in contrast with most shorter-term results, including those of King *et al*. (2001). Consequently, they conclude "the positive effects of elevated CO_2 on belowground net primary productivity may not be offset by negative effects of O_3."

Andrew and Lilleskov (2009) note sporocarps (the reproductive structures of fungi) can be significant carbon sinks for the ectomycorrhizal fungi that develop symbiotic relationships with plants by forming sheaths around their root tips, where they are the last sinks for carbon in the long and winding pathway that begins at the source of carbon assimilation in plant leaves. The researchers say "it is critical to understand how ectomycorrhizal fungal sporocarps are affected by elevated CO_2 and O_3" because "sporocarps facilitate genetic recombination, permit long-distance dispersal and contribute to food webs."

They sampled aboveground sporocarps for four years at the Aspen FACE site, which provided, they write, a "unique opportunity to examine the effects of both elevated CO_2 and O_3 on a forested ecosystem." They conducted their examination during years 4 through 7 of the long-term study. They report total mean sporocarp biomass "was generally lowest under elevated O_3 with ambient CO_2," and it "was greatest under elevated CO_2, regardless of O_3 concentration." They state there was "a complete elimination of O_3 effects on sporocarp production when [extra] CO_2 was added," noting they "expect that the responses seen in the present study were conservative compared to those expected under regional to global changes in CO_2 and O_3."

By itself, or in combination with rising ozone concentrations, the rise in the air's CO_2 content appears destined to enhance the genetic recombination and long-distance dispersal of the ectomycorrhizal fungi that form symbiotic relationships with the roots of aspen and other trees, thereby positively contributing to various food webs that will be found in Earth's forests of the future.

Zak *et al*. (2011) noted how both insufficient soil nitrogen (N) and an overabundance of atmospheric ozone have been claimed to either partially or totally repress the many positive effects of elevated atmospheric CO_2 concentrations on plant growth and development, especially in the case of long-lived woody plants such as trees. However, they write, the combined effects of elevated CO_2 and elevated O_3 (eCO_2 and eO_3) "remain undocumented in the context of long-term, replicated field experiments." In 1997 the four researchers planted at the Rhinelander (Wisconsin, USA) FACE facility one-half of each of 12 FACE plots with various trembling aspen (*Populus tremuloides*) genotypes (8, 42, 216, 259, 271) of differing CO_2 and O_3 sensitivities. They planted one-quarter of each ring with a single aspen genotype (226) and paper birch (*Betula papyrifera*), and another quarter of each ring with the same single aspen genotype and sugar maple (*Acer saccharum*). The authors maintained each FACE plot for 12 years at either ambient CO_2 and O_3 (aCO_2 and aO_3), aCO_2 and eO_3, eCO_2 and aO_3, or eCO_2 and eO_3—where eCO_2 was 560 ppm, and where eO_3 was in the range of 50–60 nmol/mol—while they collected numerous types of pertinent data.

In reference to the progressive nitrogen limitation hypothesis, Zak *et al*. (2011) say they "found no evidence of this effect after 12 years of eCO_2 exposure." Relative to net primary production (NPP) under aCO_2, they found a 26% increase in NPP in the eCO_2 treatment over the last three years of the study, which for a more standard 300-ppm increase in atmospheric CO_2 concentration equates to an approximate 42% increase in NPP. The increase "was sustained by greater root exploration of soil for growth-limiting N, as well as more rapid rates of litter decomposition and microbial N release during decay."

With respect to the concomitant stress of O_3 pollution, the researchers report, "despite eO_3-induced reductions in plant growth that occurred early in the experiment (i.e., after three years of exposure), eO_3 had no effect on NPP during the 10th-12th years of exposure." This response, they write, "appears to result from the compensatory growth of eO_3-tolerant genotypes and species as the growth of eO_3-sensitive individuals declined over time (Kubiske *et al*., 2007; Zak *et al*., 2007), thereby causing NPP to attain equivalent levels under ambient O_3 and elevated O_3."

Zak *et al*. (2011) write, "NPP in the three plant communities responded similarly to the combined eCO_2 and eO_3 treatment." And "given the degree to which eO_3 has been projected to decrease global NPP (Felzer *et al*., 2005), the compensatory growth of eO_3-tolerant plants in our experiment should be considered in future simulations and, depending on the generality of this response, could dramatically diminish the negative effect of eO_3 on NPP and carbon storage on land."

The four researchers ultimately conclude if forests of similar composition growing throughout northeastern North America respond in the same manner as those in their experiment (Cole *et al*., 2009), enhanced forest NPP under eCO_2 may be sustained for a longer duration than previously had been thought possible. They conclude, "the negative effect of eO_3 may be diminished by compensatory growth of eO_3-tolerant plants as they begin to dominate forest communities (Kubiske *et al*., 2007; Zak *et al*., 2007), suggesting that aspects of biodiversity like genetic diversity and species composition are important components of ecosystem response to this agent of global change."

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3.8.2.2 Beech

- Even when faced with the generally negative influence of atmospheric ozone pollution on their leaves, shoot axes, coarse roots, and fine roots, as well as the carbohydrate (starch and soluble sugar) contents and concentrations of those plant parts, these adverse effects of ozone on beech trees are typically more than counteracted by atmospheric CO_2 enrichment.

In discussing the problem of elevated tropospheric ozone (O_3) concentrations, Liu *et al*. (2004) write, "ozone is considered to be one of the air pollutants most detrimental to plant growth and development in both urban and rural environments (Lefohn, 1992; Skarby *et al*., 1998; Matyssek and Innes, 1999)," because it "reduces the growth and yield of numerous agronomic crops as well as fruit and forest trees (Retzlaff *et al*., 1997; Fumagalli *et al*., 2001; Matyssek and Sandermann, 2003)." In addition, they note ozone concentrations are "currently two to three times higher than in the early 1900s (Galloway, 1998; Fowler *et al*., 1999)," and likely "will remain high in the future (Elvingson, 2001)." This section addresses studies that have examined the effects of ozone on European beech (*Fagus sylvatica* L.) trees.

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

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

Grams *et al*. (1999) grew European beech seedlings in glasshouses maintained at average atmospheric CO_2 concentrations of either 367 or 667 ppm for one year. Throughout the following year, in addition to being exposed to the same set of CO_2 concentrations, the seedlings were exposed to either ambient or twice-ambient levels of O_3. Elevated O_3 significantly reduced photosynthesis in beech seedlings grown at ambient CO_2 concentrations by a factor of approximately three. In the CO_2-enriched air, the seedlings did not exhibit any photosynthetic reduction due to the doubled O_3 concentration. The photosynthetic rates of the CO_2-enriched seedlings rose by 8% when simultaneously fumigated with elevated O_3, leading the five researchers to conclude long-term acclimation to elevated CO_2 supply does indeed counteract the O_3-induced decline of photosynthetic light and dark reactions.

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

These results add more evidence of the ability of increased CO_2 concentrations to fight—and overpower—the deleterious consequences of one of the world's most devastating air pollutants.

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3.8.2.3 Birch

- Birch trees are generally harmed by rising ozone concentrations, but when the air's CO_2 concentration is also rising, these negative effects are generally eliminated and replaced by positive responses.

At the free-air CO_2 enrichment (FACE) facility located near Rhinelander, Wisconsin (USA), King *et al*. (2001) grew a mixture of paper birch and quaking aspen trees in 30-m-diameter plots maintained at atmospheric 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 two years. The extra O_3 had no effect on the growth of fine roots over that period, but elevated O_3 and CO_2 together increased the fine-root biomass of the mixed stand by 83%.

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

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

Riikonen *et al.* (2004) harvested the same trees and reported "the negative effects of elevated O_3 were found mainly in ambient CO_2, not in elevated CO_2." Doubling the air's O_3 concentration decreased total biomass production by 13% across both clones, but simultaneously doubling the air's CO_2 concentration increased total biomass production by 30%, more than compensating for the deleterious consequences of doubling the atmospheric ozone concentration.

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

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

At the Rhinelander, Wisconsin (USA) FACE facility, Agrell *et al.* (2005) examined the effects of ambient and elevated concentrations of atmospheric CO_2 and O_3 on the foliar chemistry of birch and aspen trees, plus the consequences of these effects for host plant preferences of forest tent caterpillar larvae. They note "the only chemical component showing a somewhat consistent co-variation with larval preferences was condensed tannins," and they report "the tree becoming relatively less preferred as a result of CO_2 or O_3 treatment was in general also the one for which average levels of condensed tannins were most positively (or least negatively) affected by that treatment."

The researchers found the mean condensed tannin concentration of birch leaves was 18% higher in the elevated CO_2 and O_3 treatment. Consequently, as atmospheric concentrations of CO_2 and O_3 continue to rise, the increases in condensed tannin concentrations likely to occur in the foliage of birch trees should lead to their leaves becoming less preferred for consumption by the forest tent caterpillar, which according to Agrell *et al.* is "an eruptive generalist defoliator in North American hardwood forests, causing extensive damage during outbreak years (Fitzgerald, 1995)."

King *et al.* (2005) evaluated the effect of CO_2 enrichment alone, O_3 enrichment alone, and the net effect of both CO_2 and O_3 enrichment together on the growth of the Rhinelander birch trees. In the ambient-air control treatment, elevated CO_2 increased total biomass by 45% in the aspen-birch community; elevated O_3 caused a 13% reduction in total biomass relative to the control. The combination of elevated

CO_2 and O_3 resulted in a total biomass increase of 8.4% relative to the control aspen-birch community. King *et al.* conclude "exposure to even moderate levels of O_3 significantly reduces the capacity of net primary productivity to respond to elevated CO_2 in some forests."

Kostiainen *et al.* (2006) studied the effects of elevated CO_2 and O_3 on various wood properties of silver birch. They found the elevated CO_2 treatment had no effect on wood structure but increased annual ring width by 21%, woody biomass by 23%, and trunk starch concentration by 7%. Elevated O_3 decreased stem vessel percentage in one of the clones by 10% but had no effect on vessel percentage in the presence of elevated CO_2.

Kostiainen *et al.* note, "in the xylem of angiosperms, water movement occurs principally in vessels (Kozlowski and Pallardy, 1997)," and "the observed decrease in vessel percentage by elevated O_3 may affect water transport." They continue, "elevated CO_2 ameliorated the O_3-induced decrease in vessel percentage." In addition, they note "the concentration of nonstructural carbohydrates (starch and soluble sugars) in tree tissues is considered a measure of carbon shortage or surplus for growth (Korner, 2003)." They conclude "starch accumulation observed under elevated CO_2 in this study indicates a surplus of carbohydrates produced by enhanced photosynthesis of the same trees (Riikonen *et al*., 2004)." In addition, they report, "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."

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

Darbah *et al*. report "the seeds produced under elevated O_3 had much less stored carbohydrate, lipids, and proteins for the newly developing seedlings to depend on and, hence, the slow growth rate." They conclude, "seedling recruitment will be enhanced under elevated CO_2 but reduced under elevated O_3," another important reason to hope the atmosphere's CO_2 concentration continues to climb as long as the air's O_3 content is doing so as well.

Riikonen *et al*. (2008) studied physiological consequences of increases in the atmospheric concentrations of CO_2 (+36%) and O_3 (+39%)—both alone and in combination—in paper birch trees during the eighth and ninth years of growing-season CO_2 enrichment at the Rhinelander FACE site. They determined elevated O_3 decreased net photosynthesis in birch short-shoot leaves by 27%, averaged over the growing season, and in birch long-shoot leaves by 23% in the late season, whereas elevated CO_2 increased net photosynthesis in birch short-shoot leaves by 49% averaged over the growing season. They also report, for birch long-shoot leaves, measured in the late-season only, elevated CO_2 enhanced net photosynthesis by 42%. In addition, "elevated CO_2 delayed, and elevated O_3 tended to accelerate, leaf abscission in autumn." When both treatments were applied together, the scientists note, "elevated CO_2 generally ameliorated the effects of elevated O_3," adding "leaf stomatal conductance was usually lowest in the combination treatment, which probably caused a reduction in O_3 uptake."

Darbah *et al*. (2008) at various times over the 2004–2007 growing seasons collected many types of data pertaining to flowering, seed production, seed germination, and new seedling growth and development of young paper birch trees at the Rhinelander FACE site. Giving results for O_3 elevation first and CO_2 enrichment second (as best can be determined from Darbah *et al*.'s graphs and text), the following percentage changes were derived for:

- number of trees producing male flowers: (+86%, +140%) in 2006, (+70%, +70%) in 2007,
- total number of male flowers produced (+58%, +260%) in 2006, (+68%, +82%) in 2007,
- mean catkin or flower cluster mass (-8%, +12%) in 2004,
- mean seed mass (-22%, +10%) in 2004, (-24%, +17%) in 2005, (-22%, -2%) in 2006,

- mean seed germination success (-70%, +70%) in 2004, (-60%, +110%) in 2005, (-50%, +20%) in 2006,
- mean seedling mortality, where the greatest reductions represent the greatest benefits, (-9%, -73%) in 2004,
- mean seedling root length (+15%, +59%) in 2004,
- mean seedling shoot length (-7%, +21%) in 2004,
- mean seedling cotyledon length (-5%, +13%) in 2004, and
- mean seedling dry mass after approximately five months growth in ambient air (-38%, +69%) in 2004.

Summarizing their findings, the six researchers write, "in this study, we found that elevated CO_2 enhances and elevated O_3 decreases birch reproduction and early seedling growth," while in the concluding sentence of their abstract, they write, "the evidence from this study indicates that elevated CO_2 may have a largely positive impact on forest tree reproduction and regeneration while elevated O_3 will likely have a negative impact."

Kostiainen *et al.* (2008) investigated the interactive effects of elevated concentrations of CO_2 and O_3 on the wood chemistry of paper birch saplings at the FACE facility in Rhinelander, where the saplings had been exposed to four treatments—control, elevated CO_2 (560 ppm), elevated O_3 (1.5 x ambient), and their combination—for five growing seasons. They found the paper birch saplings exhibited a tendency for increased stem diameter in elevated CO_2, that also caused "an increase in extractives," such as fats, waxes, triterpenoids, and steroids, that have important roles to play in defense against pathogens and other biotic attacks. The nine researchers conclude the increased growth they observed in response to elevated CO_2 "can be foreseen to shorten rotation lengths, with only moderate changes in wood properties," which is good. However, "in response to elevated O_3, stem wood production decreased and was accompanied by changes in vessel properties, which may indicate decreasing efficiency of water and nutrient transport," which is not good. Here, too, the major negative effects of the elevated O_3 concentration were reversed by the positive effects of the elevated CO_2 concentration.

Uddling *et al.* (2008) studied how a 40% increase in CO_2 and O_3, alone and in combination, affected tree water use of mixed aspen-birch forests in the Rhinelander FACE study, where sap flux and canopy leaf area index (L) were measured during two growing seasons, when steady-state L had been reached after more than six years of exposure to elevated CO_2 and O_3. The 40% increase in atmospheric CO_2 concentration increased tree size and L by 40%, and the 40% increase in O_3 concentration decreased tree size and L by 22%. The combined effect of the two trace gas increases was an 18% increase in maximum stand-level sap flux in the mixed tree stands.

Pregitzer *et al.* (2008) write, "all root biomass sampling [at the Rhinelander FACE facility] previous to 2002 showed that O_3 exposure, alone or in combination with elevated CO_2, consistently resulted in lower coarse root biomass for all plant communities." In their analysis of subsequent data, however, they found $+O_3$ in combination with $+CO_2$ increased coarse root biomass in birch/aspen communities, leading them to conclude the amount of carbon being allocated to fine-root biomass under elevated O_3 was increasing over time relative to the control, especially in the $+CO_2$ $+O_3$ treatment, in contrast with most shorter-term results. They conclude, "the positive effects of elevated CO_2 on belowground net primary productivity may not be offset by negative effects of O_3."

For three years (1999–2001) Vapaavuori *et al.* (2009) grew 20 initially seven-years-old individual trees of each of two different silver birch (*Betula pendula* Roth) clones—4 and 80 (V5952 and K1659, respectively, in the Finnish forest genetic register)—out-of-doors at the Suonenjoki Research Unit site of the Finnish Forest Research Institute in individual open-top chambers maintained at all combinations of ambient CO_2 and ambient O_3, ambient CO_2 and double O_3, double CO_2 and ambient O_3, and double CO_2 and double O_3, where CO_2 treatments were imposed 24 hours per day and O_3 treatments were imposed for 12, 12, and 14 hours per day in 1999, 2000, and 2001, respectively. Throughout the course of the experiment they measured a variety of plant physiological responses to the four treatments, including net photosynthesis, leaf stomatal conductance, leaf soluble proteins, leaf phenolic compounds, leaf nutrient concentrations, trunk and branch growth, physiology of the foliage and root systems, crown structure, wood properties, and interactions with folivorous insects.

The 12 scientists report the negative effects of elevated O_3 on the various growth parameters and properties of the trees "were mainly found in ambient CO_2," noting elevated CO_2 typically "reversed or diminished the effects of elevated O_3."

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3.8.2.4 Yellow Poplar

- As the air's CO_2 content rises, yellow-poplar trees likely will display substantial increases in photosynthetic rate and biomass production, even under conditions of elevated O_3 concentrations, and the soils in which the trees grow should therefore sequester increasing quantities of carbon.

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

Loats and Rebbeck (1999) grew yellow-poplar seedlings for 10 weeks in pots placed in growth chambers filled with ambient air, air with twice the ambient CO_2 concentration, air with twice the ambient O_3 concentration, and air with twice the ambient CO_2 and O_3 concentrations, to determine the effects of elevated CO_2 and O_3 on photosynthesis and growth in this deciduous tree species. They found doubling the air's CO_2 concentration increased the rate of net photosynthesis by 55% in ambient O_3 air; at twice the ambient level of O_3 it stimulated net photosynthesis by an average of 50%. The doubled CO_2 concentration significantly increased total biomass by 29%, and the doubled O_3 concentration had little impact on growth.

Rebbeck *et al.* (2004) grew yellow poplar seedlings for five years in open-top chambers in a field plantation at Delaware, Ohio (USA), exposing them continuously from mid-May through mid-October of each year to charcoal-filtered air to remove ambient O_3, ambient O_3, 1.5 times ambient O_3, or 1.5 times ambient O_3 plus 350 ppm CO_2 above ambient CO_2. The trees were never fertilized during the study, and they received no supplemental water beyond some given in the first season.

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

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3.8.2.5 Miscellaneous

- The positive effects of atmospheric CO_2 enrichment generally more than compensate for the negative effects of elevated ozone concentrations on tree growth.

Ozone (O_3) is the primary air pollutant responsible for visible foliar injury and reduced growth in trees the world over. Most studies of the subject suggest it gains entrance to leaves through their stomata, where it interferes with the process of photosynthesis and thereby reduces plant productivity. Fowler *et al*. (1999) described the global significance of the phenomenon in some detail by estimating O_3 to have been negatively affecting a quarter of Earth's forests at the close of the twentieth century, and calculating it to have the potential to negatively affect one-half of the planet's forests by 2100.

In one of the earlier studies of the subject, Kainulainen *et al*. (1998) constructed open-top chambers around Scots pine (*Pinus sylvestris* L.) trees about 20 years old and fumigated them with combinations of ambient or CO_2-enriched air (645 ppm) and ambient or twice-ambient (20 to 40 ppb) ozone-enriched air for three growing seasons, to study the interactive effects of these gases on starch and secondary metabolite production. They discovered elevated CO_2 and O_3 had no significant impact on the trees' starch production, even after two years of treatment exposure. Near the end of the third year, elevated CO_2 alone significantly enhanced starch production in current-year needles. But neither elevated CO_2 nor O_3, acting alone or together, had any significant effects on the concentrations of the secondary metabolites the researchers investigated.

Kainulainen *et al*.'s paper made clear the need for long-term studies of tree responses to atmospheric CO_2 enrichment. Whereas no effects of elevated CO_2 on starch production were found after two years of treatment exposure, starch concentrations in needles ultimately increased significantly in the CO_2-enriched trees late into the third year of the study. It's hardly surprising that long-lived perennial plants, such as trees, require long-term CO_2-enrichment studies to reveal how they will respond to the rising concentration of atmospheric CO_2. This study suggests over time, Scots pine trees may respond to the rising CO_2 content of the air with increases in starch concentration, which can be mobilized to provide carbohydrates for active plant sinks to increase total tree size and biomass. In addition, if ozone continues to accumulate in the lower atmosphere, Scots pine may not display any adverse response to it, as atmospheric CO_2 enrichment seems able to protect against O_3-induced harm.

Broadmeadow *et al*. (1999) studied several species of young trees, including sessile oak (*Quercus petraea*), European beech (*Fagus sylvatica*), and sweet chestnut (*Castanea sativa*), to determine how their responses to ozone exposure are affected by elevated CO_2 and other environmental variables. They found elevated CO_2 generally reduced the amount of ozone damage by inducing stomatal closure, which decreased the uptake of this air pollutant. This study suggests, as the air's CO_2 concentration continues to rise, many tree species likely will exhibit reductions in stomatal conductance, which should reduce the negative effects of tropospheric ozone on their growth and development.

Herman *et al*. (2001) note air pollution by SO_2, Pb, NOx, and NH_3 had been significantly reduced in central Europe over the two decades prior to their study, but ozone levels were still on the rise, based on trends derived from European databases that included ozone measurements from about 100 stations in Austria and Germany. The parameter Herman *et al.*

used to express the significance of these ozone trends was the *AOT40* Critical Level set by the UN-ECE (1994), which had a value of 10 ppm.h and was defined as accumulated ozone exposure above a threshold of 40 ppb 24 hours per day over the six-month growing season of April–September, which in controlled experiments had been documented to cause approximate 10% reductions in tree biomass production.

As a measure of how bad ozone pollution had become in central Europe, in most of the grid plots of the Austrian Forest Inventory Grid, and based on 1993 ozone data, Herman *et al*. report "the Critical Level of 10 ppm.h had been exceeded up to sevenfold," and "where standards had been exceeded to such an alarming extent, serious damage of forest trees should be expected."

So what did the trees in these highly ozone-polluted grid plots look like? Were they absolutely devastated? Or dead? Herman *et al*. report, "the results of the Austrian monitoring surveys did not reflect such damage." They note, for example, "neither the general evaluation of the foliage losses in the context of the crown condition inventories nor the development of the growing stock reflect a dramatic situation." Not only were there no "dramatic" reductions in tree health and productivity, there were typically none at all, and in many areas there were actually improvements, such as crown conditions in Austria looking slightly better and the growing stock increasing.

Herman *et al*. acknowledge that although ozone-related losses of biomass could not be confirmed on old trees, under the ozone levels of that day they did show some reductions in photosynthetic CO_2 uptake. This phenomenon was particularly evident in old trees at high altitudes, where AOT40 values were much more extreme, and in trees experiencing "additional climatic stress." But the researchers were careful to add "the reductions of the CO_2 uptake were in no proportion to the massive excess of the AOT40."

Ozone exposures more than sevenfold greater than the Critical Level (which Critical Level alone should have decreased tree productivity by 10%) were occurring all across the Austrian Forest Inventory Grid, and such conditions could have been expected to reduce the growth rates of the exposed trees by 70% or more. Yet there was no evidence of any widespread damage or productivity reduction. In fact, growth conditions seemed to have improved almost everywhere, except at high altitudes and under conditions of more-than-usual climatic stress.

Herman *et al*. suggest these observations imply the once-adequate Critical Level of ozone exposure was no longer suitable for application. Why? Because "the significant parameter for the assessment of the risk" is not the atmospheric concentration of ozone, but "the absorbed dose." Therefore, they advise the creation of a new Critical Level that "takes into account leaf conductance and the environmental parameters influencing it."

This latter statement is an example of the proper approach to risk assessment, for there are many concurrent and ongoing changes in Earth's atmosphere and the net result of all of them acting in concert must be considered when predicting the consequences of changes in any individual factor. In the case of Earth's climate, for example, the surface air temperature effects of an increase in the air's CO_2 content cannot be adequately evaluated without considering the effects of concurrent changes in atmospheric aerosol quantities and properties. Likewise, in the case of ozone and forest health, the biological consequences of rising tropospheric ozone concentrations cannot be adequately evaluated without considering the effects of the concurrent rise in the air's CO_2 content, which is known to have a significant impact on leaf conductance and, hence, largely determines a tree's critical "absorbed dose" of ozone. When this more rational approach has been followed, numerous laboratory and field experiments have shown realistically scaled concurrent increases in atmospheric CO_2 and ozone concentrations typically lead to very little change in plant net productivity. The lack of substantial negative ozone-induced impacts on the forests of central Europe, as described by Herman *et al*., may have been the result of the compensatory beneficial impacts of the historical and still-ongoing rise in the air's CO_2 content.

King *et al*. (2005) note preindustrial concentrations of tropospheric O_3 were estimated to have been less than 10 ppb, but subsequently rose to the 30–40 ppb background levels of their day, referencing Levy *et al*. (1997). In addition, they report the rising boundary-layer O_3 concentration caused by increasing industrialization around the globe has had negative continent-scale implications for carbon sequestration (Felzer *et al*., 2004). Thus they sought to evaluate the net effect of the positive CO_2 and negative O_3 impacts of possible future increases in these trace atmospheric gases on the productivity of the most widespread tree species found in North America—trembling aspen (*Populus tremuloides* Michx.)—and two-member mixed communities of trembling aspen-paper birch (*Betula papyrifera* Marsh.) and trembling aspen-sugar maple (*Acer saccharum* Marsh.).

Working at the Aspen FACE site (Dickson *et al*., 2000) near Rhinelander, Wisconsin (USA), King *et al*. allowed pure stands of aspen and mixed stands of aspen-birch and aspen-maple to grow for seven years in ambient air, air enriched with an extra 200 ppm of CO_2, air enriched with an extra 50% O_3. or air thus enriched by both CO_2 and O_3. Relative to the ambient-air control treatment, the eight researchers found elevated CO_2 increased "total biomass 25, 45, and 60% in the aspen, aspen-birch and aspen-maple communities, respectively," while elevated O_3 "caused 23, 13, and 14% reductions in total biomass relative to the control in the respective communities." The combination of elevated CO_2 and O_3 "resulted in total biomass responses of -7.8, +8.4, and +24.3% relative to the control in the aspen, aspen-birch and aspen-sugar maple communities, respectively."

King *et al*. conclude "exposure to even moderate levels of O_3 significantly reduces the capacity of net primary productivity to respond to elevated CO_2 in some forests."

Gardner *et al*. (2005) grew pre-flushed hardwood stem cuttings of the inter-American (*Populus trichocarpa* Torr. & Gray ex Hook. *x P. deltoides* Bartr. ex Marsh) hybrid poplar clone 'Boelare' out-of-doors in eight open-top chambers for two growing seasons of 132 and 186 days (first and second years, respectively), measuring a number of plant properties and physiological processes. Two of the eight chambers were maintained at ambient carbon dioxide (350 ppm) and ozone concentrations (A), two at ambient CO_2 with daily O_3 episodes rising to a mid-day peak of 100 ppb (AO), two at elevated CO_2 (700 ppm) and ambient O_3 (E), and two at elevated CO_2 and O_3 (EO) throughout the first year of the study. Only CO_2 was elevated during the second year.

With respect to the effect of CO_2 alone, Gardner *et al*. write mainstem dry weight "was increased by 38% in 700-ppm CO_2 compared with that in 350-ppm CO_2 at the end of the first growing season," and "during year 2 mainstem dry weight increased by about 5-fold and the relative effect of elevated CO_2 remained similar in magnitude (32%) to that seen in the first year." During the first season of exposure, mainstem dry mass was decreased by 45% in the O_3-episode treatment in 350-ppm CO_2, and by 34% in the O_3-episode treatment in 700-ppm CO_2. Because of the strong growth-promoting effect of the extra CO_2, the O_3-induced change in growth when going from the ambient-CO_2-ambient-O_3 treatment to the elevated-CO_2-elevated-O_3 treatment was only a reduction of 10%, as compared to the O_3-induced reduction of 45% when CO_2 was not increased concurrently.

The British researchers conclude "elevated levels of CO_2 can play a key role in ameliorating the worst effects of severe ozone episodes on a relatively sensitive tree species," and "O_3 episodes are less likely to be detrimental to *P. trichocarpa x P. deltoides* in the CO_2 concentrations of the future."

Noting the "detrimental effects of ozone on plants are well known" and "CO_2 generally affects trees in opposite ways to ozone," Valkama *et al*. (2007) conducted a literature review they describe as "the first quantitative analysis of the interactive effects of elevated O_3 and elevated CO_2 on tree chemistry and herbivore performance," based on the results of 63 studies conducted on 22 tree species and 10 insect herbivore species published between 1990 and 2005.

With respect to the ways elevated O_3 may benefit insect herbivores that tend to damage trees, Valkama *et al*. write, "elevated O_3 significantly shortened development time of insect herbivores [when they are exposed and vulnerable to attack by various enemies] and increased their pupal mass in the overall dataset." In addition, the "relative growth rate of chewers was significantly increased by 3.5% under elevated O_3." They report "these effects were counteracted by elevated CO_2," such that "elevated O_3 in combination with CO_2 had no effect on herbivore performance," with the exception that when elevated CO_2 was added to the O_3-enriched air, it not only counteracted the O_3-induced increase in pupal biomass, but reduced it below what it was in ambient air by 7%. This analysis of the vast majority of experimental data obtained prior to 2006 suggests in the interaction between insect herbivores and trees, the rise in the air's CO_2 content likely plays an extremely important role in negating, and in some cases even more than negating, the damage insect pests would otherwise do to forests.

Wittig *et al*. (2007) calculated the increase in the atmosphere's O_3 concentration since the start of the Industrial Revolution had caused a mean decrease of 11% in the leaf photosynthetic CO_2 uptake of temperate and boreal forests. Based on projections derived from the A2 storyline of the *Special Report on Emissions Scenarios* included in IPCC's Fourth Assessment Report (which indicate atmospheric O_3 concentrations could rise 20–25% between 2015 and 2050, and could further increase by 40–60% by 2100 if current emission trends continue), they calculate temperate and boreal forest photosynthetic rates could decline by an additional 8–16% by the end of the century.

Fortunately, the stomatal-aperture-constricting effect of concomitant past increases and anticipated future increases in the air's CO_2 content tend to counter the negative influence of rising O_3 concentrations by retarding O_3 entry into plant leaves. In addition, the CO_2-induced increase in leaf photosynthesis (its "aerial fertilization effect") has been shown to often more than compensate for the negative influence of ozone on leaf photosynthesis rates. These welcome findings comprise only half of the good news about rising CO_2 concentrations and their impact on the ozone problem.

It is a well-established fact that vegetative isoprene emissions are responsible for the production of vast amounts of tropospheric ozone (Chameides *et al*., 1988; Harley *et al*., 1999). Poisson *et al*. (2000) calculated current levels of non-methane hydrocarbon (NMHC) emissions (the vast majority of which are isoprene, accounting for more than twice as much as all other NMHCs combined) likely increase surface ozone concentrations from what they would be in their absence by up to 50–60% over land. In addition, although little appreciated, it has been known for some time that atmospheric CO_2 enrichment typically leads to large reductions in isoprene emissions from plants. This phenomenon typically has not been factored into projections of future atmospheric O_3 concentrations.

Arneth *et al*. (2007) addressed this issue, noting future vegetative isoprene emissions typically have been modeled to rise in tandem with projected increases in vegetative biomass and productivity driven by projected changes in various environmental factors. This protocol, in an anticipated warmer and CO_2-enriched environment, generally has led to predictions of significant increases in isoprene emissions and, therefore, significant increases in future atmospheric O_3 concentrations, as Wittig *et al* predicted. However, Arneth *et al*. convincingly demonstrate "a quite different result is obtained when the direct CO_2 effect on isoprene emissions is included," noting in this more-realistic situation a properly forced model "maintains global isoprene emissions within ± 15% of present values."

The seven Swedish and UK researchers thus conclude "predictions of high future tropospheric O_3 concentrations partly driven by isoprene emissions may need to be revised."

Xu *et al*. (2012) report "levels of atmospheric CO_2 and O_3 have increased rapidly in the last five decades," and "it is predicted that at the end of this century, the average levels of CO_2 and O_3 in Earth's atmosphere are going to reach 700 ppm and 80 ppb, respectively (IPCC, 2007)." Thus, in an experiment designed to evaluate the opposing effects of these two atmospheric trace gases on Chinese pine (*Pinus tabulaeformis*) trees at the year AD 2100, they grew four-year-old trees in loamy soil with no extra fertilizer in 12 open-top chambers in May 2006 in the populated central area of Shenyang city in northeastern China, where the trees were exposed to either current ambient air of about 400 ppm CO_2 and 40 ppb O_3 or 700 ppm CO_2 and 80 ppm O_3, plus all combinations thereof.

This study revealed elevated CO_2 by itself increased growth but "did not significantly affect net photosynthetic rate, stomatal conductance, chlorophyll content, the maximum quantum yield of photosystem II, or the effective quantum yield of photosystem II electron transport after 90 days of gas exposure." Elevated O_3 by itself "decreased growth, net photosynthetic rate and stomatal conductance after 90 days of exposure," but Xu *et al*. note "its negative effects were alleviated by elevated CO_2."

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3.9 Non-Ozone Air Pollutants

- Despite being labeled by the United Nations and U.S. Environmental Protection Agency as a dangerous air pollutant, not only is CO_2 not a "pollutant," as those entities claim it is; it is actually an anti-pollutant that helps plants overcome the negative effects of real air and soil pollutants and better enables their removal from polluted areas.

In addition to ozone, many other airborne substances can damage plant life. This section explores the scientific literature pertaining to the negative effects of some of these other harmful components of the planet's atmosphere and how these negative effects can be alleviated by atmospheric CO_2 enrichment.

Lee *et al*. (1997) note, "several studies using controlled-environment chambers have shown that CO_2 may compensate for sulfur dioxide (SO_2)-induced leaf injury (Black, 1982; Carlson and Bazzaz, 1982; Darrall, 1989; Sandhu *et al*., 1992; Rao and De Kok, 1994; Niewiadomska and Miszalski, 1995; Tausz *et al*., 1996)." They conducted a similar study out-of-doors using open-top chambers placed over soybeans (*Glycine max* L. Merr. cv. Essex) growing in a typical field situation, to determine whether the positive effects of atmospheric CO_2 enrichment would compensate for the negative effects of elevated SO_2 concentrations on soybean photosynthetic rates. They exposed the soybeans to either ambient (350 ppm) or elevated (500 ppm) atmospheric CO_2 concentrations in combination with atmospheric SO_2 concentrations of either 0.00 or 0.12 ppm. They describe the latter concentration as being sufficient to produce "potentially toxic effects over long term exposure."

