# 1

# $CO_2$, Plants, and Soils

Key Findings

Introduction

**1.1 Plant Responses to Atmospheric $CO_2$ Enrichment**

**1.2 Ecosystem Responses to $CO_2$ Enrichment**

## Key Findings

The key findings of the present chapter are listed below.

- Results from 3,586 separate experimental conditions conducted on 549 plant species reveal nearly all plants will experience increases in dry weight or biomass in response to atmospheric $CO_2$ enrichment. Results from an additional 2,094 separate experimental conditions conducted on 472 plant species reveal nearly all plants will experience increases in photosynthesis in response to atmospheric $CO_2$ enrichment.

- Long-term $CO_2$ enrichment studies confirm the findings of shorter-term experiments, demonstrating the effects of elevated atmospheric $CO_2$ likely persist across plant lifetimes.

- Several studies indicate plants are not harmed by super-elevated atmospheric $CO_2$ concentrations an order of magnitude or more greater than the globe's current mean. Instead, positive growth responses are reported, some of which are particularly large. Most plants will display enhanced rates of photosynthesis and biomass production as the atmosphere's $CO_2$ concentration rises.

- Forest growth rates throughout the world have increased over the years in concert with, and in response to, the historical