They found, throughout the period of pod filling, the mean photosynthetic rate of plants growing in ambient-CO_2 but elevated-SO_2 air was 17.2% lower than the mean rate of plants growing in ambient-CO_2 and SO_2-free air, and the mean photosynthetic rate of plants growing in CO_2-enriched but SO_2-free air was 25.1% higher than the mean rate of plants growing in ambient-CO_2 and SO_2-free air. The mean photosynthetic rate of plants growing in CO_2-enriched and elevated-SO_2 air was 33.4% greater than the mean rate of plants growing in ambient-CO_2 and SO_2-free air. Enriching the air with CO_2 more than compensated for the negative effects of the elevated SO_2 on the photosynthetic rates of the soybeans the five researchers studied.

Deepak and Agrawal (2001) grew two cultivars of soybeans (*Glycine max* L. Merr. Cv. PK472 and Bragg) in open-top chambers at atmospheric CO_2 concentrations of either 350 or 600 ppm, both alone and in combination with 60 ppb SO_2, to determine the individual and interactive effects of elevated CO_2 and SO_2 on the growth and yield of this important crop. Exposure to the elevated SO_2 significantly reduced total plant biomass and grain yield by approximately 18% in both cultivars. In contrast, elevated CO_2 significantly increased total plant biomass and grain yield in both cultivars by averages of 30 and 34%, respectively. When the plants were exposed simultaneously to elevated SO_2 and CO_2, the negative effects of SO_2 were completely ameliorated.

Agrawal and Deepak (2003) conducted a similar study of two cultivars of wheat (*Triticum aestivum* L. cv. Malviya 234 and HP1209) in open-top chambers maintained at atmospheric CO_2 concentrations of 350 and 600 ppm both alone and in combination with 60 ppb SO_2, to study the individual and interactive effects of elevated CO_2 and SO_2 on another of the world's major crops. They found exposure to elevated CO_2 boosted photosynthetic rates by 58 and 48% in M234 and HP1209, respectively, and fumigation with elevated SO_2 had no significant impact on rates of photosynthesis in either cultivar. Plants grown in the combined treatment of elevated CO_2 and elevated SO_2 displayed slightly lower photosynthetic rates, but they were still 42 and 38% greater than those measured in control plants for M234 and HP1209, respectively.

The plants grown in elevated CO_2 in this experiment also displayed an approximate 20% reduction in stomatal conductance, and those grown in elevated SO_2 exhibited an average conductance increase of 15%. When exposed simultaneously to both gases, the plants displayed an average 11% reduction in stomatal conductance. This phenomenon contributed to an approximate 32% increase in water-use efficiency (plant growth per unit of water used) for plants simultaneously exposed to increased concentrations of both gases, whereas plants exposed to elevated SO_2 alone displayed an average decrease in water-use efficiency of 16%. In addition, plant exposure to elevated SO_2 caused an average 13% decrease in foliar protein concentrations in both cultivars, but when the plants were concurrently exposed to an atmospheric CO_2 concentration of 600 ppm, leaf protein levels decreased by only 3% in HP1209 and increased by 4% in M234.

As the air's CO_2 content rises, it likely will reduce the stress and growth reductions of these specific wheat cultivars and others as a consequence of SO_2 pollution. Agrawal and Deepak's study demonstrates CO_2-induced increases in photosynthesis will be only partially offset by elevated SO_2 concentrations, which should allow greater wheat yields to be produced in the future under similar conditions. In addition, since SO_2-induced reductions in plant water-use efficiency were essentially eliminated by concurrent plant exposure to elevated CO_2, these cultivars should be able to grow better in areas with limited water availability and in areas close to industrial complexes emitting large quantities of SO_2. Also, wheat plants growing in SO_2-polluted air should not suffer as large a reduction in foliar protein content in a future high-CO_2 world as they do today.

Izrael *et al.* (2002) evaluated the effects of sulfur dioxide pollution on Russian forests. Among other things, the five researchers report "sulfur dioxide (SO_2) causes widespread damage to plants, because it can spread through large distances, and its emissions into the atmosphere are large." In 1996, for example, they found "total SO_2 emission from the industrial areas of Russia comprised 5866.76 thousand tons, or 42.2% of the total emission of liquid and gaseous pollutants." They determined 1.3 million hectares of Russian forest land had been adversely affected by SO_2 pollution. They estimated total forest destruction occurs on 2–5% of this area, and heavy, moderate, and slight damage occur on 10–15%, 30–40%, and 40–50% of this area, respectively.

These results indicate the seriousness of SO_2 pollution for forest health, and they highlight the fact that atmospheric CO_2 enrichment can significantly alleviate SO_2's adverse biological consequences. Hallgren (1984), for example, demonstrated a 300 ppm increase in the air's CO_2 concentration stimulated the photosynthetic rate of Scots pine trees by 64% in unpolluted air and by 77% in air with abnormally high SO_2 concentrations. Hallgren also found a 600-ppm increase in atmospheric CO_2 stimulated photosynthetic rates in this important forest species by 85% in unpolluted air and 110% in air of high SO_2 concentration. Similarly, Carlson (1983) found a 900-ppm increase in the air's CO_2 concentration boosted photosynthetic rates of soybeans by 87% in unpolluted air and 715% in high-SO_2 air. Thus the rise in the air's CO_2 content can do much to prevent or significantly alleviate the adverse consequences of SO_2 pollution.

Several studies have been conducted at naturally occurring CO_2 springs in Tuscany, Italy, providing a unique opportunity to examine the effects of long-term atmospheric CO_2 enrichment on plant growth and development. These springs also emit elevated concentrations of the major phytotoxic air pollutants H_2S and SO_2 (Schulte *et al*., 1999). Consequently, the springs provide a suitable setting in which to study the relative strengths of two competing phenomena: the growth-promoting effect of elevated CO_2 and the growth-retarding effects of elevated H_2S and SO_2.

Grill *et al*. (2004) analyzed various properties of leaves and acorns produced on two species of oak tree (*Quercus ilex* L. and *Quercus pubescens* L.) growing in air of double-to-triple the normal atmospheric CO_2 concentration near the CO_2 springs, and the same characteristics of leaves and acorns growing on similar trees located some distance away in ambient-CO_2 air. They also analyzed several characteristics of seedlings they sprouted from acorns produced by the CO_2-enriched and ambient-treatment trees, and they used chromosome stress tests "to investigate whether alterations in sulfur-regime have negative consequences for seedlings."

The six scientists report "acorns from CO_2 springs contained significantly higher sulphur concentrations than controls (0.67 vs. 0.47 mg g^{-1} dry weight in *Q. ilex* cotyledons and 1.10 vs. 0.80 in *Q. pubescens*)," indicating the trees were indeed significantly affected by the H_2S- and SO_2-enriched air in the vicinity of the CO_2-emitting springs. They also note *Q. ilex* seedlings grown from CO_2-spring acorns showed elevated rates of chromosomal aberrations in root tips, suggestive of a permanent stress. Nevertheless, as demonstrated by the results of several studies conducted on mature trees from these sites, the CO_2-enriched air—even in the presence of significantly elevated concentrations of phytotoxic H_2S and SO_2—significantly enhanced the trees' photosynthetic capacity: by 26–69% (Blaschke *et al*., 2001), 36–77% (Stylinski *et al*., 2000), and 175–510% (Tognetti *et al*., 1998).

Jia *et al*. (2010) note "mining and smelting, disposal of sewage sludge and the use of cadmium rich phosphate fertilizers (Wagner, 1993; Liu *et al*., 2007) have contaminated a large proportion of the agricultural land throughout the world, causing an increase in the soil concentration of many heavy metals." They further note, "as one of the most toxic environmental pollutants (Zhang *et al*., 2009) cadmium (Cd) has a strong influence on metabolic activities of crop plants by inducing a number of physiological changes, such as growth inhibition, changes in water and ion metabolism, photosynthesis inhibition, enzyme activity changes, and free radical formation (Ekmekci *et al*., 2008)," stating "even at relatively low concentrations cadmium can exert strong toxic effects on crops (Seregin and Ivanov, 2001)."

The seven scientists grew Italian and perennial ryegrass (*Lolium mutiflorum* and *L. perenne*) in pots filled with soil from a long-term experimental rice field in Guangdong Province, China, which they treated to contain either 0, 25, or 100 mg Cd per kg soil. They fertilized the soils to contain 150 mg N/kg, 100 mg P/kg, and 150 mg K/kg, after which (once the ryegrass seeds had sprouted) the pots were taken outdoors and distributed among six open-top chambers. Three of these (one each for the three soil cadmium concentrations) were maintained at the ambient atmospheric CO_2 concentration of 375 ppm, and three were maintained at an elevated CO_2 concentration of 810 ppm from 0800 to 1700 hours throughout all 58 days of the summer study. During this time and at the conclusion of the study, they measured a number of plant physiological processes and parameters.

Jia *et al*. found elevated CO_2 significantly increased both net photosynthesis and plant water use efficiency, which led to increases in both shoot and root biomass at harvest. "When compared with the ambient CO_2 control, the increase in total biomass due to elevated CO_2 was about 32 and 31% for *L. multiflorum* and *L. perenne*, respectively, grown on the control soil; 37 and 45% on soil amended with 25 mg/kg Cd; [and] 46 and 52% on soil spiked with 100 mg/kg Cd, respectively." In addition to these very positive results, compared to the ambient CO_2 control, under elevated CO_2 both *Lolium* species had decreased Cd concentrations in their shoots and roots, where "the decreased magnitude of Cd concentration in *L. multiflorum* and *L. perenne* grown on soil spiked with 25 mg/kg Cd was 10.3 and 3.8% for the shoots, and 18.6 and 14.7% for the roots, respectively; for those [plants] grown on soil spiked with 100 mg/kg Cd, it was 8.4 and 8.9% for the shoots, and 12.5 and 13.9% for the roots, respectively."

Thus atmospheric CO_2 enrichment not only spurred both ryegrass species to produce more root and shoot biomass, but this greater amount of plant material contained reduced concentrations of a toxic soil pollutant. Jia *et al*. conclude, “given expected global increases in CO_2 concentration, elevated CO_2 may help plants better survive in contaminated soil and reduce the food safety risk due to CO_2-induced reduction and dilution in heavy metal concentration.”

Not only is carbon dioxide not a “pollutant,” as the United Nations and U.S. Environmental Protection Agency claim, it is actually an *anti*-pollutant that helps plants overcome the negative effects of real air and soil pollutants and remove them from polluted areas.

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3.10 Phosphorus Insufficiency

- Plants growing in CO_2-enriched air typically respond by increasing their biomass production, even under conditions of low soil phosphorus content, especially if the plants possess the ability to increase root phosphatase activity.

Under current ambient conditions, plant growth and development are typically carbon-limited, which is why plants generally exhibit increased growth and biomass production in response to atmospheric CO_2 enrichment. Next to carbon, nitrogen is usually the second-most-limiting nutrient to plant growth, followed by phosphorus. Although it is a less-significant component of plant tissues than carbon and nitrogen, phosphorus is still required for successful life-cycle completion in many plant species. It is thus important to investigate aspects of plant phosphorus acquisition and biomass production in response to atmospheric CO_2 enrichment when phosphorus concentrations in soils are less than optimal.

In an early study of the subject, Barrett *et al.* (1998) demonstrated a doubling of the air's CO_2 content under continuous phosphorus deficiency increased wheat root phosphatase activity by 30 to 40%, thus increasing the inorganic phosphorus supply available for plant utilization. As phosphatase is the primary enzyme responsible for the mineralization of organic phosphate, which thereby makes phosphorus available for plant use, an increase in its activity with elevated CO_2 could facilitate sustained plant growth responses to the rise in the air's CO_2 content, even in areas where growth is currently limited by phosphorous deficiencies. And because these increases in phosphatase activity also were observed under sterile growing conditions, this response can be mediated directly by plant roots without involving soil microorganisms, which are known to aid in phosphorus mineralization.

As the air's CO_2 content continues to rise, phosphatase activity in wheat roots should increase, increasingly converting organic phosphorus into inorganic forms that support the increased plant growth and development stimulated by higher CO_2 concentrations. As a similar increase in phosphatase activity at elevated CO_2 already has been reported for a native Australian pasture grass, these results may be applicable to most of the planet's vegetation. If that turns out to be true, plants that are currently phosphorus-limited in their growth might increase their phosphorous acquisition from soil organic supplies as the atmosphere's CO_2 concentration rises, and this phenomenon, in turn, may allow them to sequester even greater amounts of carbon from the air.

Other studies also have investigated plant biomass responses to atmospheric CO_2 enrichment under conditions of limiting phosphorus supply. Staddon *et al.* (1999), for example, found *Plantago lanceolata* and *Trifolium repens* effectively increased their phosphorus-use efficiency under elevated CO_2 conditions by reducing shoot phosphorus content as a component of CO_2-induced photosynthetic acclimation. Walker *et al.* (1998) found ponderosa pine seedlings grown for a year at atmospheric CO_2 concentrations of 525 and 700 ppm exhibited significantly greater root, shoot, and total dry weights than control plants grown at ambient CO_2, with little influence of a superimposed phosphorus treatment (low vs. high).

Niklaus *et al.* (1998) explored the effects of elevated CO_2, nitrogen, and phosphorus supply on calcareous grassland communities. At low phosphorus concentrations, biomass nitrogen contents were unaffected by elevated CO_2 (600 ppm), whereas at high phosphorus concentrations, community biomass-nitrogen increased by 28%, suggesting community biomass nitrogen will increase in the future if soil phosphorus contents are increased. A companion study of these grasslands published by Stocklin and Korner (1999) showed community total biomass (the actual dry weight of plant material, not the amount of nitrogen in the plant material) increased with atmospheric CO_2 enrichment even under low phosphorus concentrations, with or without nitrogen-fixing legumes present in the grassland swards.

Nguyen *et al.* (2006) grew seedlings of two N-fixing woody plants (*Acacia auriculiformis* Cunn. ex Benth and *Acacia mangium* Willd) well irrigated and fertilized—except for phosphorus (P), of which there were three treatments (low, medium, and high) composing 10, 50, and 100 mg P/liter of soil mixture—in growth chambers maintained at atmospheric CO_2 concentrations of either ambient or ambient + 800 ppm. They found plant biomass of *A. auriculiformis* was enhanced by 19%, 21%, and 57%, respectively, at high, medium, and low P. Biomass in *A. mangium* was enhanced by 5%, 32%, and 47%, respectively. Nguyen *et al.* also note, "in both species the increase in plant growth [caused] by elevated CO_2 was accompanied by increased P use efficiency," "increased N use efficiency[,] and total N accumulation." In addition, they write, "elevated CO_2 also increased P use efficiency for N_2 fixation." Consequently, under ambient CO_2, "plant growth and the amount of N fixed symbiotically in N_2-fixing seedlings decreased with the decrease of supplied P," but "this relationship did not occur under elevated CO_2," because "elevated CO_2 alleviated [the] low P-induced reduction in plant growth," mainly by "increasing the use efficiency of internal P for plant growth and N_2 fixation."

Nguyen *et al.* note in many parts of the world "*Acacia* species are grown for environmental protection and energy plantations on degraded soils," and their findings indicate these soils' low nutrient levels may not impede the growth of these important plants.

Khan *et al.* (2008) note the faster and more vigorous plant growth typically observed in CO_2-enriched air "has to be sustained by a sufficient nutrient supply," because "if increased biomass production is to continue, [nutrient] availability in the soil has to match increasing demand for major nutrients," such as nitrogen (N) and phosphorus (P), two of the elements "often considered to limit productivity in terrestrial ecosystems." Khan *et al.* set out to test this hypothesis as it pertains to phosphorus at the EuroFACE facility near Viterbo in central Italy. They grew three genotypes of *Populus*—*P. alba*, *P nigra,* and *P. x euroamericana*—under ambient and elevated (ambient + 200 ppm) atmospheric CO_2 concentrations for five years.

The four UK researchers report "increased tree growth under elevated CO_2 has not resulted in the depletion of phosphorus pools in soils as originally hypothesized, but rather in the replenishment and increased storage of P in the rooting zone," and thus "P may not, therefore, limit tree growth in a high CO_2 world." Kahn *et al.* conclude "biogenically driven weathering of primary minerals in the rooting zone is sufficient to maintain the replenishment of plant available inorganic P," and "since future levels of elevated CO_2 may stimulate biomass production in a diverse range of forests (Norby *et al*., 2005), this increase of P availability is of global consequence."

Kahn *et al.* (2010) report similar findings in the same EuroFACE experiment, writing, "the availability of P can actually increase in elevated CO_2, forming a positive feedback with increased biomass production on P limited soils." They conclude "phosphorus limitation may therefore not reduce tree growth in a high CO_2 world."

Plants growing in CO_2-enriched air likely will respond by increasing their biomass production, even under conditions of low soil phosphorus concentration, especially if plants have the ability to increase root phosphatase activity, as Barrett *et al.* (1998) observed regarding wheat.

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3.11 The Progressive Nitrogen Limitation Hypothesis

The progressive nitrogen limitation hypothesis suggests low concentrations of soil nitrogen will impede the productivity-enhancing and carbon-sequestering effects of rising atmospheric CO_2 concentrations over the long term. The following three sections explore this possibility as it pertains to Earth's grasslands, loblolly pine trees, and other types of vegetation.

3.11.1 Grasslands

- Real-world data from several multiyear experiments indicate CO_2-induced increases in carbon input to the soil stimulate microbial decomposition and thus lead to more available soil nitrogen, contrary to the progressive nitrogen limitation hypothesis.

Richter *et al*. (2003) measured gross rates of N mineralization, NH_4^+ consumption, and N immobilization in soils on which monocultures of *Lolium perenne* and *Trifolium repens* had been exposed to ambient (360 ppm) and elevated (600 ppm) concentrations of atmospheric CO_2 for seven years in the Swiss FACE study conducted near Zurich. After seven years of exposure to elevated CO_2, "gross mineralization, NH_4^+ consumption and N immobilization in both the *L. perenne* and the *T. repens* swards did not show significant differences," and the size of the microbial N pool and immobilization of applied mineral ^{15}N were not significantly affected by elevated CO_2. The five researchers conclude their observations "did not support the initial hypothesis," which was "that increased below-ground translocation of photoassimilates at elevated pCO_2 would lead to an increase in immobilization of N due to an excess supply of energy to the roots and rhizosphere" and would ultimately lead to a reduction in the size of the growth-promoting effect of elevated atmospheric CO_2.

After five years of exposure of a nutrient-poor low-productivity calcareous grassland in northwestern Switzerland to atmospheric CO_2 concentrations of 360 and 660 ppm via screen-aided CO_2 control or SACC technology (Leadley *et al*., 1997), Thurig *et al*. (2003) measured the vegetative and reproductive responses of the plants comprising the ecosystem. They write, "the effect of elevated CO_2 on the number of flowering shoots (+24%, $P < 0.01$) and seeds (+29%, $P = 0.06$) at the community level was similar to [the] above ground biomass response." They also found a 42% ($P < 0.01$) increase in the mean seed number of graminoids and a 33% ($P = 0.07$) increase in the mean seed number of forbs, and in most species mean seed weight also tended to be greater (+12%, $P < 0.01$). Atmospheric CO_2 enrichment significantly increased both vegetative and reproductive biomass production. The researchers note many studies have shown heavier seeds result in seedlings that "are more robust than seedlings from lighter seeds (Baskin and Baskin, 1998)." Thus the continued rise of the air's CO_2 content would bode well for these and other nutrient-poor, low-productivity grasslands.

Reich *et al*. (2006) described the first six years' results of a FACE study of perennial grassland species conducted at the Cedar Creek Natural History Area in central Minnesota (USA). On natural ambient-N soil (where N limits growth) or natural soil receiving an extra 4 g N m^{-2} yr^{-1} (applied as NH_4NO_3), they planted 296 field plots to support the growth of either 1, 4, 9, or 16 grassland species (four C_3 grasses, four C_4 grasses, four N-fixing legumes, and four non-leguminous forbs). The plots were fumigated with either ambient air of ~370 ppm CO_2 or air enriched to a CO_2 concentration of 560 ppm throughout each year's growing season. The nine researchers conclude "low availability of N progressively suppresses the positive response of plant biomass to elevated CO_2."

Their data, however, do not support this conclusion. As best as can be determined from their graph of total plant biomass vs. time in their ambient-N plots (see Figure 3.11.1.1), the percent increase in plant biomass production induced by the extra ~190 ppm of CO_2 supplied to the CO_2-enriched plots progressed from 15% in year 1 to 16% in year 2, 13% in year 3, 0% in year 4, 8% in year 5, and 12% in year 6. Over the first three years of the study, it is difficult to claim there is any meaningful trend in the data, but in year 4 it is clear something happened, as the CO_2-induced growth stimulation dropped to zero. The CO_2-induced growth stimulation reappeared in year 5, rising from 0% to 8%, and it continued its upward climb in year 6, rising from 8% to 12%. The latter value is probably not significantly different from the 13% biomass stimulation recorded in year 3.

The behavior illustrated in Figure 3.11.1.1 is not a low-soil-N-induced "progressive limitation" of the aerial fertilization effect of elevated CO_2. The percent growth enhancement experienced in year 6 of Reich *et al.*'s study was essentially the same as that experienced in year 3, and the record ends with the aerial fertilization effect in a strong ascending mode. As for years 1 and 2, where the CO_2-induced growth stimulation was slightly higher, Reich *et al.* state, "the positive response to CO_2 enrichment observed under ambient N during the first two years of the experiment may also be more characteristic of seedlings or juvenile plants than of mature well-established plants." This phenomenon (initial large CO_2-induced growth stimulation in the juvenile plant stage which subsequently decreases with time) has been observed in a number of experiments, indicating just how risky it is to predict the course of the CO_2-induced aerial fertilization effect of atmospheric CO_2 enrichment on the basis of even multiple years of data.

These observations indicate there is no compelling reason to believe, as Reich *et al.* concluded, "low availability of N progressively suppresses the positive response of plant biomass to elevated CO_2." There is not even a weak reason for doing so, as their data depict no such phenomenon. And even if the trend they postulate were apparent, the long-term sour orange tree study of Idso and Kimball (2001; see section 1.1.3.2.3 Sour Orange, this volume) shows six years of data are simply not sufficient to predict the ultimate equilibrium response of a long-lived plant or ecosystem to a large step-increase in atmospheric CO_2 concentration in either N-limiting or non-N-limiting situations. In addition, in the real world of nature the air's CO_2 concentration rises gradually, by only a ppm or two per year, a much easier situation for plants to cope with than that employed in essentially all CO_2 enrichment experiments that have been conducted to date, where a CO_2 concentration increase fully two orders of magnitude greater than that experienced each year in nature is typically imposed on the plants being studied. Thus it is important to

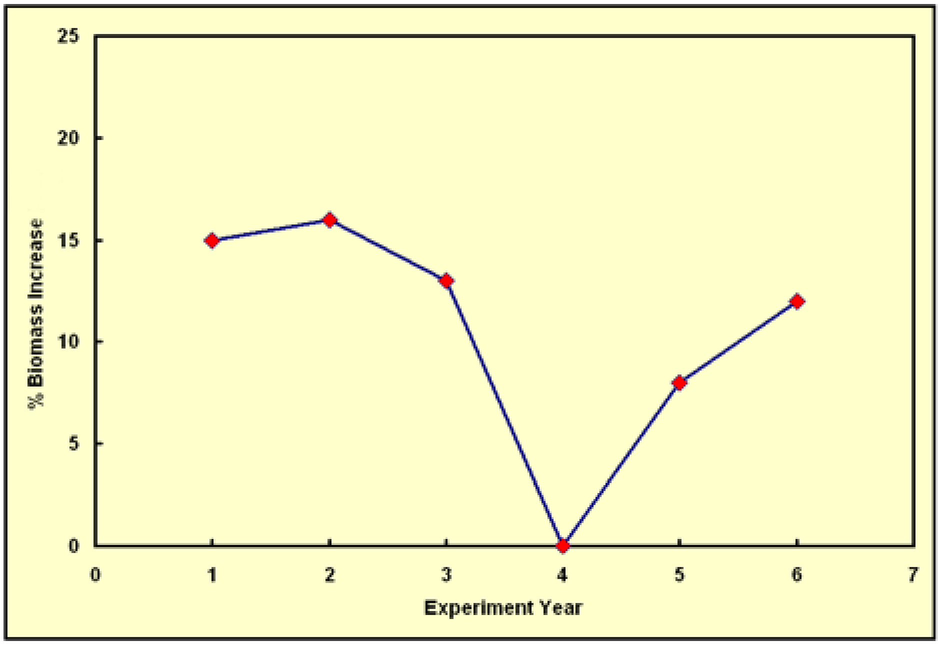

Figure 3.11.1.1. Percent increase in biomass production by the plants in the ambient-N soil plots of Reich *et al.* since the start of their long-term experiment, as a result of enriching the CO_2 concentration of the air above the plots by 190 ppm. Adapted from Reich *et al.* (2006)

conduct experiments for as long a period of time as possible—the answer is out there, but it could be far out there, several years in the future.

Zavaleta and Kettley (2006) studied an annual grassland at the Jasper Ridge Biological Preserve in the interior foothills of the central coast mountain range south of San Francisco, California (USA). They examined patterns of production, standing biomass, carbon and nitrogen storage, community composition, and soil moisture along a 25-year chronosequence of sites in various stages of invasion by the woody shrub *Baccharis pilularis*. They sought evidence for the hypothesis "*Baccharis*-invaded sites would experience increasing nitrogen limitation as nitrogen was immobilized in biomass and litter," and whether this phenomenon would preclude further increases in ecosystem biomass.

In progressing from initial grassland conditions to conditions that prevailed 25 years after shrub invasion began, the two researchers report, "net increases in biomass and tissue and soil C:N [carbon to nitrogen ratio] contributed to increases in total ecosystem carbon storage of over 125%." Even more stunning was their discovery the increases in ecosystem biomass "drove increases in ecosystem nitrogen sequestration of ~700%." In the soil alone, nitrogen content also "increased rapidly with shrub age," as the increase in soil nitrogen "was much larger than the increase in nitrogen immobilization in biomass and litter over time."

What was the source of the extra nitrogen? The two researchers mention several possibilities but say they could not be sure of them. Nevertheless, their observations repudiate the progressive nitrogen limitation hypothesis, making it clear a soil of low initial nitrogen status need not constrain long-term positive ecosystem responses to biomass-enhancing phenomena such as woody plant invasions and atmospheric CO_2 enrichment. Zavaleta and Kettley state, "while many climate models now incorporate the effects of short-term energy and resource exchanges between the atmosphere and the biosphere, most do not consider feedbacks associated with long-term vegetation changes." They also say their findings "illustrate the potential for important vegetation-mediated ecosystem responses and feedbacks to atmospheric CO_2 and climate change," while additionally noting many of the changes they observed "were progressive and did not saturate with time."

Drissner *et al*. (2007) measured soil microbial biomass and the activities of associated enzymes covering cycles of the most important elements (C, N, and P) for nine years in a FACE study conducted near Zurich, Switzerland, on three types of grassland (monocultures and mixed cultures of *Trifolium repens* L. and *Lolium perenne* L.) under two nitrogen treatments (low N = 14 g N m^{-2} $year^{-1}$; high N = 56 g N m^{-2} $year^{-1}$) and maintained at atmospheric CO_2 concentrations of either 350 or 600 ppm. They write, "the enrichment in CO_2 increased soil microbial biomass (+48.1%) as well as activities of invertase (+36.2%), xylanase (+22.9%), urease (+23.8%), protease (+40.2%) and alkaline phosphomonoesterase (+54.1%) in spring," and "in autumn, the stimulation of microbial biomass was 25% less and that of enzymes 3–12% less than in spring." All of these increases, the researchers write, "were most likely stimulated by increase in roots under enriched CO_2."

Drissner *et al*. report in their nine-year-long FACE experiment, "stimulation of enzyme activities in the enriched CO_2 indicated enhanced C, N and P cycling and greater availabilities of nutrients for microbial and plant growth." They conclude their results "support the hypothesis of positive feedback proposed by Zak *et al*. (1993), who stated that additional C stimulates microbial decomposition and thus leads to more available N under enriched CO_2." Their results and others thus contradict periodic claims that the future availability of nitrogen will be too low to support large CO_2-induced increases in plant growth over the long term.

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3.11.2 Loblolly Pine

- Extensive experimentation on loblolly pine trees (plus several understory species) at the Duke Forest long-term free-air CO_2 enrichment (FACE) site has conclusively disproven the progressive nitrogen limitation hypothesis, instead suggesting the growth-enhancing benefits of atmospheric CO_2 enrichment should continue as the air's CO_2 content rises.

The progressive nitrogen limitation (PNL) hypothesis posits low concentrations of soil nitrogen will inhibit the productivity-enhancing effect of atmospheric CO_2 enrichment, meaning increases in plant growth and ecosystem carbon sequestration rates will not be sustained over long periods of time. In this section this possibility is explored as it pertains to loblolly pine (*Pinus taeda* L.) trees.

Finzi and Schlesinger (2003) measured and analyzed pool sizes and fluxes of inorganic and organic nitrogen in the forest floor and top 30 cm of mineral soil during the first five years of differential atmospheric CO_2 treatment of a stand of initially 13-year-old loblolly pine trees at the Duke Forest FACE facility in the Piedmont region of North Carolina (USA), where half of the experimental plots were maintained at an atmospheric CO_2 concentration approximately 200 ppm above ambient. The extra CO_2 significantly increased the input of carbon (C) and nitrogen (N) to the forest floor, as well as to the mineral soil in which the trees were growing. Finzi and Schlesinger report "there was no statistically significant change in the cycling rate of N derived from soil organic matter under elevated CO_2," and "neither the rate of net N mineralization nor gross $^{15}NH_4^+$ dynamics were significantly altered by elevated CO_2." They found "no statistically significant difference in the concentration or net flux of organic and inorganic N in the forest floor and top 30-cm of mineral soil after 5 years of CO_2 fumigation," adding, "microbial biomass was not a larger sink for N." Based on these findings, they rejected their original hypothesis, which was essentially the PNL hypothesis: that the extra CO_2 provided to the experimental plots would significantly increase the rate of nitrogen immobilization by the soil microbial communities found in the CO_2-enriched FACE arrays and thereby lead to a reduction in the magnitude of the growth stimulation initially manifest in the CO_2-enriched treatment.

Schafer *et al.* (2003) measured net ecosystem exchange (NEE) and net ecosystem production (NEP) at the Duke Forest FACE facility during the third and fourth years of the long-term CO_2 enrichment study conducted there. They found the extra 200 ppm of CO_2 supplied to the loblolly pine trees in the CO_2-enriched FACE arrays increased the entire canopy's net uptake of CO_2 (NEE) by 41%, and canopy NEP was increased by 44%. They note 87% of the extra NEP "was sequestered in a moderately long-term C pool in wood." This large increase in solidly sequestered carbon is remarkable, especially given that, as noted by Finzi and Schlesinger (2003), the soil at the Duke Forest FACE site at that time was in "a state of acute nutrient deficiency that can only be reversed with fertilization," which was not provided.

Finzi *et al.* (2006) again tested the PNL concept "using data on the pools and fluxes of C and N in tree biomass, microbes and soils" obtained from the first six years of the Duke Forest FACE study. As was the case three years earlier, "there was no reduction in the average stimulation of net primary production by elevated CO_2," even though "significantly more N was immobilized in tree biomass and in the O [soil] horizon under elevated CO_2." Also, and "in contrast to the PNL hypothesis," they write, "microbial-N immobilization did not increase under elevated CO_2, and although the rate of net N mineralization declined through time, the decline was not significantly more rapid under elevated CO_2." The 12 researchers also report, "mass balance calculations demonstrated a large accrual of ecosystem N capital," and the rate of the extra N accrual was "much greater than the estimated rate of N input via atmospheric deposition or heterotrophic N fixation." Noting "there are no plant species capable of symbiotic N fixation in this ecosystem," they say some other mechanism enabled the loblolly pine trees to obtain the extra N they needed to stave off the negative effects predicted by the PNL hypothesis; possibly, Finzi *et al*. write, by roots "actively taking up N and redistributing N from deeper in the soil profile."

Moore *et al*. (2006) report finding "a sustained increase in basal area increment over the first 8 years of [their] experiment," which varied between 13 and 27% in harmony with variations in weather and the timing of growth. They also report, "there was no evidence of a decline in the relative enhancement of tree growth by elevated CO_2 as might be expected if soil nutrients were becoming progressively more limiting," which normally would be expected, considering the unfertilized state of the soil in which the experiment was conducted.

Pritchard *et al*. (2008a) published the results they obtained from minirhizotrons employed to characterize the influence of the extra 200 ppm of CO_2 on the fine roots of the Duke Forest loblolly pines over the six-year period 1998–2004. Averaged over all six years, they found the extra CO_2 increased average fine-root standing crop by 23%, which compared well with the overall stimulation of tree net primary productivity of 18–24% observed over the period 1996–2002. They noted "the positive effects of CO_2 enrichment on fine root growth persisted 6 years following minirhizotron tube installation (8 years following initiation of the CO_2 fumigation)," finding no evidence of progressive nitrogen limitation to the stimulatory effect of atmospheric CO_2 enrichment. As a possible explanation for their findings, Pritchard *et al*. point out the distal tips of fine roots are "the primary site for initiation of mycorrhizal partnerships which are critical for resource acquisition and could also influence whether or not forests can sustain higher productivity in a CO_2-enriched world."

Pritchard *et al*. (2008b) focused their attention on the role played by ectomycorrhizal (ECM) fungi over five years, based on minirhizotron observations of fungal dynamics at the Duke Forest FACE site. Summed across all years of the study, the five researchers found the extra 200 ppm of CO_2 provided to the trees in the high-CO_2 treatment did not influence mycorrhizal production in the top 15 cm of the forest soil, but it increased mycorrhizal root-tip production by 194% throughout the 15–30 cm depth interval. Production of soil rhizomorph length was 27% greater in the CO_2-enriched plots than in the ambient-air plots.

Pritchard *et al*. state the CO_2-induced "stimulation of carbon flow into soil has increased the intensity of root and fungal foraging for nutrients," and "the shift in distribution of mycorrhizal fungi to deeper soils may enable perennial plant systems to acquire additional soil nitrogen to balance the increased availability of ecosystem carbohydrates in CO_2-enriched atmospheres." This additional acquisition of nitrogen in the CO_2-enriched plots of the Duke Forest FACE study was determined to be approximately 12 g N per m^2 per year.

Pritchard *et al*. also write, "the notion that CO_2 enrichment expands the volume of soil effectively explored by roots and fungi, and that foraging in a given volume of soil also seems to intensify, provides compelling evidence to indicate that CO_2 enrichment has the potential to stimulate productivity (and carbon sequestration) in N-limited ecosystems more than previously expected." While they also speculate "it is unlikely that ecosystem productivity will be stimulated by CO_2 enrichment indefinitely," nature had to this point in time proven such speculations invalid.

Summarizing their nine years of work at the Duke Forest FACE facility, Lichter *et al*. (2008) once again warn progressive nitrogen limitation may "accompany carbon sequestration in plants and soils stimulated by CO_2 fertilization, gradually attenuating the CO_2 response." They describe what they had learned about the PNL hypothesis over the prior nine years.

The nine scientists first note their data pertaining to forest-floor carbon pools indicate the existence of "a long-term steady-state sink" of about 30 g C per m^2 per year, which represents, they write, "a substantial increase in forest-floor C storage under elevated CO_2 (i.e. 29%)," which they attribute to "increased litterfall and root turnover during the first 9 years of the study." Second, below the forest floor, they say, "approximately 20% [of the mineral soil carbon formed during the prior nine years] has been allocated to stable pools that will likely remain protected from microbial activity and associated release as CO_2."

A third important finding was "a significant widening of the C/N ratio of soil organic matter in the upper mineral soil under both elevated and ambient CO_2," which suggests, as they describe it, "enhanced rates of soil organic matter decomposition are increasing mineralization and uptake to provide the extra N required to support the observed increase in primary productivity under elevated CO_2." And at the Duke Forest FACE site, Pritchard *et al.* (2008b) say this CO_2-induced increase in productivity amounted to approximately 30% annually, adding there is "little evidence to indicate a diminished response through time." They cite Finzi *et al.* (2007), who found the same to be true at the long-term forest FACE studies at Rhinelander, Wisconsin (USA), Oak Ridge National Laboratory (USA), and Tuscania (Italy).

Contrary to the early expectations of many scientists, many forests thought to have had access to less-than-adequate soil nitrogen supplies appear to be able to acquire the extra nitrogen they need to maintain the sizable increases in their growth rates driven by elevated concentrations of atmospheric CO_2. In North Carolina's Duke Forest, for example, "even after nine years of experimental CO_2 fertilization," as Lichter *et al.* (2008) note, "attenuation of the CO_2-induced productivity enhancement has not been observed," as Finzi *et al.* (2006) also found. This finding at this location is extremely significant because the growth of pine-hardwood forests in the southeastern United States often removes so much nitrogen from the soil they induce what Finzi and Schlesinger (2003) describe as "a state of acute nutrient deficiency that can only be reversed with fertilization," which, as noted earlier in this section, was not employed at the Duke Forest FACE study.

Jackson *et al.* (2009) describe new belowground data they obtained at the Duke Forest Face site, then present a synthesis of these and other results obtained from 1996 through 2008 to determine which variables may have shown a decrease in their response to atmospheric CO_2 enrichment during that period. Among many other things, they found, "on average, in elevated CO_2, fine-root biomass in the top 15 cm of soil increased by 24%," and in recent years the fine-root biomass increase "grew stronger, averaging ~30% at high CO_2." Regarding coarse roots with diameters greater than 2 mm and extending to a soil depth of 32 cm, they report, biomass sampled in 2008 was "twice as great in elevated CO_2." The graphical representation of their results indicates the coarse-root biomass was 130% greater, quite extraordinary given that the extra 200 ppm of CO_2 supplied to the air surrounding the CO_2-enriched trees represented an enhancement of only about 55% above ambient conditions. They conclude, "overall, the effect of elevated CO_2 belowground shows no sign of diminishing."

The four researchers also remark, "if progressive nitrogen limitation were occurring in this system, we would expect differences in productivity to diminish for trees in the elevated vs. ambient CO_2 plots," but "there is little evidence from estimates of aboveground or total net primary productivity in the replicated Duke experiment that progressive nitrogen limitation is occurring there or at other forest FACE experiments," citing Finzi *et al.* (2007).

McCarthy *et al.* (2010) analyzed data from the Duke Forest FACE experiment for the years 1996–2004, calculating the net primary productivity (NPP) of the entire ecosystem—including the loblolly pines' understory of various broadleaf species (*Liriodendron tulipifera, Liquidambar styraciflua, Acer rubrum, Ulmus alata, Cornus florida*) plus various other trees, shrubs, and vines—as "the sum of the production of coarse wood (stems, branches, coarse roots), leaf litter (lagged for pines), fine roots and reproductive structures."

They report "elevated CO_2 increased pine biomass production, starting in 1997 and continuing every year thereafter"; "the CO_2-induced enhancement remained fairly consistent as the stand developed"; and "elevated CO_2 increased stand (pine plus all other species) biomass production every year from 1997 onwards with no trend over time." They also noted the average yearly increase in NPP caused by the approximate 54% increase in the air's CO_2 content was 28%. In contradiction of the PNL hypothesis, the trees, bushes, and shrubs constituting the Duke Forest has continued to maintain the extra CO_2-enabled vitality it exhibited from the start of the study, with no subsequent sign of it tapering off.

Drake *et al.* (2011) described how the CO_2-induced enhanced rates of net primary production at the Duke Forest FACE site likely were sustained by a carbon cascade through the root-microbe-soil system. They write, "increases in the flux of carbon belowground under elevated CO_2 stimulated microbial activity" that in turn "accelerated the rate of soil organic matter decomposition and stimulated tree uptake of nitrogen bound to this soil organic matter." This process "set into motion a positive feedback maintaining greater carbon gain under elevated CO_2 as a result of increases in canopy nitrogen content and higher photosynthetic nitrogen-use efficiency," the consequence of which was "the dominance of carbon storage in tree biomass."

Drake *et al.* write, "the long-term increase in forest productivity under elevated CO_2 at the Duke FACE site appears to be maintained by a belowground exchange of tree carbon for soil nitrogen, with the quantity of carbon allocated belowground set by the availability of nitrogen in the soil and the demand for nitrogen to meet growth requirements." They note, "all of the belowground carbon fluxes thought to increase decomposition rates increased under elevated CO_2, including root production and mortality (Pritchard *et al*., 2008a), root exudation (Phillips *et al*., 2011), fungal rhizomorph production (Pritchard *et al*., 2008b) and allocation of carbon to mycorrhizal fungi (Garcia *et al*., 2008)." They conclude, "the preponderance of the evidence points to increased decomposition [of organic matter] in surface soils as the primary source of additional nitrogen taken up by the trees growing under elevated CO_2."

Phillips *et al.* (2011) opine "increased root exploration alone is unlikely to sustain plant nitrogen requirements under rising CO_2 unless accompanied by the concomitant stimulation of soil microbial activity and the release of nutrients from soil organic matter." Despite the presumed importance of root exudates in this scenario, they note no studies had yet quantified the effects of CO_2 enrichment on exudation by mature trees. They set out to do so in order to understand why progressive nitrogen limitation was not observed in some long-term studies of trees growing on nutrient-poor soil (Langley *et al*., 2009; McCarthy *et al*., 2010). Working at the Duke Forest FACE facility, the three researchers examined plant-microbe interactions in the rhizospheres and bulk soils of the various treatments, measuring differences in rhizosphere microbial activity and root exudation rates.

On an annual basis, Phillips *et al.* state, "exudation increased by *c.* 50% for trees enriched with CO_2 in non-fertilized plots," but trees were unaffected in this manner by CO_2 enrichment in fertilized plots, demonstrating "increased root carbon efflux from CO_2-enriched trees stimulates rhizosphere N cycling in low fertility soils." Their work provides additional evidence that "rhizosphere microbes such as actinomycetes, which produce NAGase enzymes and respond strongly to CO_2 at this site (Billings and Ziegler, 2008), are using energy derived from exudates to synthesize enzymes that release nitrogen from soil organic matter (Cheng and Kuzyakov, 2005)." They emphasize "this dramatic contrast between the fertilized and unfertilized treatments provides evidence that enhanced exudation is a mechanism trees employ for increasing nitrogen availability."

Phillips *et al.* write "the enhanced carbon flux from roots to soil in low fertility forests exposed to elevated CO_2 creates hotspots for microbial activity that are associated with faster rates of soil organic matter turnover and N cycling." This phenomenon provides the trees the extra nitrogen they need to take full advantage of the enhanced potential for growth provided by atmospheric CO_2 enrichment, contrary to the incorrect implications of the progressive nitrogen limitation hypothesis. Phillips *et al.* state their results "provide field-based empirical support suggesting that sustained growth responses of forests to elevated CO_2 in low fertility soils are maintained by enhanced rates of microbial activity and N cycling fueled by inputs of root-derived carbon."

Hofmockel *et al.* (2011) write, "several free-air CO_2 enrichment (FACE) experiments in North America have shown a continual stimulation in forest productivity under elevated CO_2 over time scales nearly reaching a decade (Finzi *et al*., 2006; Norby and Iversen, 2006; Zak *et al*., 2007; McCarthy *et al*., 2010)." In their own examination of the effects of elevated CO_2 on nitrogen (N) cycling in the Duke Forest, where elevated atmospheric CO_2 concentrations "consistently stimulated forest productivity" throughout the decade-long experiment being conducted there, Hofmockel *et al.* provide "an integrated understanding" of this phenomenon that serves as "a basis for inferring how C and N cycling in this forest may respond to elevated CO_2 beyond the decadal time scale."

"Using natural-abundance measures of nitrogen isotopes together with an ecosystem-scale ^{15}N tracer experiment," as the six scientists describe it, they "quantified the cycling of ^{15}N in plant and soil pools under ambient and elevated CO_2 over three growing seasons to determine how elevated CO_2 changed nitrogen cycling between plants, soil and microorganisms," after having first measured natural abundances of ^{15}N in plant and soil pools in the two CO_2 treatments over the prior year. They discovered "at the Duke FACE site, the rate at which N is being sequestered in plant biomass is greater than the rate of atmospheric deposition and heterotrophic N fixation," a finding also established by Finzi *et al.* (2002), Hofmockel and Schlesinger (2007), and Sparks *et al.* (2008). These findings suggest, they write, "soil organic matter decomposition supplies a significant fraction of plant N in both ambient and elevated-CO_2 conditions, but that this is greater under elevated CO_2."

Hofmockel *et al.* conclude, "in pine forests of the southeastern United States, rising CO_2 may elicit shifts in the mechanisms by which plants acquire nitrogen, allowing a sustained increase in net primary productivity for decades," further stating, "increased mineralization of nitrogen in the organic and 0–15 cm mineral horizon and deeper rooting are likely sustaining the elevated CO_2 enhancement of net primary productivity."

Ellsworth *et al.* (2012) "compiled a comprehensive dataset measured over ten years for a temperate pine forest of *Pinus taeda*, but also including deciduous species, primarily *Liquidambar styraciflua*," derived from "over one thousand controlled-response curves of photosynthesis as a function of environmental drivers (light, atmospheric CO_2 concentration [Ca] and temperature) measured at canopy heights up to 20 meters over eleven years (1996–2006)." From that data they generated "parameterizations for leaf-scale models for the Duke free-air CO_2 enrichment (FACE) experiment."

They found the enhancement of light-saturated leaf net photosynthesis (Anet) in *P. taeda* trees produced by an elevated Ca of +200 ppm was 67% for current-year needles in the upper crown of the trees in summer conditions over the 10-year period, and previous-year foliage Anet was enhanced by 30%. They note "the mean stimulation in light-saturated Anet averaged over the growing season of all years and across canopy positions and needle age classes was 53 ± 7%." In addition, "the photosynthetic enhancement responses to elevated Ca are mirrored in part by the pine biomass accumulation responses to elevated Ca across different years."

The eight researchers also report "co-dominant and sub-canopy *L. styraciflua* trees showed Anet enhancement of 62%," and "various understory deciduous tree species showed an average Anet enhancement of 42%." In addition, "the photosynthetic responses of shaded, understory leaves suggest a capacity to increase photosynthetic carbon capture in elevated Ca in shade-grown plants when measured in sunflecks," citing DeLucia and Thomas (2000). They note this response suggests "a competitive advantage to shade-tolerant species adapted for carbon capture in high sunlight or sunflecks in the understory over less shade-tolerant species."

This comprehensive set of photosynthesis measurements compiled over the course of the Duke Forest FACE study rebuts the progressive nitrogen limitation hypothesis, which posits the initial growth stimulation of atmospheric CO_2 enrichment will dwindle away as time progresses, especially in the case of the pine-hardwood forests of the southeastern United States, which often remove so much nitrogen from the soils in which they grow as to induce what Finzi and Schlesinger (2003) once described as "a state of acute nutrient deficiency that can only be reversed with fertilization." Ellsworth *et al.*'s work demonstrates this is simply not true. In another implication of their findings, the eight researchers conclude the observed "differences in photosynthetic responses between the over-story pines and deciduous tree sub-canopy suggest that increased Ca may have the potential to enhance the mixed-species composition of planted pine stands," and, by extension, "naturally regenerating pine-dominated stands."

Rounding out this review of the progressive nitrogen limitation hypothesis are Phillips *et al.* (2012), who write, "after nearly two decades of research on forest ecosystem responses to global change, uncertainty about the role of roots and rhizosphere processes in soil C and N retention and loss has limited our ability to predict biogeochemical feedbacks to long-term forest productivity." Working at the Duke Forest FACE site, where eight 30-meter-diameter plots of loblolly pine (*Pinus taeda* L.) trees were enriched with an extra 200 ppm of CO_2 from 1996 to 2010, and four similar plots were maintained under then-current ambient-air conditions, Phillips *et al.* measured root-induced changes in soil C dynamics of trees exposed to CO_2 and nitrogen enrichment by combining stable isotope analyses, molecular characterizations of soil organic matter, and microbial assays.

The six scientists conclude the CO_2-enriched trees "may be both enhancing the availability of N by stimulating microbial decomposition of soil organic matter via priming and increasing the rate at which N cycles through the microbial pools owing to the rapid turnover of N-rich fungal tissues," noting "the accelerated turnover of hyphal tissues under elevated CO_2 may represent an important source of N to plants and microbes." Referring to this CO_2-induced phenomenon as the Rhizo-Accelerated Mineralization and Priming, or RAMP, hypothesis, Phillips *et al.* suggest it may have "important consequences for N availability and forest productivity," which could be expected to sustain CO_2-enhanced tree growth over their lifetimes.

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3.11.3 Other Plants

- Although the progressive nitrogen limitation hypothesis initially was embraced by many scientists, a vast array of observational data has subsequently shown it dos not explain changes in real ecosystems.

The progressive nitrogen limitation (PNL) hypothesis—which contends low concentrations of soil nitrogen will gradually inhibit the aerial fertilization effect of atmospheric CO_2 enrichment—had its origins in the writings of Hungate *et al*. (2003) and Luo *et al*. (2004). Interestingly, the first of these papers contains considerable evidence that argues against its authors' contentions, as does a subsequent publication (Luo *et al*., 2006), the senior author of which was also senior author of the second paper.

Hungate *et al*. (2003) report the C:N ratio of tree biomass increases with increases in the air's CO_2 concentration, citing Hungate (1999) and Rastetter *et al*. (1992). This indicates increasing amounts of carbon can be stored in tree tissues per unit of nitrogen stored therein as the air's CO_2 content rises; as Hungate and his coauthors state, "soil C:N could also increase with rising atmospheric CO_2 concentration, allowing soil carbon accumulation without additional nitrogen."

Lou *et al*. (2006) conducted a meta-analysis of various C and N processes in plants and soils in response to atmospheric CO_2 enrichment based on experimentally derived data contained in 104 scientific publications. In response to atmospheric CO_2 enrichment, the carbon and nitrogen contents in all the plant and soil pools studied significantly increased, "leading to more net C and N accumulations in ecosystems at elevated than ambient CO_2." They found the mean CO_2-induced increases in C pools of shoot, root, whole plant, litter, and soil were 22.4%, 31.6%, 23.0%, 20.6%, and 5.6%, respectively, and the corresponding CO_2-induced increases in N pools were 4.6%, 10.0%, 10.2%, 25.4%, and 11.2%. In addition, "N accumulations in ecosystems have long been documented in association with C accumulations during both primary and secondary successions (Crocker and Major, 1955; Binkley *et al*., 2000; Vitousek, 2004)." They conclude, "the net C and N accumulations revealed in this study," which were produced by atmospheric CO_2 enrichment, "together with studies of C and N dynamics during succession over hundreds to millions of years, suggest that ecosystems may have intrinsic capabilities to stimulate N accumulation by C input," which is typically increased by atmospheric CO_2 enrichment. They further conclude "net N accumulation likely supports long-term C sequestration in response to rising atmospheric CO_2 concentration." They state "concomitant increases in C and N contents in plant and soil pools at elevated CO_2 as shown in this study point toward a long-term trend of terrestrial C sequestration in response to rising atmospheric CO_2 concentration," just the opposite of what the PNL hypothesis predicts.

Norby and Iverson (2006) reviewed what they had learned about the PNL hypothesis from "a six-year record of N dynamics of a sweetgum (*Liquidambar styraciflua*) stand exposed to elevated CO_2 in the free-air CO_2 enrichment (FACE) experiment at Oak Ridge, Tennessee, USA," focusing on N uptake, content, distribution, turnover, and N-use efficiency. They write, "net primary productivity in this stand has been significantly higher in CO_2-enriched plots, and the response has been sustained through time, thereby meeting one of the criteria for the development of PNL." They further report, "none of the measured responses of plant N dynamics in this ecosystem indicated the occurrence of PNL."

Hungate *et al*. (2006) tested the PNL hypothesis against what they had observed over seven years in an open-top chamber study of a scrub oak woodland dominated by *Quercus myrtifolia*, *Q. geminate,* and *Q. chapmanii* on an island in NASA's Kennedy Space Center on the coast of central Florida (USA). Their experiment commenced just a few months after a complete burning of the ecosystem located on well-drained but nutrient-poor soil. They report "litterfall production (one measure of aboveground primary productivity) increased initially in response to elevated CO_2, but the CO_2 stimulation declined during years five through seven, concurrent with the accumulation of N in the O [soil] horizon and the apparent restriction of plant N availability." They state these changes in N cycling were "likely to reduce the response of plant production to elevated CO_2." However, they acknowledge, "at the level of aboveground plant biomass (estimated by allometry), progressive N limitation was less apparent." In fact, there was a persistent CO_2-induced increase in aboveground plant carbon, which led them to conclude "some mechanisms are partially alleviating progressive N limitation," as Finzi *et al.* (2006) also concluded in their study of loblolly pines, where by some unknown means the pines obtained the extra nitrogen they needed.

Idso and Kimball (2001) also observed a large initial CO_2-induced increase in aboveground biomass production, followed by a rapid but slowing decline in this parameter, in their long-term sour orange tree study. Because the trees of their experiment were periodically fertilized so as never to lack nitrogen, the similar productivity vs. time pattern Hungate *et al.* observed may have had nothing to do with "restriction of plant N availability," which they characterized as being merely "apparent." It is also important to note the slow decline in the CO_2-induced growth stimulation of the sour orange trees came to a halt at the ten-year point of the experiment, when the declining growth stimulation finally leveled out at an essentially constant value that was maintained to the end of the 17-year study—a 69% increase in yearly total biomass production in response to a 75% increase in the air's CO_2 content (Kimball *et al.*, 2007).

Consequently, as Norby and Iverson (2006) and Finzi *et al.* (2006) both found, the pattern of CO_2-induced growth stimulation in the scrub oak ecosystem Hungate *et al.* studied provides no evidence for the PNL hypothesis. In fact, it and others of their observations point to one or more unknown means of ecosystem N acquisition that allow the aerial fertilization effect of atmospheric CO_2 enrichment to continue, albeit at a level of impact lower than its peak manifestation, even with "apparent" N limitations.

Johnson *et al.* (2006) studied the effects of elevated CO_2 (ambient, +175, +350 ppm) and N fertilization (unfertilized, +100, +200 kg N ha^{-1} yr^{-1}, provided as ammonium sulfate) on C and N accumulations in the biomass of ponderosa pines (*Pinus ponderosa* Laws, grown from seed) and the soils that supported them, in a six-year open-top chamber experiment conducted near Placerville, California (USA). This study, like several others according to Johnson *et al.*, "showed that growth response to elevated CO_2 more than offset declines in tissue N concentrations, necessitating increased N uptake by trees," which led them to ask, "How did the trees manage to obtain this 'extra' N in an N-limited environment?"

In the fertilized treatments, the four researchers suggest, the extra N could readily have been supplied by the added fertilizer, but in the unfertilized treatments they opine a substantial amount of the N uptake "probably came from the soil," as both wet and dry deposition were not great enough to have supplied all of the extra N, and "no symbiotic N fixer was present in the study plots." Citing other investigators' results as supplying circumstantial evidence for what they finally concluded, they write, "the additional N needed to respond to elevated CO_2 came from the soil and was facilitated by greater root exploration under elevated CO_2." Acknowledging they could not "provide an accurate prediction from the results of this study," Johnson *et al.* nevertheless state they could "see no evidence that either growth or additional N uptake at the +350 ppm CO_2 level are being inhibited by PNL as of year 6 in this study."

Studying the same trees, Phillips *et al.* (2006) collected video images every two months of roots growing against the surfaces of three minirhizotron tubes installed in each chamber. Yearly values of fine-root standing crop, production, and mortality were consistently higher in the elevated CO_2 treatments throughout the study, and they write, "in this same study, Johnson *et al.* (2000) found that elevated CO_2 increased fine-root life span." Because elevated CO_2 also increased fine-root length, Phillips *et al.* note, "the amount of root length dying per year was actually greater." Therefore, they write, "the higher rates of mortality in absolute terms for elevated CO_2 are driven by increased standing crop and not reduced life spans." In addition, they report Tingey *et al.* (2005) found "in the elevated CO_2

treatments, fine roots explored the soil more extensively and deeper, and filled in the explored areas more intensively." With respect to the PNL hypothesis, therefore, Phillips *et al.* state "the increased fine-root length reported here explains how additional N was provided to support the increased whole plant growth in elevated CO_2 treatments, and corresponds with the increased extent and intensity of the root system architecture discussed by Tingey *et al.* (2005)." This "mining of soil N," they continue, "can in some cases go on for substantial lengths of time, and there is no evidence that PNL occurred during the course of this study."

Barnard *et al.* (2006) injected ^{15}N-labelled NH_4 into the soil of mesocosms of *Holcus lanatus* (L.) grown for more than 15 months at either ambient or elevated atmospheric CO_2 concentrations to determine whether the uptake capacity of soil micro-organisms had remained higher at elevated CO_2, and to shed further light on the short-term (48 hours) partitioning of N between plants and soil micro-organisms. Their results and data from other plant-microbial ^{15}N partitioning experiments at elevated CO_2 suggest "the mechanisms controlling the effects of CO_2 on short- vs. long-term N uptake and turnover differ." They state "short-term immobilization of added N by soil micro-organisms at elevated CO_2 does not appear to lead to long-term increases in N in soil microbial biomass," noting the increased soil microbial C:N ratios they observed at elevated CO_2 "suggest that long-term exposure to CO_2 alters either the functioning or structure of these microbial communities." Barnard *et al.* conclude "short-term immobilization of inorganic soil nitrogen or exploitation of nutrient pulses may be altered under conditions of elevated atmospheric CO_2 concentration," and this alteration undermines the PNL hypothesis, likely allowing long-lived plants and ecosystems to maintain positive growth responses to atmospheric CO_2 enrichment.

Noting the photosynthetic down-regulation posited by the PNL hypothesis "may occur in ecosystems that have a low soil N availability, such as piedmont loblolly pine forests"—the setting in which the long-term Duke Forest FACE study was being conducted—Springer and Thomas (2007) tested the validity of the hypothesis on some of the site's understory tree species. They "hypothesized that after seven years of exposure to elevated CO_2, significant photosynthetic down-regulation would be observed in these tree species," which included red maple (*Acer rubrum* L.), hickory (*Carya glabra* Mill.), redbud (*Cercis canadensis* L.), and sweetgum (*Liquidambar styraciflua* L.).

During the first year of the Duke Forest FACE experiment, DeLucia and Thomas (2000) examined the photosynthetic responses of these particular saplings to the 200 ppm increase in atmospheric CO_2 concentration employed in that study. Subsequently, Springer and Thomas "reexamined the photosynthetic responses of saplings of the same four understory species to determine whether the enhancement of photosynthesis observed during the first year of exposure to elevated CO_2 was sustained in the seventh year of the experiment." They found "no evidence of photosynthetic down-regulation in any species in either early or late summer." Not only did their measurements reveal no down-regulation of photosynthesis, they observed "a small increase in the photosynthetic capacity of all of the study species in response to elevated CO_2," which they say "has been demonstrated in several studies (Campbell *et al.*, 1988; Ziska and Teramura, 1992; Idso *et al.*, 1991)."

Springer and Thomas note "the progressive N limitation hypothesis predicts a diminished response of plant productivity to elevated CO_2 as N availability decreases because of the increased nutrient demands of greater plant biomass production (Luo *et al.*, 2004)." They go on to reiterate their own finding: "after seven years of elevated CO_2 treatment in the Duke Forest FACE experiment, we see little evidence of progressive N limitation in the leaf level processes of these four species of understory trees."

Working at the EUROFACE facility in central Italy near Viterbo, Liberloo *et al.* (2007) grew three species of poplar trees—robusta poplar (*Populus x euramericana*), white poplar (*P. alba*), and black poplar (*P. nigra*)—for two three-year periods, between which times the trees were coppiced and allowed to regrow, in either ambient air or air enriched with an extra 180 ppm of CO_2 (an approximate 49% enhancement). They applied no fertilization to any of the plots over the first growth cycle, then fertilized half of the trees over the second growth cycle. During the last year of the last cycle, they measured a number of plant processes and parameters and compared them with similar observations made throughout earlier years of the experiment.

The five researchers discovered, after six years of growth under elevated atmospheric CO_2, the poplar trees did not experience any down-regulation of leaf net photosynthesis, and the long-term stimulation was substantial. In response to the 49% increase in the atmosphere's CO_2 concentration, the CO_2-induced stimulation of net photosynthesis, averaged over the three species, was 49%. In addition, they found no difference in CO_2-induced net photosynthetic stimulation between Sun and shade leaves, nor was there any difference in CO_2 effects between the fertilized and non-fertilized trees.

After thus finding "photosynthetic stimulation of poplar leaves was sustained in elevated CO_2 after six years of fumigation, even under non-fertilized conditions," Liberloo *et al*. state "these results give optimistic perspectives for the future, as the maintained enhancement of photosynthesis in poplar trees is likely to continue over several rotations, thereby providing more carbon for growth in a closed canopy forest."

Finzi *et al*. (2007) evaluated the PNL hypothesis based on data obtained from four well-known FACE experiments conducted on forests—the Rhinelander, Duke, and Oak Ridge National Laboratory (ORNL) studies in the United States and the POP-EUROFACE study in Europe—where previous research described by Norby *et al*. (2005) showed net primary production (NPP) increased by 23 ± 2% in response to a CO_2 concentration increase of 174 ppm (46%) above the mean ambient-air concentration. Finzi *et al*. found the CO_2-induced increase in forest productivity at the POP-EUROFACE site, which they note was "located on former agricultural land where soil nitrogen availability was high and not limiting," not to have been supported by greater nitrogen uptake from the soil but instead by an increase in nitrogen use efficiency (NUE). At the other three sites, however, the CO_2-induced increase in forest productivity was supported by greater N uptake from the soil, with no change in NUE. They state this result was "unexpected," especially for the Duke and ORNL sites, where they say "tree growth is demonstrably N-limited."

Focusing on the findings of the three U.S. studies, Finzi *et al*. state "the response of N uptake and NUE in these young temperate forests exposed to FACE is the opposite of that predicted by the current generation of biogeochemical models," meaning those based on the PNL hypothesis. After discussing how these forests might be obtaining the seemingly impossible-to-obtain nitrogen they needed to maintain their significantly CO_2-enhanced growth rates, the scientists conclude, "regardless of the specific mechanism, this analysis demonstrates that larger quantities of carbon entering the below-ground system under elevated CO_2 result in greater N uptake, even in N-limited ecosystems."

Zak *et al*. (2007) initiated a year-long ecosystem-level ^{15}N tracer experiment at the Rhinelander, Wisconsin (USA) FACE facility at the seven-year point of a long-term study of aspen (*Populus tremuloides*) and aspen-birch (*P. tremuloides-Betula papyrifera*) communities exposed to treatments of CO_2 (ambient and elevated to 200 ppm above ambient) and O_3 (ambient and elevated to 30–40 ppb above ambient). One year after adding tracer amounts of $^{15}NH_4^+$ to the forest floor of the young tree stands, they found "both forest communities exposed to elevated CO_2 obtained greater amounts of ^{15}N (29%) and N (40%) from soil, despite no change in soil N availability or plant N-use efficiency." They attribute this to greater belowground root growth and a more thorough exploration of the soil for nitrogen in the CO_2-enriched treatment. In contrast, they note the elevated O_3 treatment "decreased the amount of ^{15}N (-15%) and N (-29%) in both communities." These decreases were significantly smaller than the corresponding CO_2-induced increases. Consequently, Zak *et al*. conclude "progressive nitrogen limitation is presently not a factor governing plant growth response to elevated CO_2 in these young, developing forest communities." In addition, they state their findings "are consistent with those in young sweet gum (*Liquidambar styraciflua*) and loblolly pine (*Pinus taeda*) forests exposed to elevated CO_2 (Finzi *et al*., 2006; Norby and Iversen, 2006)."

Langley *et al*. (2009) "employed an acid-hydrolysis-incubation method and a net nitrogen-mineralization assay to assess stability of soil carbon pools and short-term nitrogen dynamics in a Florida scrub-oak ecosystem after six years of exposure to elevated CO_2" at the multiple open-top-chamber facility at NASA's Kennedy Space Center. Their research showed elevated atmospheric CO_2 (to 350 ppm above ambient concentrations) tended to increase net N mineralization in the top 10 cm of the soil, but it also decreased total soil organic carbon content there by 21%. That loss of carbon mass was equivalent only to "roughly one-third of the increase in plant biomass that occurred in the same experiment." They found the strongest increases in net N mineralization were in the 10–30 cm depth increment, and "release of N from this depth may have allowed the sustained CO_2 effect on productivity in this scrub-oak forest," which over the four years leading up to their study "increased litterfall by 19–59%."

Thus yet another experiment demonstrates atmospheric CO_2 enrichment generally enables plants to find the extra nitrogen they need to take full advantage of the aerial fertilization effect of elevated atmospheric CO_2 concentrations, thus increasing total ecosystem carbon content. Although the PNL hypothesis sounds logical enough and many scientists initially embraced it as a fact, a vast array of observational data has subsequently proven it unfounded.

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3.12 Salinity Stress

- The buildup of soil salinity from repeated irrigation can produce growth stresses in agricultural plants, but the rise in the air's CO_2 concentration can overcome these stresses.

In agricultural enterprises the buildup of soil salinity from repeated irrigations can reduce crop yields. Similarly, in unmanaged ecosystems where exposure to brackish or salty water is commonplace, saline soils can induce growth stresses in plants not adapted to these conditions. It is important to understand how rising atmospheric CO_2 concentrations may interact with soil salinity to affect plant growth. Experiments addressing this issue are discussed below.

Ball *et al.* (1997) grew two Australian mangrove species—*Rhizophora stylosa* and *Rhizophora apiculata*, the former of which has a slower relative growth rate than the latter but a greater salt tolerance—for 14 weeks in glasshouses with different combinations of atmospheric CO_2 (340 and 700 ppm), relative humidity (43 and 86%), and salinity (25 and 75% of seawater), to determine the effects of these variables on their development and growth. Averaged across the entire experiment, the elevated CO_2 treatment significantly increased the rates of net photosynthesis in both species, but only at the lower salinity level.

Mavrogianopoulos *et al.* (1999) grew parnon melons (*Cucumis melo*) in greenhouses subjected to atmospheric CO_2 concentrations of 400, 800, and 1,200 ppm for the first five hours of each day, irrigating them with nutrient solutions containing 0, 25, and 50 mM NaCl to determine the interactive effects of elevated CO_2 and salinity on plant growth and yield. Exposure to CO_2 concentrations of 800 and 1,200 ppm increased net photosynthetic rates by averages of 75 and 120%, respectively—regardless of salinity—relative to rates measured at 400 ppm CO_2. The CO_2 enrichment partially reversed the negative effects of salinity on shoot growth, leaf growth, and leaf chlorophyll content, and although melon yields were significantly increased with atmospheric CO_2 enrichment at all salinity levels, the greatest CO_2-induced enhancement was observed at the lowest salinity level.

Also working in the agricultural sector, Maggio *et al.* (2002) grew tomato (*Lycopersicon esculentum* Mill.) plants in controlled-environment chambers maintained at atmospheric CO_2 concentrations of either 400 or 900 ppm in combination with varying degrees of soil salinity for one month. They found plants grown in the elevated CO_2 treatment tolerated an average root-zone salinity threshold value about 60% greater than plants grown in the low CO_2 treatment, and the water-use of the CO_2-enriched plants was about half the low-CO_2 plants. In addition, the amount of chloride in the leaves of the CO_2-enriched plants was significantly lower than in the leaves of the low-CO_2 plants.

Poorter and Perez-Soba (2001) reported very similar findings in a review paper. They found the positive effects of elevated CO_2 on the growth responses of most plants over a wide range of soil salinities remained the same, which concurred with the earlier findings of Idso and Idso (1994) in their review. Hence, there is abundant evidence indicating plants respond positively to increases in the air's CO_2 content, even where high soil salinity levels present mild to moderate stresses.

Syvertsen and Levy (2005) reviewed what was known about salinity stress in citrus trees and how atmospheric CO_2 enrichment might modify it. They note rapidly growing plants almost always use more water than slower-growing plants, and "in citrus, many vigorous rootstocks that produce fast-growing trees also tend to have poor salt tolerance (Castle *et al*., 1993)," possibly because they accumulate more salt in their tissues because of their greater uptake of water. When growing plants in CO_2-enriched air, however, plant stomatal conductance and water use are often decreased at the same time net photosynthesis and growth are increased, so, in the words of the two scientists, "elevated CO_2 almost always leads to higher water use efficiency as it disconnects rapid tree growth from high water use." They explain, "if salt uptake is coupled with water uptake, then leaves grown at elevated CO_2 should have lower salt concentrations than leaves grown at ambient CO_2 (Ball and Munns, 1992)."

"As expected," Syvertsen and Levy continue, "all citrus rootstock species studied increased growth and water use efficiency in response to elevated CO_2 that was twice ambient," and generally, but not always, "the salinity-induced accumulation of sodium (Na^+) in leaves was less when seedlings were grown at elevated CO_2 than at ambient CO_2." One exception—where Na^+ accumulation was not affected by elevated CO_2—was Rangpur lime (*Citrus reticulata*), but they report this citrus variety was already relatively salt-tolerant, and another variety of the same species (Cleopatra mandarin) had lower leaf chloride concentrations in CO_2-enriched air than in ambient air.

Rasse *et al*. (2005) reported on the long-term effects of atmospheric CO_2 enrichment on the net CO_2 exchange, shoot density, and shoot biomass of the wetland sedge, *Scirpus olneyi*, as well as how those effects were influenced by salinity (one of the main environmental stressors of the wetlands), in one of the longest (17 years) *in situ* atmospheric CO_2 enrichment experiments ever conducted—in a natural wetland located at the Smithsonian Environmental Research Center on the Chesapeake Bay (USA). In every year of that period, the net CO_2 exchange rate and shoot biomass and density of the plants growing in the CO_2-enriched (ambient +340 ppm) air were greater than they were among the plants growing in ambient air. In the case of the net CO_2 exchange rate, for example, the extra CO_2 boosted it by 80% in the first year of the study, but the enhancement declined to about 35% by the end of the third year and remained relatively constant at that value over the following 15 years. Shoot biomass and density also increased; while the CO_2-induced stimulation of the net CO_2 exchange rate remained essentially constant over the past 15 years, the CO_2-induced stimulations of shoot biomass and density increased over time. After five years of a nearly constant stimulation of 16%, for example, shoot density increased in near-linear fashion to a value 128% above the ambient-air value at the end of year 17. The response of shoot biomass to CO_2 enrichment was also nearly linear, reaching a value approximately 70% above ambient at year 17. The trends in shoot density and biomass did not appear to be leveling off.

Net CO_2 exchange, shoot density, and shoot biomass were also closely correlated with salinity—the higher the salinity, the more detrimental were its effects on these variables. But even at the highest levels of salinity reported, atmospheric CO_2 enrichment was able to produce a positive, albeit reduced, stimulation of net CO_2 exchange. For shoot biomass and density, the responses were better still. Not only did atmospheric CO_2 enrichment essentially eradicate the detrimental effects of salinity, there was, Rasse *et al*. write, "evidence suggesting that salinity stress increased the stimulation of shoot density by elevated atmospheric CO_2 concentration."

This experiment demonstrated several important facts. First, as the researchers state, their results "leave no doubt as to the sustained response of the salt marsh sedge to elevated atmospheric CO_2 concentration." Second, as the initial responses of the three growth variables declined or remained low during the first few years of the study, but leveled out or increased thereafter, it is clear long-term research must be carried out to ascertain the full and correct impacts of atmospheric CO_2 enrichment on plants. In the wetland sedge of this study, for example, it took about 10 growing seasons before an increasing trend in the shoot density could be recognized. Finally, there is what the researchers called their "most important finding": "a species response to elevated atmospheric CO_2 concentration can continually increase when [it] is under stress and declining in its natural environment."

Garcia-Sanchez and Syvertsen (2006) grew well-watered and -fertilized three-month-old rootstock seedlings of Cleopatra mandarin (*Citrus reticulata* Blanco) and Carrizo citrange (*Citrus sinensis* (L.)

Osb. x *Poncirus trifoliata* L.), with or without salt stress (an additional 50 mM NaCl), for eight additional weeks, one plant each in 1.5-liter containers located in controlled-environment greenhouses maintained at either 360 or 700 ppm CO_2. During that time and at the end of the experiment, they measured a number of plant properties and physiological processes that allowed them to determine whether "salinity tolerance of citrus rootstock seedlings would be increased when grown in elevated CO_2."

The two researchers found "elevated CO_2 increased plant growth, shoot/root ratio, leaf dry weight per area, net assimilation of CO_2, chlorophyll, and water-use efficiency." The increase in the last parameter was caused by a decrease in transpiration and an increase in plant biomass. In Cleopatra mandarin, biomass received a 27% CO_2-induced boost in the salt-stress treatment and a 40% boost in the non-salt-stress treatment; in Carrizo citrange, biomass received a 49% boost in the salt-stress treatment and 43% in the non-salt-stress treatment. They note "elevated CO_2 increased salinity tolerance in the relatively salt-sensitive Carrizo more than in the salt-tolerant Cleopatra."

Takagi *et al*. (2008) grew well-watered and well-fertilized *Solanum lycopersicum* (formerly *Lycopersicon esculentum*) tomato plant seedlings for two weeks at two levels of irrigation-water salinity (0 or 100 mM NaCl) in 3-L pots inside the greenhouse of Hiroshima University (Japan), at atmospheric CO_2 concentrations of either 370 or 1,000 ppm, measuring various plant properties and physiological responses. They report the "salt-stress treatment severely decreased whole-plant biomass" and "leaf photosynthesis and transport of carbon assimilates," but "the impact of stress on these activities was alleviated under elevated CO_2 concentration." This alleviation, they write, "was promoted when sink activity relative to source activity was higher," which they say was "probably owing to improvement of oxidative stress," due "at least partially to the higher constitutive antioxidant enzymes' activities" as well as improved water status "through stomatal closure at high CO_2 concentration." They conclude their study "corroborates earlier reports that the interaction between salinity stress and CO_2 concentration results in the alleviative effect of elevated CO_2 on the negative effects of salinity on plant growth."

Geissler *et al*. (2009a) note, "desertification is often accompanied by soil salinization ... leading to growth conditions unacceptable for most conventional crops." They suggest "a promising solution" to the problem is "the desalinization and reclamation of degraded land by making sustainable use of naturally salt-tolerant halophytes under seawater irrigation (including drainage mechanisms which avoid salt accumulation in the soil)."

The three researchers grew well-fertilized two-month-old *Aster tripolium* plants in a hydroponic system maintained at seawater salinity (sws) levels of 0, 50, and 100% in open-top chambers at atmospheric CO_2 concentrations of either 380 ppm (ambient) or 520 ppm (elevated), during which time they measured several plant properties and processes. Growing the plants with water of 100% sws (as opposed to 0% sws) resulted in "a significant decrease in photosynthesis and water use efficiency and to an increase in oxidative stress." When they raised the air's CO_2 concentration by 37% (from 380 to 520 ppm), there was a subsequent increase of 84% in photosynthesis and 60% in water use efficiency. The researchers note "the improved water and energy supply was used to increase the investment in mechanisms reducing water loss and oxidative stress." They conclude, because "elevated CO_2 concentration enhances the energy and water supply of *Aster tripolium*, ameliorates oxidative stress, and thus enhances the survival of this plant in saline habitats," it "can help in desalinizing and reclaiming degraded land and sequestering CO_2, thus counteracting the greenhouse effect."

Geissler *et al*. (2009b) write halophytes are "naturally salt tolerant plants which are able to complete their life cycle on a substrate rich in NaCl," and cash-crop halophytes "can be used for various economical and ecological purposes, e.g. for food, fodder, for obtaining timber, fibers, reeds or chemicals, as ornamental plants, for coastal protection, land reclamation or greenification of deserts." They note *Aster tripolium*, in particular, "can be used for food (the leaves have a high nutritional value and can be eaten as salad or vegetable), for fodder and as an ornamental plant."

The three scientists state the 40% increase in the air's CO_2 content in their experiment increased the light-saturated rate of net photosynthesis by 56%, 82%, and 71%, respectively, in the plants irrigated with water of 0, 50, and 100% sws, and it increased their water use efficiencies by 14, 26, and 61%, respectively. Other positive impacts of the CO_2-enriched air were "an enhanced synthesis of proline, carbohydrates and proteins," and "these mechanisms led to a higher survival rate under saline conditions, i.e. to an improved salt tolerance." Thus, they conclude "*A. tripolium* is a promising cash crop halophyte which will probably benefit from rising atmospheric CO_2 concentrations in the future," and "its sustainable use can help feeding the growing world population."

Working with a more common crop, Perez-Lopez *et al*. (2009a) grew two barley (*Hordeum vulgare* L.) cultivars, Alpha and Iranis, in controlled-environment growth chambers at either ambient (350 ppm) or elevated (700 ppm) atmospheric CO_2 concentrations in a 3:1 perlite:vermiculite mixture watered with Hoagland's solution every two days (until the first leaf was completely expanded at 14 days), after which they administered a salinity treatment by adding 0, 80, 160, or 240 mM NaCl to the Hoagland's solution every two days for 14 more days. After a total of 28 days, the primary leaf of each barley plant was harvested and assessed for a number of biochemical properties.

In the various ambient-air salinity treatments, the deleterious effects of reactive oxygen species on barley leaves were made apparent through ion leakage and increases in thiobarbituric acid reactive substances (TBARS), which rose as salt concentrations rose. "On the other hand," the seven scientists continue, "when [the] salinity treatment was imposed under elevated CO_2 conditions, lower solute leakage and TBARS levels were observed, suggesting that the oxidative stress caused by salinity was lower." They conclude "elevated CO_2 protects barley cultivars from oxidative stress," noting "the relief of oxidative stress damage observed in our barley leaves grown under a CO_2 enriched atmosphere has also been observed in alfalfa (Sgherri *et al*., 1998), pine (Vu *et al*., 1999) and oak (Schwanz and Polle, 2001)."

Working with the same plants in the same experiment, but focusing on different phenomena, Perez-Lopez *et al*. (2009b) measured relative water content, water potential and its components, transpiration rate, hydraulic conductance, and water use efficiency, computed as plant dry weight produced per unit of water transpired. They found "elevated CO_2 improves barley water relations under saline conditions because elevated CO_2 permits a greater osmotic adjustment, most likely due to a greater carbon supply from increased photosynthesis, and a lower passive dehydration due to reductions in stomatal conductance and hydraulic conductance." Specifically, by the end of their study the water use efficiency of salt-stressed plants grown in the elevated CO_2 treatment was 61% greater in Alpha and 43% greater in Iranis than that of plants grown in the ambient CO_2 treatment. The five researchers conclude, "elevated CO_2 will mitigate the negative impact of salinity on barley growth and will enable plants to remain turgid and functional for a longer period and for a higher salt concentration," noting "these facts open the possibility of a future successful development of this species in saline areas in which nowadays growth is not possible." This finding has enormous implications, as Frommer *et al*. (1999) have estimated approximately one-third of the world's irrigated land is currently unsuitable for crop production because of its high salinity.

Also working with barley plants grown in the same experiment, Perez-Lopez *et al*. (2010) measured midday leaf water potential, osmotic potential, osmotic potential at full turgor, dehydration, and osmotic adjustment; they subsequently harvested the primary leaf of each plant and made assessments of its concentrations of various minerals and organic compounds. They write, "elevated CO_2 permitted plant metabolism to be maintained at a better status under salt stress than did ambient CO_2," and "growth was reduced more at ambient than at elevated CO_2." They also report, "elevated CO_2 widens the range of salt concentrations at which osmotic adjustment continues to be efficient by providing a greater supply of carbon and Adenosine-5'-triphosphate," a multifunctional nucleotide that transports chemical energy in cells for metabolism and is "needed to perform the energetically expensive salt tolerance mechanisms." Thus, they conclude—as they had in their earlier papers—"under future environmental conditions, barley species will be able to succeed in salinized areas in which growth is not currently possible."

Azam *et al*. (2005) note "in agro-ecosystems, green manuring legumes occupy a key position in maintaining/improving soil fertility and productivity," and the important role of these plants as a source of nitrogen has increased further due to economic and pollution concerns associated with nitrogen supplied by chemical fertilizers. They state, "species of sesbania have generally been considered as most important for green manuring, especially in wheat-rice rotation systems."

In many situations, the growth of sesbania is suppressed by varying degrees of water stress and salinity, but the five Pakistani scientists state "elevated CO_2 favors different physiological processes of plants, thereby leading to increased biomass production and ecosystem functioning," citing Drake and Leadley (1991), Idso and Idso

(1994), and Azam and Farooq (2001). They report this effect is more pronounced for plants facing stresses imposed through the soil or atmosphere, citing the collection of papers compiled and edited by Koch and Mooney (1996). They hypothesized rising atmospheric CO_2 concentrations might mitigate salinity stress in sesbania, enabling the rotation cover-crop to more effectively "fix" atmospheric nitrogen and deposit the plant-usable form of it in the soil, where it could help promote the growth of such important agricultural staples as wheat and rice.

Conducting greenhouse experiments designed to assess the effects of elevated atmospheric CO_2 concentrations on growth and nitrogen fixation in *Sesbania aculeata* exposed to different salinity and water regimes, Azam *et al.* report "elevated CO_2 favored N_2 fixation leading to a greater contribution of fixed N to the total plant N." In addition, "biological nitrogen fixation decreased with salinity" but "elevated CO_2 arrested the decrease to a significant extent."

Perez-Lopez *et al.* (2012) write, "salt stress has a threefold effect on plant health" because it reduces water availability, causes ion imbalance, and causes toxicity, all of which phenomena, they write, "curtail growth, photosynthesis, protein synthesis, energy storage, and lipid metabolism," as described in detail by Munns (2005) and Parida and Das (2005). In a study designed to explore the negative consequences of potentially greater salt stress in a CO_2-enriched environment, they grew barley (*Hordeum vulgare*) plants in pots containing a 3:1 mix of perlite: vermiculite in controlled-environment chambers maintained at either ambient or elevated atmospheric CO_2 concentrations (350 or 700 ppm) for the last 14 days of a 28-day post-planting period. They also instituted four salt-stress treatments on the 15th day by supplying the plants then and thereafter with water of one of four degrees of saltiness (0, 80, 160, or 240 mM NaCl). At the end of the 28-day period they measured a number of plant physiological properties and processes related to the maximal rate of net photosynthesis (Amax) exhibited by the first fully expanded attached leaf of each plant.

The five Spanish scientists report, "in the zero-saline treatment, elevated CO_2 increased the Amax by 49% compared with the Amax measured at ambient CO_2," whereas "under ambient CO_2 conditions, saline treatments (80-, 160- and 240-mM NaCl) reduced the Amax by 18, 32 and 39%, respectively." They add, "these reductions were lower at elevated CO_2: 8, 22 and 28% for 80-, 160-, and 240-mM NaCl." Based on the graphical representations of their results, the CO_2-induced enhancements of Amax in the four saline treatments (0-, 80-, 160-, and 240-mM NaCl) appear to have been, respectively, 49%, 68%, 71%, and 76%, revealing the greater the salinity-induced percentage reduction in barley Amax becomes, the greater the CO_2-induced percentage increase in barley Amax becomes.

Also investigating salt stress in barley, Perez-Lopez *et al.* (2013) write, "soil salinization is an important growth limiting factor for most plants," citing the United Nations' Food and Agriculture Organization (FAO, 2007) and noting "around 20% of the irrigated land and one third of the world's arable soil are affected by a progressive salinization." They note "barley is one of the most extensively cultivated crops worldwide" but "salt stress reduces its productivity."

Perez-Lopez *et al.* analyzed "the effect of salinity on nitrogen acquisition, distribution and assimilation, the consequences of these effects on growth in barley (*Hordeum vulgare* L., cv. Iranis), and the possible effects on these processes provoked by elevated CO_2 levels." They sowed six barley seeds in each of several 2.5-liter pots containing a 3:1 mix of perlite: vermiculite in controlled-environment chambers maintained at either ambient (350 ppm) or elevated (700 ppm) CO_2 concentrations and watered the plants with 250 ml of Hoagland's solution containing 0, 80, 160, or 240 mM concentrations of NaCl every two days until the end of the 28-day study.

The six Spanish scientists report, "under ambient CO_2 conditions, 80, 160, and 240 mM NaCl reduced the total plant biomass by 12%, 30%, and 44%, respectively." By contrast, "growth at elevated CO_2 levels led to 24%, 20%, and 33% higher total biomass than under ambient CO_2 levels for 80, 160, and 240 mM NaCl, respectively." And because "the relative stimulation of total plant biomass in response to elevated CO_2 levels was higher in salt-stressed plants than in non-stressed ones," they conclude, "barley plants subjected to elevated CO_2 levels will likely overcome mild saline conditions."

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3.13 Temperature Stress

As the atmosphere's CO_2 content rises, nearly all agricultural crops, grassland plants, and trees will exhibit enhanced rates of photosynthesis and biomass production that will not be diminished by any global warming that might accompany it. If ambient air temperatures rise concurrently, the growth-promoting effects of atmospheric CO_2 enrichment likely will rise even more, as the Earth gets "greener."

3.13.1 Agricultural Crops

- As the air's CO_2 concentration rises, nearly all agricultural crops will exhibit enhanced rates of photosynthesis and biomass production that will not be diminished by any concomitant global warming. If air temperatures rise concurrently, the growth-promoting effects of atmospheric CO_2 enrichment likely will rise even more.

As the air's CO_2 content rises, most plants exhibit increased rates of photosynthesis and biomass production (see Chapter 1), which should increase the amount of food, fiber, and timber production that can be utilized to feed, clothe, and shelter the expanding human population. However, some researchers argue the growth-promoting effects of atmospheric CO_2 enrichment may be largely negated by the global warming predicted to occur in the near future by a number of state-of-the-art climate models. Such an outcome could compromise the planet's ability to sustain a greater human population without increasing use of land for agriculture. This section examines the scientific literature to see whether plants will continue to exhibit CO_2-induced growth increases under conditions of predicted future warming, reviewing what has been learned about the photosynthetic and growth responses of CO_2-enriched agricultural crops grown at both current and projected future growing-season temperatures.

The optimum growth temperatures of several plants have been shown to rise substantially with increasing levels of atmospheric CO_2 (Berry and Bjorkman, 1980; Stuhlfauth and Fock, 1990; McMurtrie *et al*., 1992; McMurtrie and Wang, 1993). This phenomenon was explained by Long (1991), who calculated from well-established plant physiological principles that most C_3 plants should increase their optimum growth temperatures by approximately 5°C for a 300 ppm increase in the air's CO_2 concentration. Thus plant photosynthetic rates should rise in response to concomitant increases in both the air's CO_2 concentration and temperature, as Idso and Idso (1994) and Cowling (1999) have shown to be typically the case. These positive CO_2 x temperature interactions have been observed in subsequent scientific studies, as indicated below.

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

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

Elevated CO_2 also helps plants recover from high-temperature- and drought-induced reductions in photosynthetic capacity, as Ferris *et al.* (1998) demonstrated. They grew soybeans for 52 days under normal air temperatures and soil water conditions at atmospheric CO_2 concentrations of 360 and 700 ppm, then subjected the plants to an eight-day period of high temperature and water stress. When the researchers restored normal air temperatures and soil water conditions, the CO_2-enriched plants attained photosynthetic rates 72% of their unstressed controls, and the plants grown at ambient CO_2 attained photosynthetic rates only 52% of their controls. At the end of the growing season, Ferris *et al.* (1999) report, plants growing in the elevated CO_2 treatment exhibited an average biomass 24% greater than plants grown in ambient CO_2, and a seed yield 32% greater.

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

These studies make it clear elevated air temperatures often significantly enhance the beneficial effects of elevated atmospheric CO_2 on agricultural crop yields. In some cases, however, rising air temperatures do not interact with rising atmospheric CO_2 concentrations to further increase the growth-promoting effects of atmospheric CO_2 enrichment. Instead, they simply do not interfere with the status quo.

Demmers-Derks *et al.* (1998) found sugar beets grown at 700 ppm CO_2 produced 25% more biomass than ambient-grown plants, regardless of air temperature, which was increased by 3°C. Similarly, Fritschi *et al.* (1999) found significant warming (4.5°C above ambient) had no impact on the growth of rhizoma peanut, whereas a 300 ppm increase in the air's CO_2 content increased the plant's total biomass by 52% regardless of air temperature. In the unlikely event the air's CO_2 content were to cease rising or have no effect on the productivity of certain plants, it is possible the temperature increase itself may promote plant growth and development, as was found in the experiment conducted by Wurr *et al.* (2000), where elevated CO_2 had essentially no effect on the yield of French beans but a 4°C increase in air temperature increased their yield by approximately 50%.

Aloni *et al.* (2001) grew bell pepper (*Capsicum annuum* L. cv. Mazurka) plants under optimal conditions until eight days prior to anthesis, then placed the plants in greenhouses maintained at atmospheric CO_2 concentrations of either 350 or 800 ppm and normal (28/22°C) or elevated (32/26°C) day/night air temperatures to determine the effects of these two environmental changes on reproductive parameters associated with pollen, which is extremely sensitive to high temperatures. The high temperature stress reduced pollen germination by 75% at ambient CO_2, but atmospheric CO_2 enrichment completely ameliorated this negative effect. The high temperature treatment also reduced the number of seeds produced per fruit by 68%, but the elevated CO_2 treatment nearly compensated for this deleterious effect, reducing the warming-induced seed-per-fruit reduction to only 9%.

Tako *et al.* (2001) grew rice (*Oryza sativa* L. cv. Mutsu-homare) plants hydroponically in controlled-environment chambers having atmospheric CO_2 concentrations of 350 and 700 ppm and day/night air temperatures of 24/17 (ambient) and 26/19°C (elevated), to study the interactive effects of elevated

CO_2 and temperature on the growth of this important crop. After 18 weeks, elevated CO_2 had no effect on whole-plant biomass at ambient growth temperatures, but with the additional 2°C of warming, atmospheric CO_2 enrichment produced a whole-plant biomass enhancement of 22%.

Bunce (2001) grew strawberry (*Fragaria x ananassa* Duchesne cv. Honeoye) plants in the field in open-top chambers maintained at atmospheric CO_2 concentrations of 350, 650, and 950 ppm for two years to study the effects of elevated CO_2 on photosynthesis in this important fruit crop. They took measurements weekly to evaluate the temperature dependence of the photosynthetic stimulation resulting from the two levels of atmospheric CO_2 enrichment. Plants grown at 650 and 950 ppm CO_2 exhibited mean photosynthetic rates 77 and 106% greater, respectively, than those of control plants exposed to ambient air.

Prasad *et al*. (2003) grew peanuts (*Arachis hypogaea* L. cv. Georgia Green, of the Virginia Runner type) from seed to maturity in sunlit controlled-environment growth chambers maintained at atmospheric CO_2 concentrations of 350 and 700 ppm and daytime-maximum/nighttime-minimum air temperatures of 32/22, 36/26, 40/30, and 44/34°C. During this study, leaf photosynthetic rates were unaffected by air temperatures over the range studied, but they rose by approximately 27% in response to the experimental doubling of the air's CO_2 content. Vegetative biomass increased by 51% and 54% in ambient air and CO_2-enriched air, respectively, as temperatures rose from 32/22 to 40/30°C. A further temperature increase to 44/34°C caused moderate to slight declines in vegetative biomass in ambient and CO_2-enriched air, respectively, so the final biomass increase over the entire temperature range investigated was 27% in the ambient air and 53% in the CO_2-enriched air. Going from the lowest-temperature, ambient CO_2 treatment to the highest-temperature, elevated CO_2 treatment led to a 106% increase in vegetative biomass.

In contrast, seed yields in both the ambient and CO_2-enriched air dropped dramatically with each of the three temperature increases studied, declining at the highest temperature regime to but a small percentage of what they were at the lowest temperature regime. Nevertheless, Prasad *et al*. report, "seed yields at 36.4/26.4°C under elevated CO_2 were similar to those obtained at 32/22°C under ambient CO_2," describing the latter pair of temperatures as "present-day seasonal temperatures." Even an unrealistically large warming of 4.4°C above present-day growing temperatures for peanut production would have essentially no effect on peanut seed yields, as long as the atmosphere's CO_2 concentration rose concurrently by something on the order of 350 ppm. And more realistic values of CO_2-induced global warming—temperature increases on the order of 0.4°C or less for a doubling of the air's CO_2 content (Idso, 1998)—likely would lead to a significant increase in peanut production.

Vu (2005) grew peanut plants of the cultivar Florunner from seed to maturity in greenhouses maintained at atmospheric CO_2 concentrations of 360 and 720 ppm and at air temperatures 1.5 and 6.0°C above outdoor air temperatures, measuring a number of parameters related to the plants' photosynthetic performance. They report rubisco photosynthetic efficiency—the ratio of midday light-saturated carbon exchange rate to rubisco initial or total activity—of the elevated-CO_2 plants was 1.3- to 1.9-fold greater than rubisco efficiency of the ambient-CO_2 plants at both growth temperatures. In addition, leaf soluble sugars and starch of plants grown at elevated CO_2 were 1.3- and 2-fold higher, respectively, than those of plants grown at ambient CO_2. Leaf transpiration of the elevated-CO_2 plants relative to the ambient-CO_2 plants was 12% less at near-ambient temperatures and 17% less in the higher temperature regime, and the water use efficiency of the elevated-CO_2 plants relative to the ambient-CO_2 plants was 56% greater at near-ambient temperatures and 41% greater in the higher temperature environment. Because less rubisco protein was required by the elevated-CO_2 plants, the subsequent redistribution of excess leaf nitrogen "would increase the efficiency of nitrogen use for peanut under elevated CO_2," just as the optimization of inorganic carbon acquisition and greater accumulation of the primary photosynthetic products in the CO_2-enriched plants "would be beneficial for peanut growth at elevated CO_2," Vu writes. Consequently, in the absence of other stresses, "peanut photosynthesis would perform well under rising atmospheric CO_2 and temperature predicted for this century," Vu concludes.

Crafts-Brandner and Salvucci (2004) explored the concurrent effects of elevated atmospheric CO_2 concentration and temperature on photosynthetic CO_2 fixation in cotton (*Gossypium hirsutum* L. cv. Coker 100A-glandless), using "intact plants and biochemical measurements to directly determine how environmental change impacts specific physiological mechanisms important to plant productivity." They report "net photosynthesis of cotton leaves at ambient levels of CO_2 was inhibited at leaf temperatures above about 32°C." At a leaf internal CO_2 concentration 4.3 times greater than ambient, however, net photosynthesis did not begin to decline until leaf temperatures rose above 40°C. Viewed another way, the net photosynthetic rate of cotton leaves exposed to ambient air declined by approximately 77% as leaf temperature rose from 32 to 40°C, whereas in leaves exposed to the CO_2-enriched air it rose by about 9%, indicating the increase in atmospheric CO_2 concentration more than compensated for the dramatic decrease in photosynthetic rate that would ordinarily result from the 8°C increase in temperature.

Aranjuelo *et al.* (2005) grew the forage crop alfalfa (*Medicago sativa* L.) in 13-L pots for three consecutive June–July periods (2001–2003) out-of-doors in polyethylene-covered temperature gradient tunnels maintained at atmospheric CO_2 concentrations that averaged 405 and 730 ppm at ambient (AT) and elevated (ET) temperatures (ET = AT + 4°C) and at high (HW) and low (LW) soil water contents (LW = 0.5HW). They fed all of the plants adequate nutrients except for nitrogen, to ensure the only source of nitrogen for the plants was that which was fixed by their nodules in response to inoculation with *Sinorhizobium meliloti* strain 102F78. The researchers report "the effect of elevated CO_2 on plant growth interacted positively with temperature," and "higher dry mass production of plants grown under elevated CO_2 and temperature was a consequence of enhanced photosynthetic rates." Mean CO_2-induced increases in leaf net photosynthesis over the entire experiment were found to be: +5% (HW, AT), +50% (HW, ET), +17% (LW, AT), and +42% (LW, ET), as best as can be determined from the bar graphs in the paper describing their study. Mean CO_2-induced increases in leaf biomass were +4% (HW, AT), +54% (HW, ET), +23% (LW, AT), and +58% (LW, ET), with the same caveat.

For both leaf net photosynthesis and biomass production, Aranjuelo *et al.* found the stimulatory effect of the elevated CO_2 was about 2.5 times greater in the warmer of the two temperature treatments in the low soil water regime and 10 times greater in the high soil water regime. In addition, the extra CO_2 benefited plant water loss via transpiration, which declined by 25% (HW, AT), 41% (HW, ET), 31% (LW, AT), and 31% (LW, ET). Under both well-watered and droughty conditions in this study, atmospheric CO_2 enrichment enhanced photosynthesis and biomass production in alfalfa, and simultaneously decreased transpirational water losses.

Bencze *et al.* (2005) grew specimens of three varieties (Emma, Martina, and Mezofold) of winter wheat (*Triticum aestivum*) in controlled-environment chambers under ambient (375 ppm) and elevated (750 ppm) CO_2 at minimum, maximum, and mean temperature regimes of 10,12, and 10.7°C, respectively. Twelve days after the average date of heading, they subjected several plants of each variety to 15 more days of elevated temperatures (min/max/mean of 20, 35, and 25.2°C) to assess the independent effects of both elevated CO_2 and temperature on wheat growth and yield.

They found the temperature treatment accelerated the aging process in the three wheat varieties, and concurrent atmospheric CO_2 enrichment generally helped them maintain a higher and longer level of photosynthetic activity during grain-filling and maturation. Bencze *et al.* report the CO_2-enriched plants "suffered less damage from heat stress and produced a higher yield than at the ambient level." In addition, the extra CO_2 supplied to the Emma cultivar plants meant the difference between life and premature death, since by the end of the 15-day high-temperature treatment the plants growing in ambient air were dead, whereas those growing in elevated CO_2 survived for a few more days. In a future world of higher atmospheric CO_2 concentrations, wheat crops should be better able to withstand the stress of potentially higher temperatures, suffering less damage and producing greater yields.

Cen and Sage (2005) grew well-watered and well-fertilized sweet potato (*Ipomoea batatas* L.) plants in 20-L pots of soil in a greenhouse, periodically measuring light-saturated rates of net photosynthesis in new but fully expanded leaves in response to short-term changes in air temperature and atmospheric CO_2 concentration. In response to an approximate 370 ppm increase in the air's CO_2 concentration, the optimum leaf temperature for net photosynthesis—the leaf temperature at which net photosynthesis proceeds at its maximum rate—rose by approximately 4.5°C, and its maximal rate of net photosynthesis rose by about 75%. The doubling of the air's CO_2 concentration had no impact on net photosynthesis at a leaf temperature of 15°C but boosted it by 28% at 21°C, by 43% at 27°C, by 56% at 33°C, and by 70% at 39°C. In order for the net photosynthetic rate of sweet potatoes growing in air of 740 ppm CO_2 to drop below the maximum rate exhibited by plants growing in air of 370 ppm CO_2 (which occurred at a leaf temperature of 30°C), leaf temperature would have to rise by 12°C to a value of 42°C.

De Costa *et al.* (2006) write, "doubts have been expressed whether the expected yield increases [of rice] in response to increased CO_2 could be sustained under high temperature regimes." The investigators set out to learn whether this might happen in sub-humid Sri Lanka, where weekly maximum temperatures during both the maha (January to March) and yala (May to August) growing seasons typically range from 30 to 33°C. They grew two crops of rice (one in the maha season and one in the yala season) in open-top chambers maintained at atmospheric CO_2 concentrations of either 363 or 567 ppm under normal field conditions at the Rice Research and Development Institute of Sri Lanka, measuring a number of meteorological and plant physiological parameters throughout both seasons, as well as total biomass production and grain yield at the times of final harvest. They found the CO_2-induced increase in total plant biomass at the time of final harvest was 23% in the maha season and 37% in the yala season, and final grain yields were enhanced by 24% and 39% in the maha and yala seasons, respectively. These increases occurred even though air temperatures in the CO_2-enriched chambers were on average 1.6°C higher than air temperatures in the ambient-air chambers.

Borjigidai *et al.* (2006) grew rice (cv Akitakomachi) plants from seed in greenhouses maintained at atmospheric CO_2 concentrations of 370 and 570 ppm and then transplanted them to the field and grew them in a well-fertilized paddy culture in a FACE study at the same CO_2 concentrations under which the seeds were sprouted in both 2003 and 2004. At various times throughout the two growing seasons during the field portion of the experiments, the researchers made photosynthetic measurements of the most recently fully expanded leaves in full sunlight at a variety of different leaf temperatures. They report "the optimal temperature of photosynthesis (T_{opt}, the value where the photosynthetic rate was maximum) was significantly higher at elevated CO_2: it ranged from 22 to 34.5°C with an average value of 28.9°C at ambient CO_2, and from 29.5 to 37°C with an average value of 33.5°C at elevated CO_2."

Bernacchi *et al.* (2006) grew soybeans (*Glycine max* (L.) Merr.) for three years at the SoyFACE facility of the University of Illinois at Urbana-Champaign, Illinois (USA) at atmospheric CO_2 concentrations of either 375 or 550 ppm under natural field conditions, measuring a number of weather and plant physiological parameters from pre-dawn to post-dusk on several days during the three growing seasons. They found the mean daily integral of leaf-level net photosynthesis (A) was enhanced by nearly 25% in the CO_2-enriched air. In addition, the 11 scientists write, "there was a strong positive correlation between daytime maximum temperatures and mean daily integrated A at elevated CO_2." Their graphical representation of this relationship indicates at a daily maximum temperature of approximately 26.5°C, the CO_2-enriched air stimulated leaf-level net photosynthesis by about 14%, and at a daily maximum temperature of approximately 34.5°C, CO_2 enrichment stimulated photosynthesis by about 35%.

Koti *et al.* (2007) used Soil-Plant-Atmosphere-Research (SPAR) chambers at Mississippi State University (USA) to investigate the effects of doubled atmospheric CO_2 concentration (720 vs. 360 ppm) on the growth and development of six well-watered and well-fertilized soybean genotypes they grew from seed in pots filled with fine sand and exposed to the dual stresses of high day/night temperatures (38/30°C vs. 30/22°C) and high UV-B radiation levels (10 vs. 0 $kJ/m^2/day$). They found the elevated CO_2 partially compensated for the damaging effects on vegetative growth and physiology caused by high temperatures and enhanced UV-B radiation levels, and elevated CO_2 had a positive influence on plant height, leaf area, total biomass, net photosynthesis, total chlorophyll content, phenolic content, and wax content, as well as relative plant injury.

Mishra *et al.* (2008) documented the positive impact of atmospheric CO_2 enrichment on the photosynthetic rates of field-grown soybean plants subjected to the simultaneous negative effects of acute heat stress and elevated atmospheric ozone (O_3) concentrations at the SoyFACE facility of the University of Illinois. The seven scientists discovered elevated ozone exacerbated heat-related decreases in photosynthetic electron transport, but "elevated CO_2 minimized or prevented light-dependent O_3-related decreases in electron transport (and thus photoinhibition) during heat stress."

Alonso *et al.* (2009) sequentially grew well-watered and well-fertilized plants of the wheat cultivar Alcala in 16-liter pots of perlite (sown at a rate of 35 seeds per pot) in a controlled-environment growth chamber—first at an atmospheric CO_2 concentration of 370 ppm and then at 700 ppm—from sowing through anthesis. They measured gas exchange in flag leaves at ear emergence to obtain the values of various plant physiological parameters required for the biochemical photosynthesis model developed by Farquhar *et al.* (1980), along with the responses of those parameters to changes in temperature. They found "photosynthesis response to temperature was negative at low air CO_2 concentrations and became progressively positive as CO_2 increased," which might have been expected "from the increase in photorespiration with temperature and the gradual inhibition of this process as CO_2 increases (Long, 1991)." In addition, "at high chloroplastic CO_2, photosynthesis in elevated growth CO_2 was lower at 15–25°C and higher at 30–35°C, than in ambient growth CO_2, implying an enhanced photosynthesis response to temperature in plants grown in elevated CO_2."

In 2004 and 2005, Gutierrez *et al.* (2009) grew well-watered and well-fertilized spring wheat (*Triticum aestivum* L. cv. Gazul) plants from seed to maturity out-of-doors in Salamanca, Spain in temperature-gradient chambers maintained at ambient (370 ppm) and elevated (700 ppm) atmospheric CO_2 concentrations and ambient air temperature (TA) and elevated air temperature (TE = TA plus 4°C). They titled their paper, "Acclimation to future atmospheric CO_2 levels increases photochemical efficiency and mitigates photochemistry inhibition by warm temperatures in wheat." They report net photosynthesis was increased by 62–72% in both years in the CO_2-enriched chambers; at the conclusions of the two growing seasons, total plant biomass production in the CO_2-enriched chambers was increased by 12–18%. They conclude, "future increases in atmospheric CO_2 and temperature may have a positive effect on photochemical efficiency," noting their work "provides evidence that with air CO_2 enrichment a reallocation of resources favoring light capture may occur."

Xiao *et al.* (2010) note "the impact of future climate change on crop production has been widely predicted by modeling the interaction between crops and climate change," adding it is currently thought "overall crop yields will decrease by 5–10% in China by 2030 as a result of climatic changes, and that the yields of wheat, rice and maize will be greatly reduced." They further note "the direct fertilization effect of rising CO_2 will offset these losses," citing Ewert *et al.* (2002) and Long *et al.* (2006). In addition, they remark, few real-world observations of the impacts of climate change on crop production have been reported.

The seven scientists conducted two sets of field experiments to evaluate the effects of warming on the productivity of winter wheat from 2006 to 2008 in the semiarid northwestern part of China: one set of experiments at the Tongwei County station located at the foot of Lulu Mountain (35°13'N, 105°14'E) at an altitude of 1,798 meters above sea level, and another set at the mountain's summit at an altitude of 2,351 meters. At each of these locations, they established four air temperature treatments (ambient and ambient plus 0.6, 1.4, and 2.2°C), which they created by placing electric heating wires on the surface of the soil between the rows of wheat, which induced the 0.6–2.2°C air temperature increases they measured at a height of 20 cm above the tops of the wheat canopies. They found this increase in temperature "will lead to a significant change in the growth stages and water use of winter wheat," and "crop yields at both high and low altitudes will likely increase," by 2.6% at low altitudes and 6.0% at high altitudes. Even without the benefits of the aerial fertilization and anti-transpiration effects of the rise in the air's CO_2 content, the increase in temperature predicted by climate models for the year 2050 likely will lead to increases in winter wheat production in the northwestern part of China, not the decreases some modeling studies have predicted.

Yoon *et al.* (2009) grew well-watered and well-fertilized cotton plants from seed to maturity—one plant to each container of washed sand, with spacing between plants similar to the plant spacing found in typical cotton fields—in the Georgia Envirotron at the University of Georgia Griffin Campus. They placed the containers with their plants in chambers maintained at all combinations of two day/night air temperatures regimes (25/15°C and 35/25°C) and three atmospheric CO_2 concentrations (400, 600, and 800 ppm). At the lower of the two air temperature regimes, the authors found "final boll weight at harvest was 1.59 times (at 600 ppm) and 6.3 times (at 800 ppm) higher compared to ambient CO_2." Further increasing the temperature tremendously increased this difference, as "the final boll weight was 34.1 times (at 600 ppm) and 23.3 times (at 800 ppm) higher compared to ambient CO_2." In addition, "the response of final lint yield to CO_2 was more or less similar to the response of boll weight."

Thus a significant body of scientific literature suggests a continuation of the rise in the air's CO_2 content likely will lead to enhanced rates of photosynthesis and biomass production by agricultural crops, which will not be diminished by any global warming that might occur concurrently. If the ambient air temperature rises, the growth-promoting effects of atmospheric CO_2 enrichment likely will rise right along with it, in agreement with the experimental observations reviewed by Idso and Idso (1994). The biosphere will continue producing the food and fiber needed for an increasing population.

Beyond this natural phenomenon, Meerburg *et al*. (2009) describe how crop yields will continue to increase in the future because of "the development and adoption of new technologies and improved farm management," citing Ewert *et al*. (2005), who demonstrated continuing advances in agricultural technology historically have been the most important drivers of productivity change. Between 1961 and 2007, Meerburg *et al*. report, "average US corn yields increased by 240%, from 3.9 tons per hectare per year to 9.4 tons per hectare per year," citing the FAO (2009) and noting some researchers have predicted "advances in agronomics, breeding, and biotechnology will lead to an average corn yield in the US of just over 20 tons per hectare per year in 2030," citing Duvick (2005).

Meerburg *et al*. also note farmers in Brazil successfully increased the productivity of soybeans, maize, and cotton during the past decade even though the cumulative number of days of exposure to temperatures above the three crops' optimum values "is far greater than in the US." In the Brazilian state of Mato Grosso, for example, "maximum average day temperature exceeds 35°C for 118 days per year, of which 75 days are in the average soybean-growing season." Nevertheless, they report the average production of soybeans in 2008 was about 3.1 tons per hectare per year in Mexico, and the average yield in the United States was 2.8 tons per hectare per year. Similarly, they note the mean cotton yield in Brazil in 2006/2007 was 1.4 tons per hectare per year, while in the United States it was 0.9 tons per hectare per year.

The seven scientists thus conclude "temperatures higher than currently experienced in the US do not necessarily need to coincide with lower crop yields and … already existing technology and future advances (new varieties, optimized farm management, biotechnology, etc.) can overrule the negative effect of increasing temperatures on yield."

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3.13.2 Grasslands

- As the air's CO_2 content rises, grassland plants likely will exhibit enhanced rates of photosynthesis and biomass production that will not be diminished by any global warming that might occur. If the ambient air temperature does rise, the growth-promoting effects of atmospheric CO_2 enrichment likely will rise also. Grasslands are likely to produce increasingly greater amounts of forage and perhaps reclaim areas of barren ground in certain environments.

As the atmosphere's CO_2 content rises, most plants, including those of various grassland ecosystems, will exhibit increased rates of photosynthesis and biomass production. This increase in productivity should increase the amount of forage available for grazing animals and possibly reduce the land area occupied by bare soil in certain environments. However, some researchers claim global warming will negate the growth-promoting effects of atmospheric CO_2 enrichment and cause the opposite to occur. This section reviews the results of experimental studies of the photosynthetic and growth responses of grassland plants to atmospheric CO_2 enrichment when exposed to higher-than normal-temperatures.

The optimum growth temperatures of many plants have been demonstrated to rise substantially with increasing concentrations of atmospheric CO_2 (Berry and Bjorkman, 1980; Stuhlfauth and Fock, 1990; McMurtrie *et al*., 1992; McMurtrie and Wang, 1993), as has been described in more detail by Long (1991), Idso and Idso (1994), and Cowling and Sykes (1999). These previously observed positive CO_2 x temperature interactions have continued to appear in more recent studies of the subject for grassland species.

Lilley *et al*. (2001) grew swards of subterranean clover (*Trifolium subterraneum*) at 380 and 690 ppm CO_2 in combination with simultaneous exposure to ambient and elevated (ambient plus 3.4°C) air temperatures. After one year of these treatments, they found elevated CO_2 increased foliage growth by 19% at ambient air temperatures. At elevated air temperatures, the CO_2-enriched plants displayed a growth enhancement of only 8%, but the plants grown at ambient CO_2 exhibited a 28% reduction in foliage growth. Similarly, Morgan *et al*. (2001) determined twice-ambient levels of atmospheric CO_2 increased aboveground biomass in native shortgrass steppe ecosystems by an average of 38%, despite an average air temperature increase of 2.6°C. And when bahiagrass was grown across a temperature gradient of 4.5°C, Fritschi *et al.* (1999) found a 275 ppm increase in the air's CO_2 content boosted photosynthesis and aboveground biomass by 22 and 17%, respectively, independent of air temperature.

Greer *et al.* (2000) grew five pasture species at 18 and 28°C and found plants concomitantly exposed to 700 ppm CO_2 displayed average photosynthetic rates 36 and 70% greater, respectively, than average rates of control plants grown in air of ambient CO_2 concentration. The average CO_2-induced biomass increase for the five species rose dramatically with increasing air temperature, from only 8% at 18°C to 95% at 28°C.

Stirling *et al.* (1998) had found much the same thing. They nurtured five fast-growing native annual species in glasshouses maintained at two combinations of CO_2 (ambient and ambient plus 340 ppm) and temperature (ambient and ambient plus 3°C) for eight weeks, to assess their growth responses to elevated CO_2 and temperature. Elevated CO_2 significantly increased photosynthetic rates, by 18–36% for all species, independent of growth temperature, for the entire eight weeks of the experiment. The persistence of this photosynthetic enhancement led to total plant biomass increases for CO_2-enriched plants, on average, 25% greater than those of control plants grown in ambient-CO_2 air. And although elevated CO_2 and elevated temperature together had few significant interactive effects on the various metrics of growth, the overall CO_2 growth response was generally slightly larger at elevated than at ambient temperatures.

In a similar study with similar findings, Newman *et al.* (2001) grew two perennial grassland species (rhizoma peanut-*Arachis glabrata* and bahiagrass-*Paspalum notatum*) native to South America and common to Florida (USA) in greenhouses fumigated with air of either 360 or 700 ppm CO_2 for three full growing seasons. The C_3 and C_4 grasses were simultaneously exposed to air temperatures ranging from ambient to 4.5°C above ambient. Averaged across the three growing seasons, elevated CO_2 increased dry matter production in rhizoma peanut and bahiagrass by 25 and 15%, respectively. Here too, the researchers found no significant interactive effects of elevated CO_2 and temperature on dry mass production in these species, and on their own, air temperatures 4.5°C above ambient increased dry matter production in both species by an average of 13% across all three years.

Niklaus *et al.* (2001) established experimental plots in a nutrient-poor calcareous grassland in northwestern Switzerland that contained either 31, 12, or five species, removing selected species from some of the plots so the proportion of plant functional types in each of the plots remained unchanged (55% graminoids, 15% legumes, and 30% non-legume forbs). They fumigated the plots with air of either 360 or 600 ppm CO_2 for four years, to determine the ecological effects of elevated CO_2 across a biodiversity gradient in this grassland community. As plant community diversity decreased at ambient CO_2, soil nitrate concentrations increased, the scientists report. Elevated CO_2, however, reduced soil nitrate concentrations at all the studied levels of plant diversity. In addition, nitrification—a biological process that yields nitrate—increased with decreasing species diversity at ambient CO_2, and at elevated CO_2, rates of nitrification were 25% lower than those observed at ambient CO_2 at all levels of community diversity, suggesting a CO_2-enriched environment would reduce the risk of nitrate pollution of groundwater.

Hakala and Mela (1996) grew field-sown meadow fescue (*Festuca pratensis* cv. Kalevi) in open-top chambers and glasshouses maintained at atmospheric CO_2 concentrations of 350 and 700 ppm in combination with ambient and elevated (ambient plus 3°C) air temperatures for four consecutive years to determine the effects on aboveground biomass production in this important forage crop. They found elevated CO_2 significantly increased aboveground biomass by an average of 18% in each of the four study years, but the effect occurred only when plants were concomitantly exposed to elevated air temperatures.

Sinclair *et al.* (2007) note it has long been assumed global warming would be bad for plants that appear to be adapted to cool temperatures and typically exhibit reduced growth rates in warmer environments. Using climate-controlled mini-greenhouses, the five researchers tested this assumption by examining the interacting effects of air temperature and vapor pressure deficit (VPD) on the growth of tall fescue (*Festuca arundinacea* Schreb), a cool-season grass that from past studies was expected to show declining growth with warmer temperatures over the range of 18.5 to 27°C. They grew well-watered and -fertilized plants in two sets of six-week-long experiments, one in which air VPD was held constant at 1.2 kPa while air temperature was maintained at either 18.5, 21, 24, or 27°C, and one in which air temperature was held constant at 22°C while air VPD was maintained at either 0.9, 1.2, 1.4, or 1.7 kPa.

In the experiment where the air VPD was held constant, they write, "in direct contrast to the anticipated results, the weekly growth of the tall fescue was substantially increased with increased temperature," as "growth at 24 and 27°C was about 2.3 times that at 18.5°C and 1.4 times that at 21°C." In the experiment where air temperature was held constant, "there was a strong, negative influence of increasing VPD on plant growth." In addition, "transpiration rates were similar across treatments," indicating "water movement through the plants did not increase in response to increasing VPD." This led them to conclude limitation of water movement through the plant "is likely a result of stomatal closure in response to elevated VPD (Bunce, 2006)." This phenomenon also would restrict the CO_2 diffusion pathway into the plants and result in a decrease in photosynthesis, which is likely what caused the decreased growth at increased VPD. Nonetheless, their results indicate as long as the air VPD does not rise concurrently, increasing temperatures do not lead to growth reductions in this cool-season plant. In fact, they observe just the opposite to be true—warming dramatically increased tall fescue growth.

Sinclair *et al*. note, "during the past 50 years, VPD has remained virtually constant (Szilagyi *et al*., 2001) due to an increase in atmospheric dew point temperature (Gaffen and Ross, 1999)," even in the face of what IPCC describes as unprecedented global warming. In a future warmer world, they conclude, "tall fescue, and perhaps other cool season species, could experience a substantial benefit with temperature increases expected in temperate zones if VPD were to remain unchanged."

Wolfe-Bellin *et al*. (2006) write, "nocturnal temperatures are predicted to increase more than diurnal temperatures," as has been observed in the real world over much of the twentieth century, and it might be expected "increased nocturnal temperature would increase dark respiration rate" and thereby "diminish the positive effects of elevated CO_2 on whole-plant growth, as measured by total biomass." In an experiment designed to explore this hypothesis, they grew the C_3 forb *Phytolacca americana* L. from the four-leaf stage to maturity under well-watered and well-fertilized conditions in 6.2-L containers filled with a general purpose growing medium in controlled-environment glass chambers maintained at either 370 or 740 ppm CO_2 at diurnal/nocturnal temperatures of either 26°/20°C or 26°/24°C. They periodically measured the plants' light-saturated photosynthetic rates and whole-plant biomass. They found "plant photosynthetic rate was greater under elevated CO_2 [+69% during the first part of the growing season], and dark respiration rate, predicted to increase under higher nocturnal temperatures, exhibited no response to the nocturnal temperature treatment." In contrast to their prediction, the forb they studied "exhibited no diminishment of total plant size in response to elevated nocturnal temperature," and "time to flowering decreased and biomass allocation to reproduction increased under conditions of elevated nocturnal temperatures." They conclude, "elevated CO_2 and high nocturnal temperatures of the future could have a neutral or even positive effect on the growth of northern *P. americana* populations," even to the extent of "increasing population sizes, at least for plants growing at the northern edge of the species' range."

Niu *et al*. (2010) note, "most modeling studies predict ecosystem carbon storage will decrease as respiration is stimulated more than photosynthesis by rising temperature, with a consequent positive feedback to climate warming." Working in a tallgrass prairie in McClain County, Oklahoma (USA) dominated by C_4 grasses and C_3 forbs that had not been grazed for the prior 40 years, they conducted a warming experiment in which they used infrared heaters to elevate soil temperature at a depth of 2.5 cm by an average of 1.96°C from 2000 to 2008, and "yearly biomass clipping mimicked hay or biofuel feedstock harvest."

They found the experimental warming "significantly stimulated carbon storage in aboveground plant, root, and litter pools by 17%, 38%, and 29%, respectively, averaged over the nine years," but it "did not change soil carbon content or nitrogen content in any pool." They conclude increased plant nitrogen use efficiency played a more important role than soil nitrogen availability in regulating carbon cycling in this ecosystem, as the tallgrass prairie experienced a significant increase in productivity caused solely by the warming of its soil and not promoted by any addition of nitrogen to it. They explain this result by stating, "increased inputs of more recalcitrant [higher carbon:nitrogen ratio] material into soil counterbalanced any direct warming stimulation of carbon release, leading to little change in soil carbon stock and no apparent feedback to climate warming."

Morgan *et al*. (2011) write, "global warming is predicted to induce desiccation in many world regions through increases in evaporative demand," but "rising CO_2 may counter that trend by improving plant water-use efficiency." However, they note, "it is not clear how important this CO_2-enhanced water use efficiency might be in offsetting warming-induced desiccation because higher CO_2 also leads to higher plant biomass, and therefore greater transpirational surface."

Morgan *et al*. conducted a prairie heating and CO_2 enrichment (PHACE) experiment in which they evaluated the productivity of native mixed-grass prairie west of Cheyenne, Wyoming (USA) to two levels of atmospheric CO_2 concentration (385 and 600 ppm, supplied via standard FACE technology) and two temperature regimes—ambient and elevated (ambient plus 1.5/3.0°C warmer day/night temperatures) for three full growing seasons (2007–2009) by means of T-FACE technology (Kimball *et al*., 2008)—after first having measured grassland productivity under unmodified conditions for one growing season (2005) and with CO_2 enrichment alone for a second season (2006).

The 10 researchers report their warming treatment reduced annual soil water content by 13.1%, but their elevated CO_2 treatment increased annual soil water content by 17.3%, demonstrating "the water conservation effects of elevated CO_2 can completely cancel the desiccating effects of moderately warmer temperatures." In addition, they write, "exposure of the prairie to 600 ppm CO_2 increased peak total above-ground biomass by an average 33% in the first 3 years of the experiment when annual precipitation amounts were in 7% of the site's 132-year average of 388 mm," but "CO_2 enrichment had no effect on above-ground biomass in 2009," when "annual precipitation was 17% higher than the long-term mean." They speculate the "higher soil water content in 2009 minimized the potential water-relations benefit of CO_2 enrichment on plant productivity."

Morgan *et al*. write, "many believe that CO_2-induced reductions in transpiration at the leaf level will be largely offset at the canopy level by increases in leaf area," citing McNaughton and Jarvis (1991), Piao *et al*. (2007), Frelich and Reich (2010), and Seager and Vecchi (2010). They say their results "clearly illustrate the importance of compensating CO_2 and warming effects in semi-arid ecosystems" and "indicate that in a warmer, CO_2-enriched world, both soil water content and productivity in semi-arid grasslands may be higher than previously expected." In an accompanying commentary on their paper, Baldocchi (2011) writes, "Morgan and colleagues provide one of the first and best views of how a mixed-grass ecosystem growing in a semi-arid climate will respond to future CO_2 and climatic conditions." Morgan *et al*.'s findings help explain the great CO_2-induced greening of the Earth phenomenon (see section 4.2, this volume), especially as manifested in semi-arid regions of the planet.

Even if the air's CO_2 content were to cease rising or have no effect on plants, it is still possible temperature increases alone would promote plant growth and development in some situations. Norton *et al*. (1999) found this to be the case. Elevated CO_2 had essentially no effect on the growth of the perennial grass *Agrostis curtisii* after two years of fumigation, whereas a 3°C increase in air temperature increased the growth of the species considerably.

The recent scientific literature indicates grassland plants likely will exhibit enhanced rates of photosynthesis and biomass production as the air's CO_2 content rises, and those benefits will not be diminished by any global warming that might occur. If the ambient air temperature does rise, the growth-promoting effects of atmospheric CO_2 enrichment likely will rise right along with it, becoming increasingly robust in agreement with the experimental observations reviewed by Idso and Idso (1994). As long as the air's CO_2 content continues to rise, grasslands will likely produce increasingly great amounts of forage, and perhaps reclaim areas of barren ground in certain environments.

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3.13.3 Woody Plants

- As the air's CO_2 content rises, trees likely will exhibit enhanced rates of photosynthesis and biomass production that will not be counteracted by any global warming that might occur. If the ambient air temperature rises, the growth-promoting effects of atmospheric CO_2 enrichment likely will rise also. Trees are likely to produce greater amounts of biomass and, therefore, more timber products to meet the increasing needs of Earth's growing human population in the future.

As the air's CO_2 content rises, most trees likely will exhibit increased rates of photosynthesis and biomass production, which can help meet human demands for wood products. However, some researchers claim global warming will negate the growth-promoting effects of atmospheric CO_2 enrichment and actually reduce tree growth. To determine whether this claim has any validity, this section examines the results of several studies designed to reveal the net effect of both elevated CO_2 and air temperature on the growth of trees and other woody plants.

The optimum growth temperature for several plants already has been shown to rise substantially with increasing levels of atmospheric CO_2 (Berry and Bjorkman, 1980; Stuhlfauth and Fock, 1990; McMurtrie *et al*., 1992; McMurtrie and Wang, 1993). Long (1991) described this phenomenon at length, having calculated from well-established plant physiological principles that most C_3 plants should increase their optimum growth temperature by approximately 5°C in response to a 300 ppm increase in the atmosphere's CO_2 concentration. In a subsequent review of the pertinent scientific literature, Cowling and Sykes (1999) demonstrated this was true for a number of plants. The photosynthetic rates of woody plants also are likely to rise in tandem with increases in the air's CO_2 concentration and temperature, as previously documented by Idso and Idso (1994) and by more recent studies for various trees and shrubs.

Kellomaki and Wang (2001) grew birch seedlings at atmospheric CO_2 concentrations of 350 and 700 ppm in combination with ambient and elevated (ambient plus 3°C) air temperatures. After five months, the photosynthetic rates of the CO_2-enriched seedlings were 21 and 28% greater than their ambient-grown counterparts at ambient and elevated air temperatures, respectively. Carter *et al.* (2000) report a 300 ppm increase in the air's CO_2 content allowed leaves of sugar maple seedlings to remain green and non-chlorotic when exposed to air temperatures 3°C above ambient air temperature, and seedlings fumigated with ambient air exhibited severe foliar chlorosis when exposed to the same elevated air temperatures. At elevated air temperatures, rates of photosynthesis are greater and foliar health is typically better in CO_2-enriched as opposed to ambient air.

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

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

The list of recent studies of woody plants that experience a CO_2-induced enhancement of growth in response to environmental warming is extensive, starting with Hamerlynck *et al.* (2000), who grew seedlings of the evergreen perennial shrub *Larrea tridentata* in glasshouses maintained at atmospheric CO_2 concentrations of 360, 550, and 700 ppm for one year. The researchers withheld water from half of the seedlings for three months prior to a nine-day high-temperature treatment. Elevated CO_2 largely offset the detrimental effects of drought and high temperature on water relations and photosynthesis in this species. Averaged across the entire experiment, the photosynthetic rates of seedlings grown at 550 and 700 ppm CO_2 were 31 and 90% greater, respectively, than the rates of the ambient-grown control plants.

Usami *et al.* (2001) grew two-year-old saplings of *Quercus myrsinaefolia*, an evergreen broad-leaved oak species, in controlled-environment chambers having various atmospheric CO_2 concentrations and air temperatures for approximately one year, to study the interactive effects of elevated CO_2 and temperature on the development and growth of this important tree, which is widely distributed throughout Laos, Vietnam, China, Taiwan, South Korea, and southwestern Japan. In ambient air, 3 and 5°C increases in air temperature boosted final sapling biomass by 53 and 47%, respectively. At elevated CO_2 concentrations 1.5 or 2 times greater than the ambient CO_2 concentration, the same 3 and 5°C increases in air temperature enhanced final biomass by 110 and 140%, respectively.

Turbull *et al.* (2002) manipulated day/night air temperatures around 4-m-tall cottonwood (*Populus deltoides* Bartr. Ex Marsh) trees growing in large experimental enclosures, to study the effects of temperature on carbon relations. A 6°C increase in daytime temperature, coupled with a 10°C increase in nighttime temperature, enhanced rates of net photosynthesis by 64% and rates of dark respiration by 77%. On an absolute scale, the photosynthetic carbon gains due to the daytime temperature increase were nearly an order of magnitude greater than the nocturnal carbon losses caused by the greater increase in nighttime temperature. Consequently, if Earth were to begin to warm again, carbon uptake by cottonwood trees should increase significantly.

Peltola *et al.* (2003) constructed closed chambers around 20-year-old Scots pine (*Pinus sylvestris* L.) trees growing on a low-nitrogen-containing soil, and for three years thereafter they fumigated the trees in the chambers with air containing either 350 or 700 ppm CO_2 at either ambient or elevated air temperatures (about 4°C above ambient temperatures), to study the effects of elevated CO_2 and air temperature on stem development in this coniferous species when growing on a soil low in nitrogen. After three years, they found cumulative stem diameter growth in the CO_2-enriched trees grown at ambient air temperature was 57% greater than that of control trees grown at ambient CO_2 and ambient air temperature. The trees subjected to elevated CO_2 and elevated air temperature exhibited cumulative stem-diameter growth 67% greater than trees grown in ambient air at ambient air temperatures.

Sallas *et al.* (2003) grew seedlings of Scots pine and Norway spruce (*Picea abies* (L.) Karst.) for 50 days in computer-controlled environmental growth chambers in air of ambient or twice-ambient CO_2 concentration (normal or elevated (EC) treatments) at day/night temperature combinations of 19/12°C or 23/16°C (normal or elevated (ET) treatments), making a host of measurements. Seedlings of both species were shown to accumulate the most biomass in the combined EC + ET treatment.

Hymus *et al.* (2003) studied net ecosystem exchange (NEE) of CO_2 in a scrub-oak ecosystem—85–90% of the aboveground biomass of which was comprised of three oak species (*Quercus myrtifolia*, *Quercus geminate,* and *Quercus chapmanii*)—on Merritt Island in NASA's Kennedy Space Center on the coast of central Florida (USA). This ecosystem was completely burned in January 1996, after which 16 open-top chambers (OTCs) were placed on it in the spring of that year, half of which were maintained at the ambient atmospheric CO_2 concentration while the other half were maintained at ambient plus 350 ppm, with routine measurements being started in June 1999 and continuing for 25 months through July 2001. The scientists found the extra CO_2 supplied to the CO_2-enriched OTCs "increased maximum NEE and the apparent quantum yield of the NEE during the photoperiod," and the magnitude of the stimulation of maximum NEE, expressed per unit ground area, "was seasonal, rising from 50% in the winter to 180% in the summer," in accord with what is known about the interactive effects of atmospheric CO_2 enrichment and daily, seasonal, and multiyear warming.

Turnbull *et al.* (2004) studied four- to five-meter-tall cottonwood trees (*Populus deltoides* Bartr.) grown for three years in air of different CO_2 concentrations (420, 800, and 1,200 ppm) in the three bays of the Biosphere 2 facility near Tucson, Arizona (USA). They maintained the trees at three nocturnal temperatures (15, 20, or 25°C) and a single constant daytime temperature (31 ± 1°C) in a short-term experiment in which they routinely measured maximum photosynthesis (Amax) rates at growth CO_2 concentrations. As nocturnal air temperature rose from 15 to 25°C, the researchers observed subsequent daytime Amax increased by 16% in air of 420 ppm CO_2, 12% in air of 800 ppm CO_2, and 4% in air of 1,200 ppm CO_2, leading them to conclude "at future elevated night temperatures suggested by global climate monitoring and modeling, net photosynthesis at elevated CO_2 may be increased." It appears the response could saturate at a CO_2 partial pressure of somewhat more than 1,200 ppm CO_2, but that value is far greater than anyone is suggesting will ever be reached as a consequence of mankind's burning of fossil fuels.

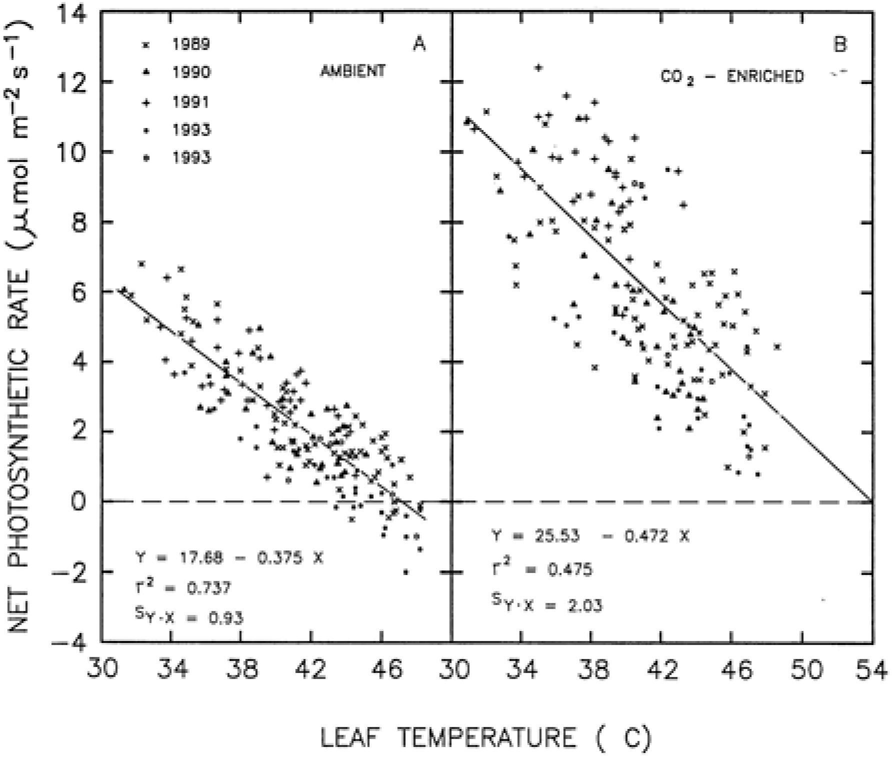

Figure 3.13.3.1. Leaf net photosynthetic rate vs. leaf temperature for the foliage of sour orange trees growing in air of either 400 or 700 ppm CO_2. Adapted from Idso *et al.* (1995).

But what if air temperatures get *really* hot, for some as-yet-unknown reason? Idso *et al.* (1995) grew well-watered and -fertilized sour orange (*Citrus aurantium* L.) trees from the seedling stage out-of-doors at Phoenix, Arizona (USA) in clear-plastic-wall open-top chambers continuously maintained at mean atmospheric CO_2 concentrations of either approximately 400 or 700 ppm for 5.5 years. During the warmest parts of some of the hottest days of summer, the scientists measured the temperatures and rates of net photosynthesis of fully expanded outer-canopy sunlit leaves.

Figure 3.13.3.1 portrays the results of plotting their net photosynthesis measurements against leaf temperature. Based on the linear regression lines fit to the data, it can be determined the 75% increase in the air's CO_2 content led to a 75% enhancement of leaf net photosynthesis at a leaf temperature of 31°C, a 100% enhancement at a leaf temperature of 35°C, and a 200% enhancement at 42°C. At higher leaf temperatures, the net photosynthetic rate of the foliage growing in ambient air dropped to zero at 47°C (making the CO_2-induced enhancement of photosynthesis at that point essentially infinite), and it became negative thereafter (which condition, if prolonged, would ultimately lead to plant death).

In the CO_2-enriched trees, by contrast, the net photosynthetic rate of the foliage was still substantial at 47°C, and the regression line for those trees suggests their mean rate of foliage net photosynthesis likely would not have declined to zero until leaf temperature reached 54°C, approximately 7°C above the upper-limiting temperature for positive net photosynthesis in the trees grown in ambient air.

These findings show if Earth's air temperature continues to rise significantly in the future, a concomitant rise in the air's CO_2 content would serve as a powerful antidote for the ill—and sometimes deadly—effects of temperature stress.

Lewis *et al.* (2001) reached somewhat similar conclusions when they grew Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings in sunlit chambers programmed to track either ambient atmospheric CO_2 concentration or ambient + 200 ppm CO_2, as well as either ambient air temperature or ambient + 4°C, over a 21-month period, measuring light-saturated rates of net photosynthesis at approximately monthly intervals. The extra CO_2 they supplied to the seedlings "increased net photosynthetic rates by an average of 21% across temperature treatments during both the 1996 hydrologic year, the third year of exposure, and the 1997 hydrologic year," and "elevated mean annual temperature increased net photosynthetic rates by an average of 33% across CO_2 treatments during both years." In addition, "between February and August 1996, the short-term temperature optima for photosynthesis shifted by approximately 10°C higher in both CO_2 treatments," and the elevated CO_2 treatment "increased the short-term (minutes to hours) temperature optima for photosynthesis, as has been observed in other tree species (Idso and Idso, 1994; Eamus *et al*., 1995)." The four researchers conclude "an increase of 200 ppm above current atmospheric CO_2 concentrations may shift temperature optima upward 3–4°C, paralleling the increase in mean annual temperatures predicted to occur during the next century," and "by shifting temperature optima upward, elevated CO_2 may 'acclimate' photosynthetic processes to future temperature regimes."

Huang *et al*. (2007) compared, synthesized, and evaluated the scientific literature to that point in time, describing atmospheric CO_2 enrichment experiments conducted on trees and empirical tree-ring studies designed to ascertain whether the growth-promoting effects of rising atmospheric CO_2 concentrations occur in natural forests. They found numerous CO_2-enrichment experiments have "demonstrated significantly positive physiological and growth responses of trees to CO_2, providing strong evidence to support the direct CO_2 fertilization effect (increased photosynthesis, water use efficiency, above- and belowground growth) and thus allowing prediction of which ecosystems might be most responsive to CO_2." They suggest the latter will be "warm, moderately drought-stressed ecosystems with an ample nitrogen supply," because "drought-stressed trees could benefit from increased water use efficiency to enhance growth." They note tree-ring studies on the cold and arid Tibetan Plateau also "showed significant growth enhancements as well as increased water use efficiency (24.7% and 33.6% for each species, respectively) in Qilian juniper and Qinghai spruce since the 1850s," citing Zhang *et al*. (2003), Shao *et al*. (2005), Liang *et al*. (2006), Huang and Zhang (2007), and Zhang and Qiu (2007).

Hickler *et al*. (2008) evaluated the process-based LPJ-GUESS model of vegetation dynamics and biogeochemistry (Smith *et al*., 2001; Hickler *et al*., 2004) via a site-by-site comparison with the results of four temperate forest FACE experiments (Norby *et al*., 2005). After demonstrating the model simulations adequately reproduced the magnitude of the FACE site measurements—a mean model-derived net primary productivity (NPP) increase of 25.9% for CO_2 raised to a value of 550 ppm vs. a mean measured NPP increase of 27.8% for the same CO_2 increase—they conducted what they called a "global forest FACE experiment" to see what the reality-tested model suggested about CO_2 enrichment effects on the NPP of boreal and tropical forests, as well as its temperate forests.

For the world as a whole, the model suggests raising the air's CO_2 concentration to 550 ppm would increase the NPP of temperate forests by an average of 25.7%. The NPP of boreal forests would be raised by 15.1%, and tropical forests would experience an NPP increase of 35.1%. Hickler *et al*. note warming "is likely to increase NPP more in cold northern regions than close to the equator because of a greater proportional growing season extension in temperature-limited environments."

Martinez-Vilalta *et al*. (2008) describe their use of tree-ring data from the Catalan Ecological and Forest Inventory "to study the temporal variability of Scots pine stem radial growth (period 1901–1997) across a relatively large region (Catalonia, NE Spain) situated close to the southern limit of the distribution of the species." This inventory, they write, "included a total of 10,664 plots randomly distributed throughout the forested area of Catalonia," where Scots pine was present in 30.2% of the plots and dominant in 18.4% of them. They found "an overall increase of 84% in Scots pine BAI [basal area increment] during the 20th century, consistent with most previous studies for temperate forests." They state, "this trend was associated with increased atmospheric CO_2 concentration," which they interpret to be "a fertilization effect." Over the same period, the five researchers note, "there was also a marked increase in temperature across the study region (0.19°C per decade on average)," and "this warming had a negative impact on radial growth, particularly at the drier sites." They add "its magnitude was not enough to counteract the fertilization effect."

Darbah *et al*. (2010) measured the effects of a natural and prolonged heat wave on the photosynthetic rates of quaking aspen (*Populus tremuloides* Michx) and paper birch (*Betula papyrifera*) trees grown from the seedling stage for an additional nine years in the free-air CO_2-enrichment (FACE) facility near Rhinelander, Wisconsin (USA), where from 0700 to 1900 hours each day throughout the growing season half of the trees were exposed to an extra ~190 ppm of CO_2. For the aspen trees, the heat wave produced "no visible symptoms of stress," but the birch trees exhibited "leaf curling and then yellowing of leaves and finally leaf shedding," with trees in the control treatment dropping 33% of their leaves and those in the CO_2-enriched treatment dropping 20%. Aspen clone 42E exhibited a 30% CO_2-induced increase in the rate of photosynthesis at saturating light intensities in the 32–35°C temperature range, and 218% in the 36–39°C range. Similarly, aspen clone 271 exhibited a 38% CO_2-induced increase in the 32–35°C range and a 199% increase in the 36–39°C range. The birch trees exhibited a 95% CO_2-induced increase in photosynthetic rates in the 32–35°C range and a 297% increase in the 36–39°C range.

The four researchers say their findings agree with those of Idso and Kimball (1992), who reported elevated CO_2 (ambient + 300 ppm) increased net photosynthetic rates in sour orange tree (*Citrus aurantium* L.) leaves exposed to full sunlight by 75, 100, and 200% compared to leaves in ambient CO_2 air at temperatures of 31, 35, and 42°C, respectively, suggesting "elevated CO_2 ameliorates heat stress in tree leaves." They also note their observations "agree with Veteli *et al*. (2007), who reported that elevated CO_2 ameliorated the negative effects of high temperature in three deciduous tree species," and "Wayne *et al*. (1998) reported that elevated CO_2 ameliorated high temperature stress in yellow birch trees (*Betula alleghaniensis*)." They conclude, "in the face of rising atmospheric CO_2 and temperature (global warming), trees will benefit from elevated CO_2 through increased thermotolerance."

Ghannoum, *et al*. (2010b) grew individual well-watered and -fertilized plants of two species of Australian eucalypts—faster-growing *Eucalyptus saligna* and slower-growing *E. sideroxylon*—from seed in 10-L pots filled with 9 kg of loamy sand in naturally lit glasshouse compartments maintained at either ambient or ambient + 4°C air temperature and three different CO_2 concentrations (280, 400, or 650 ppm) for 140 days, measuring various plant responses throughout the course of the experiment. They found light-saturated net photosynthesis (Asat) increased by ~50% with each step-increase in the air's CO_2 concentration—going from 280 to 400 ppm, and going from 400 to 650 ppm—and in the higher of the two temperature treatments the optimal temperature for Asat increased by 2–7°C across the three CO_2 treatments. They note these results "partly explain the strong growth responses to elevated CO_2 and temperature observed in a previous study with the same eucalypt seedlings," citing Ghannoum *et al*. (2010a).

Keenan *et al*. (2011) note climate models consistently project significant increases in temperature and decreases in precipitation in the Mediterranean basin, and they state these changes may have a large impact on current Mediterranean forests and the related ecosystem services they provide. They say niche-based models—also known as bioclimatic envelope models or habitat models—are the most commonly used method for predicting potential species distribution responses to future climatic changes, and they note these models typically predict significant negative consequences for terrestrial plants and animals in the face of increasing atmospheric CO_2 concentrations.

Keenan *et al.* say they prefer process-based models, which describe eco-physiological processes ranging from purely empirical relationships to mechanistic descriptions based on physical laws. These models, supported by experiments and growth and yield surveys, "suggest that global warming will have a positive impact on forest productivity (van der Meer *et al*., 2002; Nigh *et al*., 2004; Norby and Luo, 2004; Briceño-Elizondo *et al*., 2006; Gaucharel *et al*., 2008), due to the direct fertilization effect of increased CO_2 and indirect effects such as lengthening of the growing period." To elucidate the difference in results obtained by employing these two approaches, the five researchers assessed and compared the projections when applied to stands of three forest species (*Quercus ilex*, *Pinus halepensis,* and *Pinus sylvestris*) that have widely contrasting distributions in continental Spain.

Keenan *et al*. found CO_2 fertilization tends to show an increase in forest productivity in mechanistic process-based models (despite increased drought and presumed temperature stress) by up to three times the non-CO_2 fertilization scenario by the period 2050–2080, in stark contrast to projections of reduced habitat suitability based on niche-based models for the same period. Their results show "previous reports of species decline in continental Spain (e.g. Benito-Garzon *et al*., 2008) may be overestimated due to two reasons." One of these is the use of only one predictive niche-based model, and the other is the failure to account for positive effects of CO_2

fertilization in a warming world. They note similar studies in other regions that do not consider these two aspects are also potentially overestimating species decline due to climate change, because "niche-based model results also likely overestimate the decline in [habitat] suitability." They conclude, "an organism's niche must be modeled mechanistically if we are to fully explain distribution limits," citing Kearney (2006).

Osorio *et al.* (2011) investigated the impacts of drought and high-temperature stresses on photosynthesis, energy partitioning, and membrane lipids—as well as the potential ability of Carob or St. John's (*Ceratonia siliqua*) trees to attenuate oxidative damage. They studied seedlings growing in controlled-environment chambers and rooted in 3-dm^3 pots filled with a 2:1 mixture of a fertilized substrate and natural soil, maintained under two thermal regimes—low and high temperature (LT: 25/18°C; HT: 32/21°C)—and three soil water conditions (control, water stress, and rewetting), monitoring numerous physiological and biochemical plant properties and processes. The decrease in net photosynthesis (P_N) caused by drought was 33% in the LT chamber and 84% in the HT chamber. They note, "the negative effects of soil drying on P_N and stomatal conductance of HT plants were no longer detected 36 hours following rewatering." Also, "although *C. siliqua* seedlings exhibit clear signs of oxidative stress under drought and high temperature, they retain a remarkable ability to quickly restore normal physiological activity on rehydration." This ability was so strong the five Portuguese scientists say they "can state that although *C. siliqua* seedlings exhibit clear signs of oxidative stress under drought and high temperature, they retain a remarkable ability to quickly restore normal physiological activity on rehydration, which let us believe that they can satisfactorily deal with predicted climate warming and increased soil drying in the Mediterranean area."

Wertin *et al.* (2012) examined the influence of elevated temperature (ambient + 2°C) and atmospheric CO_2 concentration (700 ppm), applied singly and in combination, on biomass accumulation and the temperature response of net photosynthesis (Anet) and leaf respiration (Rd) of loblolly pine (*Pinus taeda* L.) seedlings grown simultaneously at a northern and a southern site in the species' range, where the long-term mean growing season temperature (from February through October) at the cool site was 15.2°C and at the warm site was 21.5°C. They grew the well-watered and -fertilized seedlings over two consecutive years in half-cylindrical polyfilm-enclosed chambers located in open fields.

Wertin *et al.* determined "biomass accumulation was substantially greater at the warmer site compared with the cooler site regardless of treatment," and "at each site, biomass accumulation was greater in the elevated temperature treatment compared with the ambient treatment." They also found "elevated CO_2 increased biomass accumulation and Anet at both sites and in both temperature treatments." The five University of Georgia (USA) researchers conclude their study "provides an indication that future projected increases in CO_2 and air temperature of 700 ppm and +2°C, respectively, are likely to increase loblolly pine growth in most, if not all, of its current range." And they state, "the large number of studies that have reported an increase in tree growth in elevated growth temperatures compared with current ambient temperature (Way and Oren, 2010) suggest that other species may respond similarly."

Ameye *et al.* (2012) note that in studies where the air's CO_2 content was doubled, "increases in net photosynthesis were reported ranging from 43% to 192% in *Pinus taeda* (Teskey, 1997; Tissue *et al.*, 1997; Ellsworth, 1999; Wertin *et al.*, 2010; Frenck *et al.*, 2011) and from 30% to 256% in *Quercus rubra* (Kubiske and Pregitzer, 1996; Anderson and Tomlinson, 1998; Cavender-Bares *et al.*, 2000)." Moreover, "generally, an increase in air temperature also has a positive effect on net photosynthesis and growth," citing Sage and Kubien (2007) and Way and Oren (2010).

Investigating how loblolly pine and northern red oak trees might respond to the extreme heat waves often predicted to occur in a future CO_2-enriched world, the scientists examined the most recent fully developed leaves of well-watered and -fertilized seedlings of *Pinus taeda* and *Quercus rubra* grown in 7.6-L pots out-of-doors at Athens, Georgia (USA) in polyethylene chambers maintained at ambient and elevated air temperatures (T_{amb} and T_{amb} + 3°C), as well as seven-day heat waves consisting of a biweekly +6°C heat wave or a monthly +12°C heat wave. These treatments were maintained throughout the growing season, and Ameye *et al.* measured rates of net photosynthesis before, during, and after the many midsummer heat waves they created. They report "an immediate and significant decline in net photosynthesis was observed in seedlings subjected to a +12°C heat wave, but not in seedlings subjected to a +6°C heat wave." They also state, "after the third day of the +12°C heat wave, net photosynthesis values stabilized at positive values and did not show signs of further reduction, indicating that the photosynthetic apparatus did not accrue additional stress or damage as the heat wave continued.” Therefore, they conclude, “if soil moisture is adequate, trees will experience negative effects in photosynthetic performance only with the occurrence of extreme heat waves.” Also, as “elevated CO_2 diminished these negative effects,” they conclude “the future climate may not be as detrimental to plant communities as previously assumed.”

In concluding this literature review, it is instructive to consider the Paleocene-Eocene Thermal Maximum (PETM) of some 56 million years ago. According to Jaramillo *et al.* (2010), it “was one of the most abrupt global warming events of the past 65 million years (Kennett and Stott, 1991; Zachos *et al.*, 2003; Westerhold *et al.*, 2009).” It was presumed to have been driven, they write, by “a massive release of ^{13}C-depleted carbon (Pagani *et al.*, 2006; Zeebe *et al.*, 2009)” that led to “an approximate 5°C increase in mean global temperature in about 10,000 to 20,000 years (Zachos *et al.*, 2003).” Earth’s tropical ecosystems “suffered extensively because mean temperatures are surmised to have exceeded the ecosystems’ heat tolerance (Huber, 2008),” according to many scientists, Jaramillo *et al.* write.

To ascertain whether the ancient warming of the world truly constituted a major problem for the planet’s rainforests, the 29 researchers from eight countries analyzed pollen and spore contents and the stable carbon isotopic composition of organic materials obtained from three tropical terrestrial PETM sites in eastern Colombia and western Venezuela. Contrary to the prevailing wisdom of the recent past, they found the onset of the PETM was “concomitant with an increase in diversity produced by the addition of many taxa (with some representing new families) to the stock of preexisting Paleocene taxa.” They determined this increase in biodiversity “was permanent and not transient.”

Jaramillo *et al.* write, “today, most tropical rainforests are found at mean annual temperatures below 27.5°C,” and several scientists have argued “higher temperatures could be deleterious to the health of tropical ecosystems,” citing Stoskopf (1981), Bassow *et al.* (1994), Lewis *et al.* (2004), Huber (2008, 2009), and Tewksbury *et al.* (2008). They report tropical warming during the PETM is actually thought to have produced intolerable conditions for tropical ecosystems, citing Huber (2008, 2009). Nevertheless, Jaramillo *et al.* reiterate that at the sites that they studied, “tropical forests were maintained during the warmth of the PETM (~31° to 34°C).” Thus they conclude, “it is possible that higher Paleocene CO_2 levels (Royer, 2010) contributed to their success.”

Their conclusion is supported by what is now the well-established fact that most woody plants tend to exhibit their greatest photosynthetic rates at increasingly warmer temperatures as the air’s CO_2 content rises. It is becoming increasingly clear that greater warmth and atmospheric CO_2 concentrations are not as detrimental as IPCC and others typically make them out to be. Quite to the contrary, they are likely to make ecosystems both more stable and more productive.

The scientific literature of the past few decades indicates a continuing rise in the air’s CO_2 content likely will lead to enhanced rates of photosynthesis and biomass production that will not be negated by any global warming that might occur. If the ambient air temperature rises, the growth-promoting effects of atmospheric CO_2 enrichment likely will rise right along with it. Trees are likely to produce greater amounts of biomass and, therefore, more timber products to meet the increasing needs of Earth’s expanding human population.

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3.14 UV-B Radiation Stress

- The rise in the air's CO_2 content is a powerful antidote to the deleterious biological impacts that might be caused by an increase in the flux of UV-B radiation at the surface of Earth due to depletion of the planet's stratospheric ozone layer.

Zhao *et al*. (2004) state "as a result of stratospheric ozone depletion, UV-B radiation (280–320 nm) levels are still high at the Earth's surface and are projected to increase in the near future (Madronich *et al*., 1998; McKenzie *et al*., 2003)," noting, "increased levels of UV-B radiation are known to affect plant growth, development and physiological processes (Dai *et al*., 1992; Nogues *et al*., 1999)." High UV-B levels often result in "inhibition of photosynthesis, degradation of protein and DNA, and increased oxidative stress (Jordan *et al*., 1992; Stapleton, 1992)." In light of these observations, it is only natural to wonder how the rise in the air's CO_2 content might affect the deleterious effects of UV-B radiation on vegetation.

Zhao *et al*. grew well-watered and -fertilized cotton plants in sunlit controlled-environment chambers maintained at atmospheric CO_2 concentrations of 360 or 720 ppm from emergence until three weeks past first-flower stage under three levels of UV-B radiation (0, 8, and 16 kJ m^{-2} d^{-1}). On five dates between 21 and 62 days after emergence, they measured a number of plant physiological processes and parameters. Over the course of the experiment, the mean net photosynthetic rate of the upper-canopy leaves in the CO_2-enriched chambers was increased relative to that in the ambient-air chambers by 38.3% 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 CO_2 was sufficient to raise net photosynthesis rates 33.7% above the rates experienced in the ambient air and no UV-B treatment (from 30.3 to 40.5 m m^{-2} s^{-1}). In the high UV-B treatment, however, the radiation damage was so great the 51.5% increase in net photosynthesis provided by the doubled-CO_2 air could not prevent the destruction, and the mean net photosynthesis rate of the cotton leaves was 14.5% less than in the ambient air and no UV-B treatment (dropping from 30.3 to 25.9 m m^{-2} s^{-1}).

The medium UV-B treatment of this study was chosen to represent the intensity of UV-B radiation presently received on a clear summer day in the major cotton production region of Mississippi (USA) under current stratospheric ozone conditions, and the high UV-B treatment was chosen to represent what might be expected there following a 30% depletion of the ozone layer, which has been predicted to double the region's reception of UV-B radiation from 8 to 16 kJ m^{-2} d^{-1}. Thus doubling the current CO_2 concentration and current UV-B radiation level would reduce the net photosynthetic rate of cotton leaves by just under 10% (from 28.7 to 25.9 m m^{-2} s^{-1}), whereas in the absence of a doubling of the air's CO_2 content, a doubling of the UV-B radiation level would reduce cotton net photosynthesis by just over 40% (from 28.7 to 17.1 m m^{-2} s^{-1}). Doubling the current atmospheric CO_2 concentration thus would compensate for more than three-fourths of the loss of cotton photosynthetic capacity caused by a doubling of the current UV-B radiation intensity. And it might do even better than that: Zhao *et al*. (2003) reported both Adamse and Britz (1992) and Rozema *et al*. (1997) found a doubling of CO_2 fully compensated for the negative effects of equally high UV-B radiation.

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

The results of this study indicate the positive effects of atmospheric CO_2 enrichment on flower and biomass production in white clover are greater at more realistic or natural values of UV-B radiation than those found in many greenhouses. Deckmyn *et al*. state their results "clearly indicate the importance of using UV-B transmittant greenhouses or open-top chambers when conducting CO_2 studies," lest the results obtained significantly underestimate the magnitude of the benefits provided by the rise in the air's CO_2 content.

Qaderi and Reid (2005) grew well-watered and well-fertilized canola plants (*Brassica napus*) from seed to maturity in pots in controlled-environment chambers maintained at either 370 or 740 ppm CO_2 with and without a daily dose of UV-B radiation in the amount of 4.2 kJ m^{-2}, measuring a number of plant parameters at various times throughout the growing season. The final seed yield was 0.98 g/plant in the control treatment (ambient CO_2, with UV-B). Doubling the CO_2 concentration increased yield by 25.5% to 1.23 g/plant, and removing the UV-B radiation flux increased yield by 91.8% to 1.88 g/plant. Doing both (doubling the CO_2 concentration while simultaneously removing the UV-B flux) increased final seed yield by 175.5% to 2.7 g/plant. Hence, doubling the air's CO_2 concentration in the presence of the UV-B radiation flux enhanced final seed yield by 25.5%, and doubling CO_2 in the absence of the UV-B radiation flux increased seed yield by 43.6%. Qaderi and Reid conclude, "elevated CO_2 may have a positive effect on plants by mitigating the detrimental effects caused by UV-B radiation."

In a follow-up paper, Qaderi *et al*. (2007) examined the effects of elevated CO_2 and UVB radiation on the photosynthetic rates and water use efficiency of the maturing husks (siliquas) that surround the canola plant's seeds. For the plants exposed to 4.2 kJ m^{-2} d^{-1} of UVB radiation, the experimental doubling of the air's CO_2 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. For the plants exposed to no UVB radiation, siliqua net photosynthesis was increased by 38%, transpiration was decreased by 22%, and water use efficiency was increased by 87% in the CO_2-enriched air.

Tohidimoghadam *et al.* (2011) grew two varieties (Okapi and Talaye) of canola out-of-doors over the 2008 and 2009 growing seasons beneath rigid frames covered with polyethylene plastic film in air maintained at ambient and elevated atmospheric CO_2 concentrations of 400 and 900 ppm, at ambient and elevated levels of UV radiation, and under well-watered and deficit-watered conditions, measuring numerous plant properties during and after the growing period. They found "water stress significantly decreased yield and yield components, oil yield, protein percentage, height, specific leaf area and the number of branches." Elevated CO_2 "increased the final yield, 1000-seed weight, oil percentage, oil yield, height, specific leaf area and number of branches." UV radiation "decreased the yield, yield components, oil and protein percentages and growth parameters." They also note "the highest seed weight was obtained from the 'Talaye' cultivar treated with compete irrigation and elevated CO_2 and grown under sunlight radiation," whereas "the seed weights of both cultivars visibly decreased due to UV-B, UV-C and water stress under an ambient CO_2 concentration." The three Iranian researchers who conducted the study state, "an increase in UV exposure deceases plant growth and development," but "elevated CO_2 ameliorate(s) the adverse effects of UV radiation in the final yield, seed weight, oil percentage, oil yield, plant height, specific leaf area and number of branches per plant." They conclude an increase in the atmosphere's CO_2 concentration "could improve yield, yield components and growth parameters for plants subjected to elevated levels of UV radiation."

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

When the plots were exposed to the enhanced UV-B radiation, the amount of C_{mic} in the soil was reduced to only 37% 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, there was no decrease in C_{mic} but an increase of 37%. When the plots were exposed to the enhanced level of UV-B radiation, the amount of N_{mic} in the soil showed a 69% increase when the air's 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 by 138%.

These findings, Johnson *et al.* write, "may have far-reaching implications ... because the productivity of many semi-natural ecosystems is limited by N (Ellenberg, 1988)." Thus, the 138% increase in soil microbial N observed in this study to accompany a

15% reduction in stratospheric ozone and a 64% increase in atmospheric CO_2 concentration should significantly enhance the input of plant litter to the soils of these ecosystems, which represents the first half of the carbon sequestration process—the carbon input stage.

As to the second stage—keeping as much of that carbon as possible in the soil—Johnson *et al.* note "the capacity for subarctic semi-natural heaths to act as major sinks for fossil fuel-derived carbon dioxide is [also] likely to be critically dependent on the supply of N," as indicated in the literature review of Berg and Matzner (1997). The latter report the presence of additional nitrogen in the soil significantly enhances the long-term storage of carbon, as more litter is chemically transformed into humic substances when nitrogen is more readily available, and these more recalcitrant carbon compounds can be successfully stored in the soil for many millennia.

Koti *et al.* (2007) investigated the interactive effects of elevated atmospheric CO_2 (720 vs. 360 ppm), UV-B radiation levels (0 vs. 10 kJ/m^2/day), and temperature (38/30°C vs. 30/22°C day/night) on the growth and development of six well-watered and well-fertilized soybean (*Glycine max* L.) genotypes. They found "elevated CO_2 partially compensated [for] the damaging effects on vegetative growth and physiology caused by negative stressors such as high temperatures and enhanced UV-B radiation levels in soybean." The authors note CO_2's positive influence on plant height, leaf area, total biomass, net photosynthesis, total chlorophyll content, phenolic content, and wax content, as well as relative plant injury. Thus, with respect to almost all of the ways high air temperatures and high UV-B radiation levels retard the growth and development of soybeans, elevated atmospheric CO_2 concentrations appear to provide significant ameliorative relief.

Estiarte *et al.* (1999) grew spring wheat in FACE plots in Arizona (USA) at atmospheric CO_2 concentrations of 370 and 550 ppm and two levels of soil moisture (50 and 100% of potential evapotranspiration). Under those conditions, leaves of plants growing in elevated CO_2 had 14% higher total flavonoid concentrations than those of plants grown in ambient air, and soil water content did not affect the relationship. One of the functions of flavonoids in plant leaves is to protect them against UV-B radiation. Hence, more studies of this nature should be conducted to see how general this beneficial response may be throughout the plant world.

These findings indicate the rise in the air's CO_2 content is a powerful counterbalance against the deleterious biological impacts that could be caused by an increase in the flux of UV-B radiation at the surface of Earth due to depletion of the planet's stratospheric ozone layer.

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3.15 Water Stress

As the CO_2 content of the air rises, nearly all plants will exhibit increases in photosynthesis and biomass production, but some researchers claim water stress will negate these benefits. This section examines the results of several CO_2-enrichment studies designed to show the net effect of elevated CO_2 and water stress on the growth of Earth's vegetation.

3.15.1 Agricultural Crops

- The rise in the atmosphere's CO_2 content likely will lead to substantial increases in the photosynthetic rates and biomass production of the world's chief agricultural crops, even in stressful situations imposed by less-than-optimum soil moisture.

As the air's CO_2 content rises, nearly all plants will exhibit increases in photosynthesis and biomass production, but some researchers claim elevated concentrations of atmospheric CO_2 will lead to more droughty conditions in many parts of the world and thereby significantly reduce or totally negate these CO_2-induced benefits. This section reviews the results of numerous studies that show atmospheric CO_2 enrichment may help important food crops cope with periods of less-than-optimal water availability.

One way atmospheric CO_2 enrichment helps plants in this regard is by stimulating them to develop larger-than-usual and more robust root systems that enable them to probe greater volumes of soil for moisture. Wechsung *et al.* (1999), for example, observed a 70% increase in lateral root dry weights of water-stressed wheat grown at 550 ppm CO_2, and De Luis *et al.* (1999) reported a 269% increase in root-to-shoot ratio of water-stressed alfalfa growing at 700 ppm CO_2. Thus, elevated CO_2 may often elicit stronger-than-usual positive root responses in agricultural species under conditions of water stress.

Elevated levels of atmospheric CO_2 also tend to reduce the openness of stomatal pores on leaves, thus decreasing plant stomatal conductance. This phenomenon, in turn, reduces the amount of water lost to the atmosphere by transpiration and, consequently, lowers overall plant water use. Serraj *et al.* (1999), for example, reported water-stressed soybeans grown at 700 ppm CO_2 reduced their total seasonal water loss by 10% relative to water-stressed control plants grown at 360 ppm CO_2. And Conley *et al.* (2001) found a 200 ppm increase in the air's CO_2 concentration reduced cumulative evapotranspiration in water-stressed sorghum by about 4%.

Atmospheric CO_2 enrichment thus increases plant water acquisition by stimulating root growth, and it reduces plant water loss by constricting stomatal apertures. These two phenomena typically enhance plant water-use efficiency, even under conditions of less-than-optimal soil water content. They have other implications as well.

CO_2-induced increases in root development together with CO_2-induced reductions in stomatal conductance often improve plant water status during times of drought. Sgherri *et al.* (1998), for example, found leaf water potential, which is a good indicator of overall plant water status, was 30% higher (less negative and therefore more favorable) in water-stressed alfalfa grown at an atmospheric CO_2 concentration of 600 ppm versus 340 ppm. Wall (2001) found leaf water potentials were similar in CO_2-enriched water-stressed plants and ambient-grown well-watered control plants, which implies a complete CO_2-induced amelioration of water stress in the CO_2-enriched plants. Lin and Wang (2002) demonstrated elevated CO_2 caused a several-day delay in the onset of the water stress-induced production of the highly reactive oxygenated compound H_2O_2 in spring wheat. Also, they found plants grown in elevated CO_2 maintained higher enzymatic activities of superoxide dismutase and catalase—two important antioxidants—relative to those observed in ambient-grown plants, following the induction of water stress.

If atmospheric CO_2 enrichment allows plants to maintain a better water status during times of water stress, it is only logical to surmise they would exhibit greater rates of photosynthesis than plants growing in similarly water-deficient soil in non-CO_2-enriched air. With the onset of experimentally induced water stress in India Mustard (*Brassica juncea*), Rabha and Uprety (1998) observed photosynthetic rates dropped by 40% in plants growing in ambient air, while plants growing in air containing 600 ppm CO_2 experienced only a 30% reduction in net photosynthesis. Ferris *et al.* (1998) imposed water-stress conditions on soybeans and allowed them to recover following complete rewetting of the soil, finding plants grown in air containing 700 ppm CO_2 reached pre-stressed rates of photosynthesis after six days, whereas plants grown in ambient air never recovered to pre-stressed photosynthetic rates.

Analogously, it is also to be expected that elevated CO_2 concentrations would enhance plant biomass production under drought conditions. Ferris *et al.* (1999) report water-stressed soybeans grown at 700 ppm CO_2 attained seed yields 24% greater than those of similarly water-stressed plants grown at ambient CO_2 concentrations, and Hudak *et al.* (1999) determined water stress had no detrimental effect on yield in CO_2-enriched spring wheat. Many studies have found the CO_2-induced biomass increase to be greater for water-stressed plants than for well-watered plants, as demonstrated in the review of the subject by Idso and Idso (1994).

Li *et al.* (2000), reported a 180 ppm increase in the air's CO_2 content increased final grain weights in the upper and lower sections of the main stems of the spring wheat they studied by 10 and 24%, respectively, under water-stressed conditions, but under well-watered conditions elevated CO_2 increased final grain weights only in the lower sections of the main stems and by only 14%. Thus elevated CO_2 had a greater positive impact on final grain weights of spring wheat under water-stressed field conditions than in non-water-stressed field conditions, once again demonstrating atmospheric CO_2 enrichment is often more important to stressed plants than to non-stressed plants.

Similarly, spring wheat grown in air containing an additional 280 ppm CO_2 exhibited 57 and 40% increases in grain yield under water-stressed and well-watered conditions, respectively (Schutz and Fangmeier, 2001). Ottman *et al.* (2001) found elevated CO_2 increased plant biomass in water-stressed sorghum by 15%, but no biomass increase occurred in well-watered sorghum. In predicting maize and winter wheat yields in Bulgaria under future scenarios of increased air temperature and decreased precipitation, Alexandrov and Hoogenboom (2000) note yield losses were likely to occur if the air's CO_2 content remained unchanged, but if the atmospheric CO_2 concentration doubled, maize and winter wheat yields likely would increase, even under the combined stresses of elevated temperature and reduced rainfall.

Widodo *et al.* (2003) grew rice (*Oryza sativa* [L.] cv. IR-72) in eight outdoor, sunlit, controlled-environment chambers at daytime atmospheric CO_2 concentrations of 350 and 700 ppm for an entire season. In one pair of chambers the plants were continuously flooded, in a second pair drought stress was imposed during panicle initiation, in a third pair it was imposed during anthesis, and in a fourth pair it was imposed at both stages. In the elevated CO_2 treatment, midday leaf photosynthetic CO_2 exchange rates (CER) and chlorophyll concentrations were higher at most sampling dates. In addition, the CO_2-enriched plants exhibited enhanced midday leaf sucrose and starch accumulation during early reproductive phases.

Near the end of the imposed drought periods, water deficits caused substantial decreases in midday leaf CER and chlorophyll concentrations, along with concomitant reductions in the primary products of photosynthesis. These drought-induced effects, Widodo *et al*. note, "were more severe for plants grown at ambient than at elevated CO_2." They report, for example, "plants grown under elevated CO_2 were able to maintain midday leaf photosynthesis, and to some extent other photosynthetic-related parameters, longer into the drought period than plants grown at ambient CO_2," as also has been observed for a number of other plants (Rogers *et al*., 1984; Jones *et al*., 1985; Idso, 1988; Bhattacharya *et al*., 1990; Chaves and Pereira, 1992; Clifford *et al*., 1993; Baker *et al*., 1997; Vu *et al*., 1998).

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

Triggs *et al*. (2004) grew sorghum (*Sorghum bicolor* (L.) Moench, a C_4 grain crop) for two full seasons in control CO_2 plots (about 370 ppm) and FACE plots (Control + 200 ppm) under both well-watered (Wet) and water-stressed (Dry, less than half the total water received by the Wet treatment via rainfall and irrigation) conditions near Maricopa, Arizona (USA). They assessed evapotranspiration (ET) on a continuous basis by means of micro-meteorological measurements designed to allow the calculation of all the other elements (net radiation, sensible heat flux, and soil surface heat flux) of the energy balance of the crop-soil interface with the atmosphere. Sorghum water use efficiency (WUE) was calculated using final grain yield data obtained by Ottman *et al*. (2001).

Triggs *et al*. write, "in the Wet treatments, a reduction in ET of about 19%, combined with only a slight increase in total biomass (+4%), resulted in a 28% increase in WUE in elevated CO_2 conditions," whereas "in the Dry treatments, the relatively large increase in total biomass (+16% for both years) more than compensated for the approximate 5% increase in total ET, giving the FACE-Dry treatments an increase in WUE of 16% over both seasons." They conclude, "even if future climate change results in less water available for agriculture, higher atmospheric CO_2 concentrations will still benefit C_4 crops," although "in regions with ample precipitation or irrigation, C_3 crops with higher growth responses may be preferable."

Kaddour and Fuller (2004) grew three commercial cultivars of durum wheat (*Triticum durum* Desf.) registered in Syria (Cham 1, Cham 3, and Cham 5) from seed in 10-liter pots in different compartments of a phytotron. Half of the compartments were maintained at an atmospheric CO_2 concentration of approximately 400 ppm and half were maintained at a concentration of approximately 1,000 ppm. Half of each of these treatments were further subdivided into two soil water treatments: well-watered, where available water content (AWC) was replenished to 90% of full capacity when it dropped to 60%, and water-stressed, where AWC was replenished to 70% of full capacity when it dropped to 45%. Averaged over the three cultivars, the extra 600 ppm of CO_2 supplied to the CO_2-enriched compartments led to total plant biomass increases of 62% in the well-watered treatment and 60% in the water-stressed treatment. The extra CO_2 also led to increases in the nitrogen concentrations of stems and ears. Nitrogen concentration of the ears was increased by 22% in the well-watered plants and by 16% in the water-stressed plants.

Kaddour and Fuller write their results "have important implications for the production of durum wheat in the future." They state "yields can be expected to rise as atmospheric CO_2 levels rise," and "this increase in yield can be expected under both water restricted and well irrigated conditions." Therefore, "where water availability is a prime limiting economic resource, it can be distributed more effectively under higher CO_2 conditions," and "for countries such as Syria where average national production is well below the physiological maximum due largely to drought stress, the predicted rise in atmospheric CO_2 could have a positive effect on production."

Richter and Semenov (2005) note, "with global warming, evapotranspiration is likely to increase and, with more variable rainfall, droughts could occur more often." They evaluated the impact of potential climate change on drought indicators and yields of winter wheat in England and Wales using a crop simulation model (*Sirius*) that also incorporates the effects of elevated atmospheric CO_2 concentration and temperature on crop growth and development, where the CO_2 scenario driving the model was of medium to high anthropogenic emissions that raise the air's CO_2 concentration from 334 ppm (the 1961–1990 baseline) to 554 ppm in the 2050s. Probability distributions derived from multiple simulations using representative weather, soil types, and sowing dates indicate maximum soil moisture deficit "is likely to increase in the future, especially on shallow soils, and the probability of potential yield reductions exceeding 25% will increase by 10% until the 2050s." Nevertheless, they write, "average wheat yields are likely to increase by 1.2 to 2 t/ha (15–23%) by the 2050s because of a CO_2-related increase in radiation use efficiency."

Bernacchi *et al*. (2006) grew soybeans (*Glycine max* (L.) Merr.) for three years at the SoyFACE facility of the University of Illinois at Urbana-Champaign, Illinois (USA) at atmospheric CO_2 concentrations of either 375 or 550 ppm under natural field conditions with and without a 23% increase in ambient atmospheric ozone concentration, measuring a number of weather and plant physiological parameters from pre-dawn to post-dusk on several days during the three growing seasons. They determined the mean daily integral of leaf-level net photosynthesis (A) was enhanced by nearly 25% in the CO_2-enriched air under ambient ozone concentrations, but by a slightly smaller 20% in the high-ozone air. In addition, "there was a strong positive correlation between daytime maximum temperatures and mean daily integrated A at elevated CO_2." From their graphical depiction of this relationship, it appears at a daily maximum temperature of approximately 26.5°C, A was stimulated by about 14%, and at a daily maximum temperature of approximately 34.5°C, it was stimulated by about 35%. The 11 researchers report "the effect of elevated CO_2 on photosynthesis tended to be greater under water stress conditions," rising from an approximate 17% enhancement of A at the most favorable soil moisture condition encountered to an enhancement close to 30% under the driest of the conditions experienced by the crop.

Robredo *et al*. (2007) grew well-watered and well-fertilized barley (*Hordeum vulgare* L.) seedlings (seven per each 2.5-liter pot filled with perlite and vermiculite) in controlled-environment chambers maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm. At the conclusion of the 18th day after seedling emergence, the treatments were split, with one continuing to be watered three times a week and the other treatment receiving no further water. At that time and on several following dates, researchers measured a number of soil and plant water parameters, along with rates of leaf transpiration and net photosynthesis. They found "during the period of drought, elevated CO_2 delayed by 3–4 days the depletion of soil water content," because of "the lower rates of transpiration in plants grown under CO_2 enrichment." As a result, "under elevated CO_2, plant water stress developed more slowly," thanks to "a slower rate of soil water depletion," They report "the stimulation of carbon assimilation by elevated CO_2 was even greater in droughted compared to well-watered plants," even though "elevated CO_2 caused stomata closure."

The seven Spanish researchers write, "exposure to high carbon dioxide concentration resulted in an increase in photosynthesis and in a reduction in whole plant transpiration, contributing to an increase in water use efficiency that was more noticeable when plants were subjected to elevated CO_2 in conjunction with drought." They conclude, "growing plants under [an] elevated CO_2 environment mitigates or delays the effects of water stress in barley."

Li *et al*. (2007) employed open-top chambers to determine net ecosystem CO_2 exchange (NEE) before, during, and after the severe Central Florida drought of 1998 in a scrub-oak ecosystem in ambient-CO_2 (AC) air and in elevated-CO_2 (EC) air enriched with an extra 350 ppm of CO_2 since May 1996. They focused on the ecosystem's dominant species (*Quercus myrtifolia* Willd.), for which they measured net photosynthetic rate (PN) throughout the daylight hours of several days. They found EC air generally increased PN, whereas drought decreased it. Under droughty conditions, PN peaked at around 0830 each day, after which it declined in a fairly steady fashion until solar noon and typically remained at a relatively low level throughout the remainder of the daylight hours. The scientists assessed the interactive impacts of elevated CO_2 and drought on tree PN by comparing the percentage reduction in PN from 0830 to 1230 in the two CO_2 treatments. They found in May 1998, PN was reduced by 77% from 0830 to 1230 at AC but by only 48% at EC, and in July 1998, when the drought had further intensified, PN was reduced by 82% at AC but by a lesser 69% at EC.

NEE responded in much the same way. In May and June 1998, for example, NEE's midday depression was 58% and 60% less at EC than at AC, and in July 1999 it was 66% less. In addition, Li *et al*. note, "the mitigation of the effects of water stress by EC was reflected in the aboveground biomass growth," such that "the relative effect of EC on biomass accumulation of the dominant species *Q. myrtifolia* was higher during the drought year (210% for 1998) compared to the non-drought years (67% for 1997)."

Manderscheid and Weigel (2007) grew spring wheat (*Triticum aestivum* cv. Minaret) in open-top chambers on an experimental field of the Federal Agricultural Research Center in Braunschweig, Germany, in two growing seasons at either current or future (current + 280 ppm) atmospheric CO_2 concentrations and under sufficient-water-supply (WET) or drought-stress (DRY) conditions. They imposed the latter just after the crop first-node stage was reached (approximately 35 days after emergence), by halving the subsequent water supplied to the plants. The researchers found, "in both years, biomass and grain yield were decreased by drought and increased by CO_2 enrichment," with the positive CO_2 effect being greater under drought conditions. Averaged over both years, "CO_2 enrichment increased biomass and grain yield under WET conditions by <=10% and under DRY conditions by >=44%." The CO_2-induced increase in crop water-use efficiency was 20% in the sufficient-water-supply treatment and 43% in the drought-stress treatment.

Veisz *et al.* (2008) grew seven cereal grain crops—winter barley (*Hordeum vulgare*, cv. Petra), winter wheat (*Triticum aestivum*, cvs. Libellula, Mv Regiment, Mv Mambo), winter durum wheat (*Triticum durum*, cv. Mv Makaroni), spring wheat (*Triticum aestivum*, cv Lona), and spring oats (*Avena sativa*, cv. Mv Pehely)—in a phytotron at the Agricultural Research Institute of the Hungarian Academy of Sciences at ambient and enriched atmospheric CO_2 concentrations (380 and 750 ppm, respectively) under both well-watered and drought conditions. For the latter condition they withheld water beginning at the 10th day after heading, and soil volumetric water content dropped from approximately 25% to 6%. They measured a number of crop characteristics at harvest.

Under the experimental conditions, the plants grown in the CO_2-enriched air "produced more organic matter, being taller, with more spikes and a higher grain number per plant than those grown at the present CO_2 level," and "thanks to the more intensive incorporation of carbohydrate, there was an increase in the mean grain mass and in the grain yield per plant" in the CO_2-enriched air. However, there was a concomitant decrease in the protein concentration of the grains produced in the high-CO_2 treatment. Nevertheless, the net effect was positive because, for the several cereal varieties averaged together, grain yield under the well-watered conditions rose by 12.37% (from 2.83 to 3.18 g/plant) in response to atmospheric CO_2 enrichment, and grain protein concentration dropped from 17.04% to 16.23%, resulting in a net increase of 7% in total grain protein production. Likewise, grain yield under the water-stressed conditions rose by 30.68% (from 1.76 to 2.30 g/plant) in response to atmospheric CO_2 enrichment, and the concentration of the grain protein dropped from 21.63% to 19.70%, leading to a net increase of 19% in total grain protein production.

Chun *et al.* (2011) grew corn plants from seed in naturally sunlit soil-plant-atmosphere-research (SPAR) units in which temperature, humidity, and CO_2 concentration were precisely controlled, the latter at either 400 ppm (ambient) or 800 ppm (elevated), beginning 21 days after emergence (DAE). These units were placed atop soil bins (2.0 m long by 0.5 m wide by 1.0 m deep) filled with a mixture of 75% coarse sand and 25% vermiculate, where soil water contents were monitored hourly by a time domain reflectometry (TDR) system that consisted of 15 TDR probes per chamber placed in three rows at depths of 0, 15, 30, 50, and 75 cm from the soil surface. By means of this system of soil water content assessment, combined with nightly "fertigation," Chun *et al.* were able to provide the plants with the nitrogen they needed while maintaining four soil water stress levels—control, mild, moderate, and severe—which were also initiated at 21 DAE. Thereafter, the height, number of leaves, leaf lengths, and growth states of the corn plants were determined twice weekly, and samples of the plants were collected, dried, and analyzed for biomass accumulation at 21 and 60 DAE (the beginning and end of the different CO_2 and soil water content treatments).

The five researchers did not find the elevated CO_2 treatment had a strong effect on plant height, leaf area, or above-ground biomass. But under both well-watered and water-stressed conditions, higher soil water contents were maintained in the elevated CO_2 treatment, even though 20–49% less water was applied to the soil of the elevated CO_2 treatment. The five researchers conclude, "under increased CO_2 concentrations as generally predicted in the future, less water will be required for corn plants than at present."

Robredo *et al.* (2011) write, "barley, an economically important and extensively cultivated cereal worldwide, increases its yield in parallel with an increase in CO_2," but "responds to drought stress through altered nitrogen metabolism and reduced productivity." They explored these complexities by growing barley (*Hordeum vulgare* L. cv. Iranis) seedlings in 2.5-L pots containing a 3:1 mix of perlite:vermiculite in a controlled-environment growth chamber, first at ambient and then at elevated atmospheric CO_2 concentrations (350 and 700 ppm, respectively). Initially, they watered the pots twice a week with a complete Hoagland solution and with deionized water between each Hoagland solution application. They initiated drought when the seedlings were 18 days old, withholding water for intervals of 9, 13, and 16 days. They analyzed the effects of these actions at the end of each drought period and analyzed water recovery three days after rewatering the 13-day droughted plants, with each complete experiment being replicated three times.

The six Spanish scientists state their barley plants showed a reduction in water use, even though under elevated CO_2 the plants had a larger leaf area, much as others also have found (Owensby *et al*., 1997; Niklaus *et al*., 1998). In addition, "during the period of drought, the depletion of soil water content was delayed by 3–4 days in plants grown under elevated CO_2 conditions," and in the CO_2-enriched plants "water stress also developed more slowly than at ambient CO_2 because of a slower rate of water depletion." They report, "leaf water potential in plants subjected to drought but grown at elevated CO_2 was less negative than in their ambient CO_2 grown counterparts."

Robredo *et al*. also note "absolute values for nitrogen uptake by barley plants were higher under elevated CO_2 compared to ambient CO_2." In addition, they "observed high nitrate reductase activity in plants grown at elevated CO_2, which should parallel an increase in photosynthesis (Robredo *et al*., 2007) and sugar content (Perez-Lopez *et al*., 2010)." Also, "under ambient CO_2 conditions, protein content decreased as the water stress progressed," but "when plants grew under elevated CO_2 conditions, the rate of photosynthesis was higher [and] drought had less effect on the protein content." They report the barley plants "showed a greater content of proteins under elevated CO_2," in harmony with Geiger *et al*. (1999), who they say "reported a similar outcome in tobacco with the same supra-optimal nitrogen concentration." They further remark these findings also mesh with the results of studies reviewed by Idso and Idso (2001), who conclude any negative effects of elevated CO_2 on crop protein content "could be ameliorated by increased use of nitrogen fertilizer." Robredo *et al*. conclude "elevated CO_2 mitigates many of the effects of drought on nitrogen metabolism and allows more rapid recovery following water stress."

Tohidimoghadam *et al*. (2011) grew two varieties (Okapi and Talaye) of canola (*Brassica napus* L.) plants over the 2008 and 2009 growing seasons out-of-doors at 35°59'N, 50°75'E beneath rigid frames covered with polyethylene plastic film in air maintained at ambient and elevated atmospheric CO_2 concentrations of 400 and 900 ppm, at ambient and elevated levels of UV radiation, and under well-watered and deficit-watered conditions, during and after which periods they measured numerous plant properties. They found "water stress significantly decreased yield and yield components, oil yield, protein percentage, height, specific leaf area and the number of branches," but elevated CO_2 "increased the final yield, 1000-seed weight, oil percentage, oil yield, height, specific leaf area and number of branches." They also found elevated UV radiation "decreased the yield, yield components, oil and protein percentages and growth parameters," but elevated CO_2 once again ameliorated "the adverse effects of UV radiation in the final yield, seed weight, oil percentage, oil yield, plant height, specific leaf area and number of branches per plant."

Varga *et al*. (2012) write, "as well as damaging numerous physiological functions, abiotic stress [such as drought] also leads to higher concentrations of reactive oxygen species, which are present in nature in all plants, but which may damage cell components and disturb metabolic processes when present in larger quantities," citing Omran (1980), Larson (1988), and Dat *et al*. (2000). They note, "many authors have demonstrated that the [atmosphere's] CO_2 concentration has a substantial influence on the stress sensitivity of plants via changes in antioxidant enzyme activity," citing Fernandez-Trujillo *et al*. (2007), Ali *et al*. (2008), and Varga and Bencze (2009).

In an experiment designed to explore this subject further, Varga *et al*. grew two varieties of winter wheat in phytotrons maintained at either 380 or 750 ppm CO_2, where the potted plants were watered daily and supplied with nutrient solution twice a week until the start of drought treatments. They induced drought in three phases—at first node appearance, heading, and grain filling—by completely withholding water for seven days, which ultimately dropped the volumetric soil water content in the pots from 20–25% to 3–5%. These actions, the four Hungarian researchers report, led to "changes in enzyme activity" that "indicated that enhanced CO_2 concentration delayed the development of drought stress up to first node appearance, and stimulated antioxidant enzyme activity when drought occurred during ripening, thus reducing the unfavorable effects of [drought] stress." They conclude the increases in the antioxidant enzymes they analyzed "may help to neutralize the reactive oxygen species induced by stress during various parts of the vegetation period," and this phenomenon should help crops cope with extremes of moisture insufficiency.

These peer-reviewed, scientific studies of the effects of water insufficiency on the productivity of the world's major agricultural crops strongly support the earlier work of Idso and Idso (1994), who concluded the rise in the air's CO_2 content likely will lead to substantial increases in the photosynthetic rates and biomass production of the world's major agricultural crops, even in less-than-optimum soil moisture conditions.

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3.15.2 Grasslands

- The peer-reviewed scientific literature demonstrates the historical and still-ongoing rise in the air's CO_2 content has led and likely will continue to lead to substantial increases in the photosynthetic rates and biomass production of various grassland plants, even under stressful environmental conditions imposed by less-than-optimum soil moisture.

As the air's CO_2 content rises, nearly all plants should exhibit increases in photosynthesis and biomass production, but some researchers have claimed water stress will negate these benefits. In reviewing the scientific literature for 1983–1994, Idso and Idso (1994) concluded water stress will not in fact negate the CO_2-induced stimulation of plant productivity. They discovered the CO_2-induced percentage increase in plant productivity was nearly always greater under water-stressed conditions than when plants were well-watered. Seven years later, Poorter and Perez-Soba (2001) conducted a similar literature review and reached the same conclusion. This section provides background for this phenomenon and highlights some of the more important work that subsequently has been done in this area.

Elevated levels of atmospheric CO_2 tend to reduce the area of open stomatal pore space on leaf surfaces, thus reducing plant stomatal conductance. This phenomenon, in turn, effectively reduces the amount of water lost to the atmosphere via transpiration. Leymarie *et al.* (1999), for example, found twice-ambient levels of atmospheric CO_2 caused significant reductions in the stomatal conductance of water-stressed *Arabidopsis thaliana*. Similarly, Volk *et al.* (2000) reported several calcareous grassland species exposed to elevated atmospheric CO_2 concentrations (600 ppm) consistently exhibited reduced stomatal conductance, regardless of soil moisture availability.

In addition, CO_2-induced increases in root development and CO_2-induced reductions in leaf stomatal conductance often combine to maintain a more favorable plant water status during times of drought. In the case of four grassland species comprising a pasture characteristic of New Zealand, for example, Clark *et al.* (1999) report leaf water potential, a good indicator of plant water status, was consistently higher (less negative and, therefore, less stressful) under elevated atmospheric CO_2 concentrations. Leaf water potentials of the water-stressed C_4 grass *Panicum coloratum* grown at 1,000 ppm CO_2 were always higher than those of their water-stressed counterparts growing in ambient air (Seneweera *et al.*, 2001). Seneweera *et al.* (1998) had earlier reported leaf water potentials observed in CO_2-enriched water-stressed plants were three-and-a-half times greater than those observed in control plants grown at 350 ppm during drought conditions (Seneweera *et al.*, 1998).

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

These observations demonstrate elevated CO_2 nearly always enhances photosynthetic rates during times of water stress. One thus would expect plant biomass production to be enhanced by elevated CO_2 concentrations under drought conditions.

On the American prairie, Owensby *et al*. (1999) observed tallgrass ecosystems exposed to twice-ambient concentrations of atmospheric CO_2 for eight years exhibited significant increases in above- and below-ground biomass only during years of less-than-average rainfall. Derner *et al*. (2001) observed a 150 ppm increase in the CO_2 content of the air increased shoot biomass in two C_4 grasses by 57%, regardless of soil water content. Seneweera *et al*. (2001) reported a 640 ppm increase in the air's CO_2 content increased shoot dry mass in a C_4 grass by 44 and 70% under well-watered and water-stressed conditions, respectively. Volk *et al*. (2000) grew calcareous grassland assemblages at 360 and 600 ppm CO_2 and documented 18 and 40% CO_2-induced increases in whole-community biomass under well-watered and water-stressed conditions, respectively.

Nelson *et al*. (2004) reported on a five-year study (1997–2001) conducted on the semi-arid shortgrass steppe (SGS) of Colorado (USA). Working at the USDA-ARS Central Plains Experimental Range in the northern portion of the SGS about 60 km northeast of Fort Collins, Colorado, they used large (15.5 m^2) open-top chambers to examine the effects of elevated CO_2 (720 vs. 360 ppm) on plant water relations, ecosystem water use efficiency, soil moisture dynamics, and root distributions of the ecosystem's dominant C_3 (*Pascopyrum smithii* and *Stipa comata*) and C_4 (*Bouteloua gracilis*) grasses.

The five Agricultural Research Service scientists and their collaborator from Colorado State University report "seasonal average soil moisture throughout the soil profile (0–15, 15–45, 45–75, 75–105 cm) was increased under elevated CO_2 compared to ambient CO_2 for much of the study period," with the greatest relative increase (16.4%) occurring in the 75–105 cm depth increment. This finding of "increased soil moisture under elevated CO_2 at the deepest soil depth suggests that water percolated deeper into the soil profile and that less moisture was lost to evapotranspiration under elevated CO_2." Noting "this phenomenon enhances water storage in the deep fine sandy loam soils underlying large portions of the SGS," they state, "this increase in soil moisture has been shown to be the major controlling factor in improved carbon assimilation rates and increased total aboveground biomass in this system (LeCain *et al*., 2003) and will likely decrease the susceptibility of the SGS to drought."

The Colorado researchers also found, when averaged over the study period, "leaf water potential was enhanced 24–30% under elevated CO_2 in the major warm- and cool-season grass species of the SGS (*Bouteloua gracilis*, C_4, 28.5%; *Pascopyrum smithii*, C_3, 24.7%; *Stipa comata*, C_3, 30.4%)." They report these results are similar to those of "studies involving other C_3 and C_4 grass species (Owensby *et al*., 1993; Jackson *et al*., 1994)," and they say the enhanced leaf water potential—"which reflects improved plant water status and increased drought tolerance (Tyree and Alexander, 1993)"—may lead to increased leaf turgor and allow the grasses "to continue growth further into periods of drought." Averaged over the five years of the study, Nelson *et al*. report, "water-use efficiency (grams aboveground biomass harvested / kilogram water consumed) was 43% higher in elevated than ambient CO_2 plots."

Nelson *et al*. say their results "suggest that a future, elevated CO_2 environment may result not only in increased plant productivity due to improved water use efficiency, but also lead to increased water drainage and deep soil moisture storage in this semi-arid grassland ecosystem." They add, "this, along with the ability of the major grass species to maintain a favorable water status under elevated CO_2, should result in the SGS being less susceptible to prolonged periods of drought."

Nelson *et al*. note their findings are common, writing, "previous studies have reported increased soil moisture under elevated CO_2 in semi-arid C_3 annual grasslands in California (Fredeen *et al*., 1997), mesic C_3/C_4 perennial tallgrass prairie in Kansas (Owensby *et al*., 1993, 1999; Ham *et al*., 1995; Bremer *et al*., 1996), and mesic C_3 perennial grasslands in Switzerland (Niklaus *et al*., 1998) and Sweden (Sindhoj *et al*., 2000)." Taken together, these studies indicate the benefits of atmospheric CO_2 enrichment will apply to grasslands generally, as the air's CO_2 content rises to double-and-beyond its current concentration.

If air temperature rises concurrently, things could get even better. Nelson *et al*. note, for example, "air temperature was on average 2.6°C higher inside the chambers than outside," and this warming "was implicated in the 36% enhanced biomass production observed in chambered-ambient compared to non-chambered plots." Consequently, since this already-enhanced biomass production was the starting point from which the 41% increase in biomass arising from the doubling of the air's CO_2 content was calculated, the increase in biomass caused by the concurrent actions of both factors (increasing air temperature and CO_2 concentration) could be on the order of 90%.

The 15-member team of Morgan *et al.* (2004) reviewed the scientific literature on the role of water relations in the response of grassland and desert ecosystems to elevated levels of atmospheric CO_2. They found it suggests "atmospheric CO_2 enrichment may stimulate plant growth either directly through (1) enhanced photosynthesis or indirectly through (2) reduced plant water consumption and hence slower soil moisture depletion, or the combination of both." They performed an analysis to determine "gas exchange, plant biomass and species responses of five native or semi-native temperate and Mediterranean grasslands and three semi-arid ecosystems to CO_2 enrichment, with an emphasis on water relations."

The team found "increasing CO_2 led to decreased leaf conductance for water vapor, improved plant water status, altered seasonal evapotranspiration dynamics, and in most cases, periodic increases in soil water content." As a result, "across the grasslands of the Kansas tallgrass prairie, Colorado shortgrass steppe and Swiss calcareous grassland, increases in aboveground biomass from CO_2 enrichment were relatively greater in dry years." In contrast, they report, "CO_2-induced aboveground biomass increase in the Texas C_3/C_4 grassland and the New Zealand pasture seemed little or only marginally influenced by yearly variation in soil water, and plant growth in the Mojave Desert was stimulated by CO_2 in a relatively wet year." In addition, "Mediterranean grasslands sometimes failed to respond to CO_2-related increased late-season water, whereas semiarid Negev grassland assemblages profited."

Although they state "vegetative and reproductive responses to CO_2 were highly varied among species and ecosystems, and did not generally follow any predictable pattern in regard to function groups," considered in their entirety, they conclude the literature results they reviewed (many of which they themselves had been instrumental in collecting) "suggest that the indirect effects of CO_2 on plant and soil water relations may contribute substantially to experimentally induced CO_2-effects."

Lazzarotto *et al.* (2010) write, "white clover (*Trifolium repens* L.) is the most important pasture legume grown in temperate climates in association with a variety of grasses, notably perennial ryegrass (*Lolium perenne* L.)," adding, "white clover improves the nutritional quality and digestibility of the herbage" and "contributes substantially to the nitrogen status of the sward through biological nitrogen fixation." They note some researchers have expressed concern future drought, such as is predicted by climate models to occur in tandem with CO_2-induced global warming, will damage clover more than the grass with which it is intermingled, thereby degrading the nutritional quality and digestibility of pasture swards.

Lazzarotto *et al.* conducted a study in which "mechanisms controlling transient responses to elevated CO_2 concentration and climate change in an unfertilized grassland on the Swiss Plateau were examined in light of simulations with PROGRASS." They used a process-based model of grass-clover interactions developed by Lazzarotto *et al.* (2009), in which "daily weather for a series of transient climate scenarios spanning the 21st century were developed for the study site with the help of the LARS-WG weather generator," as described by Semenov and Barrow (1997) and Semenov *et al.* (1998), and "changes in the length of dry and wet spells, temperature, precipitation and solar radiation defining the scenarios were obtained from regional climate simulations carried out in the framework of the PRUDENCE project," as described by Christensen and Christensen (2007).

"Compared to 1961–1990," the Swiss and UK scientists write, the climate scenarios they developed for a CO_2 increase from 370 to 860 ppm "indicated that for 2071–2100 there would be a noticeable increase in temperature (roughly 3°C in winter and 5°C in summer), a significant drop in summer precipitation (of the order of -30%) and a nearly 2-fold increase in the length of dry spells." They report "clover abundance did not decline even in the absence of CO_2 stimulation." When the atmospheric CO_2 concentration was programmed to gradually rise from an initial value of 370 ppm to a final value of 860 ppm, "clover development benefited from the overall positive effects of CO_2 on nitrogen acquisition," which they note was "the reason for increasing productivity of the [entire] sward."

These findings indicate the rather large increases in temperature and decreases in precipitation projected for the remainder of the twenty-first century, even if they come to pass, will not have much of an effect on Swiss grass-clover swards, but the concomitant increase in the air's CO_2 content will benefit them considerably. Lazzarotto *et al.* opine it is likely "technical progress in the management of grasslands and pastures," which will surely occur, will help such pastures even more.

Noting "grassland communities constitute an important fraction of the green surface of the Earth, and are worldwide an important source of cattle-food (Carlier *et al.*, 2009; Ciais *et al.*, 2011)," Farfan-Vignolo and Asard (2012) investigated several physiological and molecular (antioxidant) responses to water deficit in two major grassland species (*Lolium perenne* L. and *Medicago lupulina* L.) under current ambient (A) and future elevated (E) atmospheric CO_2 concentrations and air temperatures (T), where $ECO_2 = ACO_2 + 375$ ppm, and ET = AT + 3°C. The researchers found "drought caused significant increases in oxidative damage, i.e., in protein oxidation and lipid peroxidation levels." They also report, "in both species the impact of drought on protein oxidation was reduced in future climate conditions [ECO_2 and ET]." As to the stress-reducing effect of ECO_2, they state "this 'CO_2-protection effect' is reported for a variety of abiotic stress conditions and species," citing Schwanz and Polle (1998), Sgherri *et al.* (2000), Geissler *et al.* (2009), Perez-Lopez *et al.* (2009), Vurro *et al.* (2009), and Salazar-Parra *et al.* (2012). They say they too "find support for this effect at the level of oxidative cell damage and protein oxidation in water-deficit responses of *L. perenne* and *M. lupulina*." Even under drought stress, they note, "elevated CO_2 significantly affected shoot production in *L. perenne* (increase by 27–32%)," and "also in *M. lupulina* a biomass increase was observed (26–38%)."

Thus the conclusions of Idso and Idso (1994), based on the pre-1994 literature, are well supported by the subsequent peer-reviewed scientific literature, which indicates the rise in the air's CO_2 content likely will lead to substantial increases in plant photosynthetic rates and biomass production, even with stressful environmental conditions imposed by less-than-optimum soil moisture conditions.

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3.15.3 Woody Plants

- The rise in the air's CO_2 concentration likely will lead to substantial increases in the photosynthetic rates and biomass production of trees and shrubs, even with stressful environmental conditions imposed by suboptimal soil moisture availability.

It is widely acknowledged that as the CO_2 content of the air rises, nearly all plant types will exhibit increases in photosynthesis and biomass production, but some researchers claim future water stress will negate these benefits of atmospheric CO_2 enrichment. Much of the pertinent scientific literature of the 10-year period 1983–1994, reviewed by Idso and Idso (1994), calls that claim into question, showing water stress will generally not negate the CO_2-induced stimulation of plant growth. Idso and Idso's literature review found the CO_2-induced percentage increase in plant productivity was nearly always greater under water-stressed conditions than when plants were well-watered. This section discusses subsequent relevant literature as it pertains to woody species.

It is well-known that during times of water stress, atmospheric CO_2 enrichment often stimulates the development of larger-than-usual and more robust root systems in woody plants, enabling them to probe greater volumes of soil for scarce and much-needed moisture. Tomlinson and Anderson (1998), for example, found greater root development in water-stressed red oak seedlings grown at 700 ppm CO_2 helped them effectively deal with the reduced availability of moisture, and these trees eventually produced just as much biomass as well-watered controls exposed to air containing 400 ppm CO_2. Polley *et al.* (1999) report water-stressed honey mesquite trees exposed to an atmospheric CO_2 concentration of 700 ppm produced 37% more root biomass than water-stressed seedlings in air of 370 ppm.

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

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

If atmospheric CO_2 enrichment allows plants to maintain a better water status during times of water stress, it is only logical to surmise plants growing under such conditions will exhibit CO_2-induced increases in photosynthesis. Palanisamy (1999) found water-stressed Eucalyptus seedlings grown at 800 ppm CO_2 had greater net photosynthetic rates than their ambient-grown and water-stressed counterparts. Runion *et al.* (1999) found the CO_2-induced photosynthetic stimulation of water-stressed pine seedlings grown at 730 ppm CO_2 was nearly 50% greater than similar water-stressed pine seedlings grown at 365 ppm CO_2. Similarly, Centritto *et al.* (1999a) report water-stressed cherry trees grown at 700 ppm CO_2 displayed net photosynthetic rates 44% greater than those of water-stressed trees grown at 350 ppm CO_2. And Anderson and Tomlinson (1998) determined a 300-ppm increase in the air's CO_2 concentration boosted photosynthetic rates in well-watered and water-stressed red oak seedlings by 34 and 69%, respectively, demonstrating the CO_2-induced enhancement in net photosynthesis in this species was essentially twice as great in water-stressed seedlings as in well-watered ones.

Nevertheless, plants sometimes suffer drastically when subjected to extreme water stress, but the addition of CO_2 to the air often induces plants to react better to stress than plants growing in normal air. Tuba *et al.* (1998), for example, reported leaves of a water-stressed woody shrub exposed to an atmospheric CO_2 concentration of 700 ppm continued to maintain positive rates of net carbon fixation for a period that lasted three times longer than did leaves of equally water-stressed control plants growing in ambient air. Fernandez *et al*. (1998) discovered herb and tree species growing near natural CO_2 vents in Venezuela continued to maintain positive rates of net photosynthesis during that location's dry season, and the same species growing some distance away from the CO_2 source displayed net losses of carbon during this stressful time. Likewise, Fernandez *et al*. (1999) note that after four weeks of drought, the deciduous Venezuelan shrub *Ipomoea carnea* continued to exhibit positive carbon gains under elevated CO_2 conditions, whereas ambient-growing plants displayed net carbon losses. Polley *et al*. (2002) reported seedlings of five woody species grown at twice-ambient CO_2 concentrations survived 11 days longer (on average) than control seedlings when subjected to maximum drought conditions.

Since elevated CO_2 enhances photosynthetic rates during times of water stress, one would expect tree and shrub biomass production to be enhanced by elevated CO_2 concentrations under drought conditions. That was demonstrated by Arp *et al*. (1998), who reported six perennial plants common to the Netherlands increased their biomass under CO_2-enriched conditions even when suffering from lack of water. In some cases, the CO_2-induced percentage biomass increase is greater for water-stressed plants than for well-watered plants. Catovsky and Bazzaz (1999), for example, reported the CO_2-induced biomass increase for paper birch was 27% and 130% for well-watered and water-stressed seedlings, respectively. Schulte *et al*. (1998) noted the CO_2-induced biomass increase of oak seedlings was greater under water-limiting conditions than under well-watered conditions (128% vs. 92%), as did Centritto *et al*. (1999b) for basal trunk area in cherry seedlings (69% vs. 22%).

Knapp *et al*. (2001) developed tree-ring index chronologies from western juniper stands in Oregon (USA), finding the trees recovered better from the effects of drought in the 1990s, when the air's CO_2 concentration was around 340 ppm, than they did in 1900–1930, when the atmospheric CO_2 concentration was around 300 ppm.

In a loosely related study, Osborne *et al*. (2000) looked at the warming and reduced precipitation experienced in Mediterranean shrublands over the last century and concluded primary productivity should have been negatively impacted in those areas. However, when the concurrent increase in atmospheric CO_2 concentration was factored into their mechanistic model, a 25% increase in primary productivity was projected.

Centritto (2002) grew peach seedlings for two growing seasons in pots in open-top chambers of either ambient or CO_2-enriched air (350 or 700 ppm, respectively) inside a glasshouse, where all plants were continuously maintained at optimum soil fertility and, for the entire first growing season, at optimum soil water availability. In the second growing season, half of the seedlings had water withheld from them for four weeks. At the end of the study, there was no evidence of any downward acclimation of photosynthesis in the seedlings grown at elevated CO_2, nor was there any downward acclimation in rubisco carboxylation efficiency or in the maximum RuBP regeneration capacity mediated by electron transport.

Xiao *et al*. (2005) experimented with *Caragana intermedia* Kuanget H.C. Fu, a deciduous shrub of semi-arid northern China that occurs primarily in the country's Maowusu sandland as well as parts of Inner Mongolia, where they state it is "used by local people as feed for livestock, and as shelter for protection of soils (Zhang, 1994)," noting "it is one of the dominant shrubs that fix soil and reduce wind speed, thus actively mitigating desertification." The five Chinese scientists grew seedlings of this species for 3.5 months in 10-cm-diameter by 10-cm-deep pots filled with sand and maintained at three water regimes—well-watered (60–70% field capacity), moderate-watered (45–55% field capacity), and drought-stressed (30–40% field capacity)—in greenhouse compartments maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm. Near the end of this period, they measured leaf water potentials and several plant growth parameters.

Xiao *et al*. found, "elevated CO_2 significantly increased leaf water potential" while also increasing tree height, basal diameter, shoot biomass, root biomass, and total biomass, which was increased by 79% under the well-watered condition, by 61% under the moderate-watered condition, and by 53% under the drought-stressed condition. They report the Canopy Productivity Index (CPI, total growth per unit leaf area) was also "significantly increased by elevated CO_2, and the increase in CPI became stronger as the level of drought stress increased." They conclude their study "confirmed the beneficial effects of elevated CO_2 on *C. intermedia* seedlings exposed to drought-stressed conditions," and these findings "suggest that elevated CO_2 may enhance drought avoidance and improved water relations, thus weakening the effect of drought stress on growth of

C. intermedia seedlings."

Soule and Knapp (2006) write, "two major environmental issues have arisen regarding the increasingly CO_2-rich world of the late 20th and early 21st centuries: climatic change, and plant responses to the environment," and they note, "while the implications of atmospheric CO_2 for potential climatic change have received the majority of attention, the potential role of atmospheric CO_2 fertilization in plant growth and subsequent ecosystem dynamics may be equally important." They studied ponderosa pine trees growing at eight sites in the Pacific Northwest of the United States to see how they may have responded to the increase in the atmosphere's CO_2 concentration that occurred after 1950.

The two geographers say they chose study sites that "fit several criteria designed to limit potential confounding influences associated with anthropogenic disturbance," with "a variety of climatic and topo-edaphic conditions, ranging from extremely water-limiting environments ... to areas where soil moisture should be a limiting factor for growth only during extreme drought years." They note all their study sites were located in areas "where ozone concentrations and nitrogen deposition are typically low."

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

The two researchers report finding a post-1950 radial growth enhancement "more pronounced during drought years compared with wet years," and they add, "the greatest response occurred at the most stressed site." They write, "the relative change in growth [was] upward at seven of our [eight] sites, ranging from 11 to 133%."

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

Soule and Knapp recount how they "hypothesized that ponderosa pine ... would respond to gradual increases in atmospheric CO_2 over the past 50 years, and that these effects would be most apparent during drought stress and on environmentally harsh sites," and in the following sentence they state their results "support these hypotheses." They conclude it is likely "an atmospheric CO_2-driven growth-enhancement effect exists for ponderosa pine growing under specific natural conditions in the [USA's] interior Pacific Northwest."

Wang *et al.* (2006) conducted a similar study, seeking to ascertain how the historical increase in atmospheric CO_2 concentration had affected the growth of trees in the real world rather than experimental settings. They examined ring-width development in cohorts of young and old white spruce (*Picea glauca*) trees in a mixed grass-prairie ecosystem in southwestern Manitoba, Canada, where a 1997 wildfire killed most of the older trees growing in high-density spruce islands, but where younger trees slightly removed from the islands were not affected by the flames. "Within each of a total of 24 burned islands," the three researchers write, "the largest dominant tree (dead) was cut down and a disc was then sampled from the stump height," and "adjacent to each sampled island, a smaller, younger tree (live) was also cut down, and a disc was sampled from the stump height."

After removing size-, age-, and climate-related trends in radial growth from the ring-width histories of the trees, Wang *et al.* plotted the residuals as functions of time for the 30-year periods for which both the old and young trees would have been approximately the same age: 1900–1929 for the old trees and 1970–1999 for the young trees. During the first of these periods, the atmosphere's CO_2 concentration averaged 299 ppm, and during the second it averaged 346 ppm. The mean rate-of-rise of the atmosphere's CO_2 concentration was 0.37 ppm/year for the first period and 1.43 ppm/year for the second.

In comparison to the 1900–1929 period, the slope of the linear regression describing the rate-of-growth of the ring-width residuals for the 1970–1999 period (when the air's CO_2 concentration was 15% greater and its rate-of-rise was 285% greater) was more than twice the linear regression describing the rate-of-growth of the ring-width residuals for the 1900–1929 period. As the researchers observe, these results show "at the same developmental stage, a greater growth response occurred in the late period when atmospheric CO_2 concentration and the rate of atmospheric CO_2 increase were both relatively high," and "these results are consistent with expectations for CO_2-fertilization effects." They write, "the response of the studied young trees can be taken as strong circumstantial evidence for the atmospheric CO_2-fertilization effect."

Wang *et al.* also learned "postdrought growth response was much stronger for young trees (1970–1999) compared with old trees at the same development stage (1900–1929)." They add, "higher atmospheric CO_2 concentration in the period from 1970–1999 may have helped white spruce recover from severe drought." Similarly, young trees showed a weaker relationship to precipitation than did old trees, noting "more CO_2 would lead to greater water-use efficiency, which may be dampening the precipitation signal in young trees." Wang *et al.*'s unique study provides an exciting real-world example of the benefits the historical rise in the air's CO_2 content likely has conferred on long-lived woody species.

Davi *et al.* (2006) used a meteorological model following "a moderate CO_2 emission scenario" (B2 of IPCC) to calculate a 1960–2100 average temperature increase of 3.1°C and a mean summer rainfall decrease of 27%, which they used as input to a physiologically based multilayer process-based ecosystem productivity model (which contained a carbon allocation sub-model coupled with a soil model) to evaluate net productivity changes of six French forest ecosystems representative of oceanic, continental, and Mediterranean climates dominated, respectively, by deciduous species (*Fagus sylvatica*, *Quercus robur*), coniferous species (*Pinus pinaster*, *Pinus sylvestris*), and sclerophyllous evergreen species (*Quercus ilex*). These ecosystems, they write, "are representative of a significant proportion of forests in western Europe."

"By comparing runs with and without CO_2 effects," according to the researchers, they found "CO_2 fertilization is responsible from 1960 to 2100 for an NEP [net ecosystem productivity] enhancement of about 427 g(C) on average for all sites (= 3.05 g(C) m^{-2} $year^{-1}$),"and "the CO_2 fertilization effect" turns a warming- and drying-induced "decrease of NEP into an increase." In addition, they report, "no saturation of this effect on NEP is found because the differences between the simulations with and without CO_2 fertilization continuously increase with time." Consequently, the real-world physiological effects of atmospheric CO_2 enrichment included in the ecosystem productivity model employed by Davi *et al.* are able to more than compensate for the deleterious effects of the dramatic climate-change scenario on the productivity of major European forests.

Pardos *et al.* (2006) grew seedlings of cork oak (*Quercus suber* L., which they describe as "a typical Mediterranean species") germinated from acorns they collected from trees near Toledo, Spain, and maintained for five months, one per each 3-L pot filled with a mixture of fine sand and peat. The seedlings were maintained at either high (83%) or low (32–34%) growing medium moisture, under either high (600 $\mu mol\ m^{-2}\ s^{-1}$) or low (60 $\mu mol\ m^{-2}\ s^{-1}$) light intensity, in growth chambers maintained at either ambient (360 ppm) or elevated (700 ppm) atmospheric CO_2 concentrations. The four Spanish researchers state "elevated CO_2 caused the cork oak seedlings to improve their performance in dry and high light environments to a greater extent than under well-irrigated and low-light conditions, thus ameliorating the effects of soil water stress and high light loads on growth." Consequently, and because they assume these latter two stressful conditions are what "global change is likely to produce in the Mediterranean basin in the next decades," the rise in the air's CO_2 concentration should help the cork oak species deal successfully with those stresses, if and when they occur.

Saleska *et al.* (2007) note "large-scale numerical models that simulate the interactions between changing global climate and terrestrial vegetation predict substantial carbon loss from tropical ecosystems, including the drought-induced collapse of the Amazon forest and conversion to savanna." They used Terra satellite data—Enhanced Vegetation Index (EVI) derived from the Moderate Resolution Imaging Spectroradiometer (MODIS)—to determine whether the widespread Amazon drought of 2005, which peaked during the dry season onset (July–September), did indeed reduce whole-canopy forest photosynthesis as predicted, which they said "should have been especially observable during this period, when anomalous interannual drought coincided with the already seasonally low precipitation."

Strongly contradicting the model predictions, the four researchers found intact forest "greenness" in the region was "dominated by a significant increase ($P<0.0001$), not a decline." They say the trees of the Amazon forest may be utilizing deep roots to "access and sustain" water availability during drought. Another possibility is the historical increase in the air's CO_2 content has significantly enhanced the trees' water use efficiency, enabling them to produce considerably more biomass per unit of water transpired and thereby conserve water. And yet another possibility is the phenomenon described in Soule and Knapp (2006), Wang *et al*. (2006), Davi *et al*. (2006), and Pardos *et al*. (2006), discussed above.

Huang *et al*. (2007) compared, synthesized, and evaluated the scientific literature describing atmospheric CO_2 enrichment experiments conducted on trees and empirical tree-ring studies designed to ascertain whether the growth-promoting effects of rising atmospheric CO_2 concentrations occur in natural forests. They found numerous CO_2-enrichment experiments have "demonstrated significantly positive physiological and growth responses of trees to CO_2, providing strong evidence to support the direct CO_2 fertilization effect (increased photosynthesis, water use efficiency, above- and below-ground growth) and thus allowing prediction of which ecosystems might be most responsive to CO_2." They conclude the latter will be "warm, moderately drought-stressed ecosystems with an ample nitrogen supply," because "drought-stressed trees could benefit from increased water use efficiency to enhance growth." They also note tree-ring studies on the cold and arid Tibetan Plateau "showed significant growth enhancements as well as increased water use efficiency (24.7% and 33.6% for each species, respectively) in Qilian juniper and Qinghai spruce since the 1850s," citing Zhang *et al*. (2003), Shao *et al*. (2005), Liang *et al*. (2006), Huang and Zhang (2007), and Zhang and Qiu (2007).

Wyckoff and Bowers (2010) note, "with continued increases in global greenhouse gas emissions, climate models predict that, by the end of the 21st century, Minnesota [USA] summer temperature will increase by 4–9°C and summer precipitation will slightly decrease," citing Kling *et al*. (2003) and Christensen *et al*. (2007). They state certain "forest models and extrapolations from the paleoecological record suggest that, in response to increased temperature and/or drought, forests may retreat to the extreme north-eastern parts of the state," citing Pastor and Post (1998), Hamilton and Johnson (2002), and Galatowitsch *et al*. (2009). Working with bur oak (*Quercus macrocarpa*) trees, Wyckoff and Bowers explored the likelihood of this scenario by: "(i) using tree rings to establish the relationship between drought and *Q. macrocarpa* growth for three sites along Minnesota's prairie-forest border, (ii) calculating the current relationship between growth and mortality for adult *Q. macrocarpa* and (iii) using the distributions of current growth rates for *Q. macrocarpa* to predict the susceptibility of current populations to droughts of varying strength." In addition, they looked for "temporal trends in the correlation between *Q. macrocarpa* growth and climate, hypothesizing that increases in CO_2 may lead to weaker relationships between drought and tree growth over time," because atmospheric CO_2 enrichment typically leads to increases in plant water use efficiency, which generally makes them less susceptible to the deleterious impact of drought on growth.

The two University of Minnesota researchers report "the sensitivity of annual growth rates to drought has steadily declined over time as evidenced by increasing growth residuals and higher growth rates for a given PDSI [Palmer Drought Severity Index] value after 1950 [when the atmosphere's CO_2 concentration rose by 57 ppm from 1950 to 2000] compared with the first half of the century [when the CO_2 increase was only 10 ppm]." They state "for *Q. macrocarpa*, declining sensitivity of growth to drought translates into lower predicted mortality rates at all sites," and at one such site, "declining moisture sensitivity yields a 49% lower predicted mortality from a severe drought ($PDSI = -8$, on a par with the worst 1930s 'American Dust Bowl' droughts)." Wyckoff and Bowers conclude "the decreasing drought sensitivity of established trees may act as a buffer and delay the movement of the prairie-forest ecotone for many decades even in the face of climate change."

Noting climate models "consistently project significant increases in temperature and decreases in precipitation in the Mediterranean basin," Keenan *et al*. (2011) report these changes may have a large impact on current Mediterranean forests and the related ecosystem services they provide. They note niche-based models—also known as bioclimatic envelope models or habitat models—are the most commonly used method for predicting potential species distribution responses to future climatic changes. These models typically predict significant negative consequences for terrestrial plants and animals in the face of continued increases in atmospheric CO_2 concentrations.

Keenan *et al.* say they preferred process-based models, which describe eco-physiological processes ranging from purely empirical relationships to mechanistic descriptions based on physical laws. These models—supported by experiments and growth and yield surveys—"suggest that global warming will have a positive impact on forest productivity (van der Meer *et al*., 2002; Nigh *et al*., 2004; Norby and Luo, 2004; Briceño-Elizondo *et al*., 2006; Gaucharel *et al*., 2008), due to the direct fertilization effect of increased CO_2 and indirect effects such as lengthening of the growing period."

To demonstrate the difference in results obtained by these two approaches to forecasting, the five researchers assessed and compared the projections of each when applied to stands of three common forest species (*Quercus ilex*, *Pinus halepensis,* and *Pinus sylvestris*) with widely contrasting distributions in continental Spain. This procedure revealed, they write, "CO_2 fertilization through projected increased atmospheric CO_2 concentrations is shown to increase forest productivity in the mechanistic process-based model (despite increased drought stress) by up to three times the non-CO_2 fertilization scenario by the period 2050–2080, which is in stark contrast to projections of reduced habitat suitability from the niche-based models by the same period."

Thus the Spanish and U.S. scientists write, "previous reports of species decline in continental Spain (e.g. Benito-Garzon *et al*., 2008) may be overestimated due to two reasons: the use of only one predictive niche-based model, and the failure to account for possible effects of CO_2 fertilization." They add, "similar studies in other regions, which do not consider these two aspects, are also potentially overestimating species decline due to climate change." They note, "niche-based model results also likely overestimate the decline in [habitat] suitability," and they therefore conclude "an organism's niche must be modeled mechanistically if we are to fully explain distribution limits," citing Kearney (2006).

Osorio *et al*. (2011) write, "water deficits and high temperature are major abiotic stress factors restricting plant growth and productivity in many regions," and "the impact of climate change on temperature and rainfall patterns is of great importance in determining the future response of tree crops to new environmental conditions." They studied the Carob or St. John's tree (*Ceratonia siliqua*), which grows in the Mediterranean, where they contend water stress will be the most important factor limiting plant growth throughout the remainder of this century. They investigated the impacts of drought and high-temperature stresses on photosynthesis, energy partitioning, and membrane lipids, as well as the potential ability of Carob trees to attenuate oxidative damage, in young seedlings growing in controlled-environment chambers. They rooted the plants in 3-dm^3 pots filled with a 2:1 mixture of a fertilized substrate and natural soil and maintained them under two thermal regimes—low and high temperature (LT: 25/18°C; HT: 32/21°C)—and three soil water conditions (control, water stress, and rewetting), monitoring numerous physiological and biochemical plant properties and processes.

Osorio *et al.* report the decrease in net photosynthesis (*P*N) caused by drought was 33% in the LT chamber and 84% in the HT chamber. They say "the negative effects of soil drying on *P*N and stomatal conductance of HT plants were no longer detected 36 hours following rewatering." The five Portuguese scientists remark, "although *C. siliqua* seedlings exhibit clear signs of oxidative stress under drought and high temperature, they retain a remarkable ability to quickly restore normal physiological activity on rehydration, which let us believe that they can satisfactorily deal with predicted climate warming and increased soil drying in the Mediterranean area."

Soule and Knapp (2011) write, "in 2008, atmospheric CO_2 concentrations from the Mauna Loa, Hawaii, Observatory records exceeded 385 ppm, representing a 22% increase since 1959." They note, "as CO_2 has increased, most tree species have been able to use water more efficiently" as their "leaf stomatal apertures narrow during photosynthesis," resulting in "less transpirational water loss per biomass gained." The parameter representing this phenomenon is referred to as intrinsic water-use efficiency (iWUE), defined as the ratio of net CO_2 assimilation to stomatal conductance, and it has been documented, they write, "for various tree species in many parts of the world," citing Bert *et al.* (1997), Feng (1999), Tang *et al.* (1999), Arneth *et al.* (2002), Saurer *et al.* (2004), Waterhouse *et al.* (2004), and Liu *et al.* (2007).

They examined changes in, and relationships between, radial growth rates and the iWUE of ponderosa pine (*Pinus ponderosa*) trees, climate, and atmospheric CO_2 concentration in the western United States since the mid-nineteenth century, developing tree-ring chronologies for eight sites in three climate regions, and using carbon isotope data to calculate pentadal values of iWUE. They examined relationships among radial growth, climate, iWUE, and CO_2 via correlation and regression analyses.

Soule and Knapp report finding significant upward trends in iWUE at all sites, and they state “despite an absence of climate changes that would favor growth,” upward radial growth trends occurred at five sites. The highest iWUE values “were recorded in the last pentad at six of eight sites and follow a positive quadratic progression at all sites, suggesting that future increases in iWUE are likely for ponderosa pine within our study regions as CO_2 levels increase.” They also found “significant improvements in radial growth rates during drought years after 1950,” when the air’s CO_2 content rose at an accelerating rate.

The two researchers say their findings suggest “increased iWUE associated with rising CO_2 can positively impact tree growth rates in the western United States and are thus an evolving component of forest ecosystem processes.” They conclude, “if potential climate changes lead to increasing aridity in the western United States, additional increases in iWUE associated with future increases in CO_2 might ameliorate growth declines associated with drought conditions.”

The peer-reviewed scientific studies described in this section support the earlier conclusions of Idso and Idso (1994), who found the rise in the air’s CO_2 content likely will lead to substantial increases in photosynthetic rates and biomass production in Earth’s many woody species, even under stressful conditions imposed by suboptimal soil moisture.

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3.16 Weeds

Some researchers suggest weeds will become more aggressive as the air's CO_2 content climbs, making them greater threats to the wellbeing of natural ecosystems and farming operations. The subsections below investigate the merits of this claim regarding non-parasitic and parasitic weeds.

3.16.1 Non-Parasitic

- Non-parasitic weeds likely will be no more competitive in a high-CO_2 environment than they are today, and many could become less competitive. Atmospheric CO_2 enrichment may provide non-weeds with greater protection against weed-induced decreases in productivity, thereby increasing the competitiveness of non-weeds over weeds. And although atmospheric CO_2 enrichment increases the growth of many weeds, the fraction helped is probably not as large as non-weeds.

3.16.1.1 Competitiveness

- Non-parasitic weeds likely will be no more competitive in a high-CO_2 environment than they are today, and many could become less competitive.

Wayne *et al.* (1999) grew a common agricultural weed (field mustard) at six densities in pots exposed to atmospheric CO_2 concentrations of 350 and 700 ppm, sequentially harvesting them during the growing season. Early in stand development, the extra CO_2 increased above-ground biomass in a density-dependent manner; with the greatest stimulation (141%) occurring at the lowest weed density (20 plants per square meter) and the smallest stimulation (59%) occurring at the highest weed density (652 plants per square meter), the authors report. As the stands matured, the density-dependence of the growth response disappeared, and the CO_2-enriched weeds exhibited an average above-ground biomass 34% greater than those grown in ambient air. That response is similar to those of most herbaceous plants (a 30 to 50% increase for a doubling of the air's CO_2 content) and less than those of most woody species (50% and up). Consequently, in currently farmed or abandoned agricultural fields, as well as in regenerating forests, it is unlikely field mustard plants will benefit relative to other plants from Earth's rising atmospheric CO_2 concentration.

Caporn *et al.* (1999) grew bracken—a serious weed and potential threat to human health in the United Kingdom and elsewhere—for 19 months in controlled-environment chambers maintained at atmospheric CO_2 concentrations of 370 and 570 ppm and normal or high levels of fertilization. They found the extra 200 ppm of CO_2 increased rates of net photosynthesis by 30 to 70%, depending on soil fertility and time of year. The elevated CO_2 did not increase total plant biomass, nor did it increase the biomass of any plant organs, including rhizomes, roots, and fronds. The only significant effect of elevated CO_2 on plant growth was observed in the normal nutrient regime, where it reduced average frond area.

Gavazzi *et al.* (2000) grew one-year-old loblolly pine seedlings for four months in pots seeded with a variety of C_3 and C_4 weeds and maintained at adequate and inadequate levels of soil moisture in growth chambers maintained at atmospheric CO_2 concentrations of 360 and 660 ppm. The elevated CO_2 increased pine seedling biomass by 22%, decreased total weed biomass by 22%, and reduced the percentage of weed biomass composed of C_4 species from 53 to 35%. The additional CO_2 induced an increase in root-to-shoot ratio under water-stressed conditions in the pine seedlings, which Gavazzi *et al.* opine could "contribute to an improved ability of loblolly pine to compete against weeds on dry sites under elevated CO_2 levels."

Ziska (2003) grew Canada thistle, "the most frequently listed noxious weed species in surveys of the continental United States and southern Canada," in pots watered to the drip point daily with one of three complete nutrient solutions that differed only in nitrogen (N) concentration (3.0, 6.0, or 14.5 mM) in controlled-environment chambers maintained at 287 and 373 ppm CO_2 from seeding until flowering, which occurred at 77 days after seeding (DAS). He reports, "N supply did not affect the relative response to CO_2 for any measured vegetative parameter up to 77 DAS." Averaged across the three nitrogen treatments, the 86 ppm increase in atmospheric CO_2 concentration increased total plant biomass by 65.5%, which for the full 100 ppm CO_2 increase experienced over the course of the Industrial Revolution (initial value ~275 ppm, current value ~375 ppm) translates into an approximate 76% biomass increase.

To assess the significance of this CO_2-induced increase in weed biomass, it is necessary to compare it with what would have been expected for crops with which Canada thistle competes. Mayeux *et al.* (1997) obtained data indicating the 100-ppm increase in atmospheric CO_2 concentration experienced over the course of the Industrial Revolution should have produced yield increases of 70 and 74% in the two wheat varieties they studied when grown under well-watered conditions comparable to those studied by Ziska. In addition, based on the voluminous data Idso and Idso (2000) summarized, we can scale these results to derive comparable CO_2-induced growth enhancements of 84% for other C_3 cereals, 74% for legumes, and 80% for root and tuber crops. Thus the CO_2-induced growth enhancement likely experienced by Canada thistle over the course of the Industrial Revolution was not much different from the growth enhancements of most of the crops with which it competes, suggesting the competitive ability of this noxious weed against these crops has remained largely unaffected by the historical increase in the air's CO_2 content.

Ziska and Goins (2006) grew genetically modified (Round-up Ready) soybean plants in the field in aluminum chambers maintained at ambient and ambient + 250 ppm atmospheric CO_2 concentrations for two full growing seasons under conditions allowing a variety of different weed densities to develop among the soybeans. The elevated CO_2 conditions advanced soybean seed yields by 25, 33, 50, 90, and 250% when chamber weed biomass densities were 0, 200, 400, 600, and 800 gm^{-2}, respectively. Soybean seed yield in the ambient-air treatment fell to a value of zero at a weed density of approximately 920 gm^{-2}, whereas calculations reveal it would not drop that far in the CO_2-enriched treatment until a weed density of approximately 1,250 gm^{-2} was reached. Consequently, the atmospheric CO_2 enrichment of this study boosted crop yield by an increasing percentage as the stress of the expanding weed population grew larger, benefiting the soybean plants most when they needed it most. This phenomenon also has been shown to be true of other environmental stressors, such as plant diseases, lack of water, and high temperatures.

Kao-Kniffin and Balser (2007) grew invasive reed canary grass from seed for four months in well-watered mesocosms located in greenhouses maintained at atmospheric CO_2 concentrations of either 365 or 600 ppm in soils of either low or high nitrogen (N) supply (5 mg N l^{-1} or 30 mg N l^{-1}) under conditions where the invading species was either dominant (high invasion: >90% cover) or subdominant (low invasion: <50% cover), and where the remaining surface portions of the mesocosms were covered with native graminoids (grasses, sedges, and bulrushes) and native forbs also grown from seed. Elevating the air's CO_2 content increased belowground biomass only in the plant communities moderately invaded by reed canary grass, and the only plants to show a significant increase in aboveground biomass were the native graminoids in the moderately invaded low N treatment. The scientists conclude, "when CO_2 concentrations rise in the future, wetland plant communities comprised of native graminoids may be better able to hinder reed canary grass invasion, particularly under low N environments."

Williams *et al.* (2007) studied the impacts of a 170 ppm increase in atmospheric CO_2 concentration and a 2°C rise in air temperature at the Tasmanian free-air CO_2 enrichment (TasFACE) facility, located in a native lowland grassland in the southern midlands region of Tasmania, Australia. Between spring 2003 and summer 2006, they documented annual seed production, seedling emergence, seedling survival, and adult survival of four abundant perennial species, including the two most dominant invading weeds: *Hypochaeris radicata* L. and *Leontodon taraxacoides* (Vill.) Merat, members of the Asteraceae family. They found no significant CO_2-induced differences in the population growth rates of either weed species, but the population growth rates of both "were substantially reduced by warming." The six researchers conclude "global warming may be a more important determinant of the success of invasive species than CO_2 concentration," and both the invading weed species they studied "are likely to be excluded from the grassland community by increasing temperatures."

McPeek and Wang (2007) collected seeds from a single dandelion plant in Speedway, Indiana (USA), which they allowed to sprout and grow until reaching reproductive maturity in pots placed in each of two controlled-environment chambers, one continually flushed with ambient air of 370 ppm CO_2 and the other maintained at an elevated atmospheric CO_2 concentration of 730 ppm. After harvesting the plants and measuring numerous parameters of reproductive fitness, the two scientists conducted a second experiment in which they measured various parameters of the germination of the seeds produced in the two CO_2 treatments, along with the physical characteristics of the second-generation plants 35 days after planting.

McPeek and Wang state the dandelion plants "produced 83% more inflorescences and 32% more achenes, i.e., single-seed fruits, per plant at elevated than at ambient CO_2," and the "seeds from elevated CO_2-grown plants were significantly heavier and had a higher germination percentage, leading to larger seedlings and earlier establishment in the subsequent generation." Furthermore, "achenes from plants grown at elevated CO_2 had characteristics, such as higher stalks at seed maturity, longer beaks, and larger pappi, which would increase the distance of seed dispersal by wind."

The two researchers conclude "dandelion can potentially become more widespread and noxious as atmospheric CO_2 continues to rise."

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3.16.1.2 Biodiversity Impacts

- Rising atmospheric CO_2 concentrations will not favor the growth of non-parasitic weeds over crops and native plants. A CO_2 increase may provide the latter with greater protection against weed-induced decreases in productivity, thereby increasing the competitiveness of non-weeds over weeds.

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

Dukes (2002) grew model serpentine grasslands common to California (USA) in competition with the invasive forb *Centaurea solstitiali*s at atmospheric CO_2 concentrations of 350 and 700 ppm for one year. They found elevated CO_2 increased the biomass proportion of this weedy species in the community by 1.2%, while total community biomass increased by 28%. Similarly, Gavazzi *et al*. (2000) grew loblolly pine seedlings for four months in competition with C_3 and C_4 weeds at atmospheric CO_2 concentrations of 260 and 660 ppm, reporting elevated CO_2 increased pine biomass by 22% while eliciting no response from either type of weed. In a study of pasture ecosystems near Montreal, Canada, Taylor and Potvin (1997) determined elevated CO_2 concentrations did not influence the number of native species returning after their removal (to simulate disturbance), even in the face of the introduced presence of the C_3 weed *Chenopodium album*, which normally competes quite effectively with several slower-growing crops in ambient air. Atmospheric CO_2 enrichment did not impact the growth of this weed in any measurable way.

Ziska *et al*. (1999) studied the C_3 weed *C. album*, along with the C_4 weed *Amaranthus retroflexus*, in glasshouses maintained at atmospheric CO_2 concentrations of 360 and 720 ppm. Elevated CO_2 significantly increased the photosynthetic rate and total dry weight of the C_3 weed but had no effect on the C_4 weed. They report the growth response of the C_3 weed to a doubling of the air's CO_2 content was approximately 51%, about the same as the average 52% growth response tabulated by Idso (1992) and by Poorter (1993) for rapidly growing wild C_3 species (54%), suggesting a CO_2-enriched environment does not cause enhanced dominance of the C_3 weed over other C_3 plants.

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

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

These studies suggest atmospheric CO_2 enrichment will not favor the growth of non-parasitic weeds over crops and native plants.

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3.16.1.3 Miscellaneous Weeds

- Atmospheric CO_2 enrichment tends to increase the growth of many weeds, but possibly not by quite as great a percentage as it does for non-weeds.

Lewis *et al*. (2002) grew the common cocklebur (*Xanthium strumarium* L.) in controlled-environment growth chambers maintained at atmospheric CO_2 concentrations of 365 and 730 ppm for 70 days post-emergence. During the weed's vegetative growth phase, the photosynthetic rates of the CO_2-enriched plants were 30% greater than those of the plants growing in ambient air. During the flowering period that ensued shortly thereafter, this stimulation was reduced to 10%, after which it rose to 20% during the weed's fruiting period.

Gibeaut *et al*. (2001) grew the common weed *Arabidopsis thaliana* for seven weeks in controlled-environment chambers maintained at atmospheric CO_2 concentrations of 360 and 1,000 ppm, finding the 640 ppm increase in the air's CO_2 concentration increased the relative growth rate of the plants by about 20% during the first three weeks of the study. The extra CO_2 also increased the activity of the enzyme UDP-glucose dehydrogenase (an important enzyme involved in cell wall biosynthesis) by approximately 25%. Thereafter, relative growth rates were the same in both CO_2 treatments. Nevertheless, by the end of the study the CO_2-enriched plants had produced 2.3 times more biomass than the ambient-grown plants.

Ziska (2002) grew Canadian thistle (*Cirsium arvense* L. Scop.) plants in controlled-environment chambers maintained at atmospheric CO_2 concentrations of 280, 380, and 720 ppm for about two months. They determined the first increment of extra CO_2 enhanced photosynthesis rates and total plant biomass production by 45 and 126%, respectively, and the second CO_2 increment enhanced these two parameters by 49 and 69%.

Leishman *et al*. (1999) grew four weedy C_3 plants common to European grasslands (*Cardamine hirsute*, *Spergula arvensis*, *Senecio vulgaris*, and *Poa annua*) from seed to senescence in glasshouses maintained at atmospheric CO_2 concentrations of 350 and 550 ppm at two light intensities: full light and 67% of full light. The extra 200 ppm of CO_2 did not significantly impact vegetative growth in three of the species. For *Spergula arvensis*, it increased maximum leaf length by an average of 15%, regardless of light treatment, and total dry weight by 20 and 68% at full and reduced light levels, respectively. It significantly enhanced reproductive success in only one of the species, increasing the number of seeds in *Poa annua* by 50 and 26% at full and reduced light levels, respectively.

Nagashima *et al*. (2003) established even-aged stands of the summer annual *Chenopodium album* (a weed commonly found in open habitats, such as abandoned fields and flood plains) at ambient and twice-ambient atmospheric CO_2 concentrations and low and high levels of soil nutrient availability in open-top chambers in the experimental garden of Tohoku University, Sendai, Japan. They monitored the growth of individual plants every week until flowering. At the conclusion of the experiment, they could detect no significant effect of elevated CO_2 on aboveground biomass in the low nutrient regime; in the high nutrient regime, the extra CO_2 increased aboveground biomass by 50%. The CO_2-induced enhancement of growth in the high nutrient regime gradually waned and ultimately disappeared altogether in smaller subordinate individuals but continued in larger dominants throughout the experiment.

Ziska and Bunce (1999) grew four C_4 plants in controlled-environment chambers maintained continuously at atmospheric CO_2 concentrations of 350 and 700 ppm or at a nocturnal CO_2 concentration of 700 ppm and 350 ppm during the day for approximately three weeks. They found continuous CO_2 enrichment caused a significant increase in photosynthesis (+13%) and total dry mass (+21%) in only one of the four species, *Amaranthus retroflexus*. Nocturnal CO_2 enrichment provided no significant effects in this species, indicating the CO_2-induced increase in biomass was not facilitated by a reduction in dark respiration rate. Plants exposed to continuous CO_2 enrichment did not increase their biomass due to improved internal water balance, as leaf water potentials were not significantly different among plants of any CO_2 treatment.

Ziska *et al*. (1999) grew broad-leaved C_3 (*Chenopodium album*) and C_4 (*Amaranthus retroflexus*) weeds in glasshouses maintained at atmospheric CO_2 concentrations of 360 and 720 ppm. Both young and mature plants of each species were sprayed with one-tenth and full-strength solutions of the chemical glyphosate ("Roundup"). The elevated CO_2 significantly increased the photosynthetic rate and total dry weight (by 51%) of the unsprayed C_3 weed, regardless of maturity stage, but it had no effect on these parameters in the case of the C_4 weed. Spraying both young and mature *A. retroflexus* plants with full-strength herbicide resulted in their death, regardless of atmospheric CO_2 concentration; spraying *C. album* plants with full-strength glyphosate severely reduced, but did not eliminate, growth in the elevated-CO_2 air, whereas chemically treated plants died in ambient CO_2 air. Consequently, farmers who use glyphosate to control *A. retroflexus* should not have to modify their current chemical practices in the future, but better control of *C. album* may require application of glyphosate earlier in the season when the weeds are smaller or, if applied later, at higher concentrations, as elevated CO_2 slightly increases the glyphosate tolerance of this particular C_3 weed.

These studies suggest although atmospheric CO_2 enrichment tends to increase the growth of many weeds, it may not do so by as great a percentage as for non-weeds. (See, for example, the results of the many non-weed plants listed in Tables 1.1.1 and 1.1.2 in Appendices 3 and 4.)

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3.16.2 Parasitic

- Rising atmospheric CO_2 concentrations appear to reduce the negative effects of parasitic weed infection so infected host plants continue to exhibit positive (but somewhat reduced) growth responses to elevated CO_2.

Parasitic plants obtain energy, water, and nutrients from their host plants and cause widespread reductions in harvestable yields. This brief section examines how increasing atmospheric CO_2 concentrations may impact the growth of parasitic weeds and the relationships that exist between them and their host plants.

Dale and Press (1999) infected white clover (*Trifolium repens*) plants with *Orobanche minor*, a parasitic weed that primarily infects leguminous crops in the United Kingdom and the Middle East, and exposed them to atmospheric CO_2 concentrations of either 360 or 550 ppm for 75 days in controlled-environment growth cabinets. The elevated CO_2 had no effect on the total biomass of parasite per host plant, nor did it affect the number of parasites per host plant or the time to parasitic attachment to host roots. While infected host plants growing in ambient air produced 47% less biomass than uninfected plants growing in ambient air, infected plants growing at 550 ppm CO_2 exhibited final dry weights only 20% less than those of uninfected plants growing in the CO_2-enriched air, indicating a significant CO_2-induced partial alleviation of parasite-induced biomass reductions in the white clover host plants.

Watling and Press (1997) infected several C_4 sorghum plants with *Striga hermonthica* and *Striga asiatica* (parasitic C_3 weeds of the semi-arid tropics that infest many grain crops) and grew them, along with uninfected control plants, for approximately two months in controlled-environment cabinets maintained at atmospheric CO_2 concentrations of 350 and 700 ppm. In the absence of parasite infection, the extra 350 ppm of CO_2 increased sorghum biomass by approximately 36%. When infected with *S. hermonthica*, the sorghum plants grown at ambient and elevated CO_2 concentrations produced only 32 and 43% of the biomass displayed by their respective uninfected controls. Infection with *S. asiatica* was somewhat less stressful and led to host biomass production of about half that of uninfected controls in both ambient and CO_2-enriched air. Therefore, the doubling of the air's CO_2 content employed in this study increased sorghum biomass by 79% and 35% in the C_4 sorghum plants infected with *S. hermonthica* and *S. asiatica*, respectively.

Watling and Press (2000) grew upland rice (*Oryza sativa* L.) in pots in controlled-environment chambers maintained at 350 and 700 ppm CO_2 in either the presence or absence of the root parasite *S. hermonthica* for 80 days after sowing, after which they harvested and weighed the plants. In ambient air, the presence of the parasite reduced the biomass of the rice to only 35% of what it was in the absence of the parasite. In air enriched with CO_2 the presence of the parasite reduced the biomass of infected plants to 73% of what it was in the absence of the parasite.

These few observations suggest rising atmospheric CO_2 concentrations generally tend to reduce the negative effects of parasitic weed infection so infected host plants continue to exhibit positive growth responses to elevated CO_2. It is likely host plants infected by parasitic weeds will fare better under higher atmospheric CO_2 conditions than they do currently.

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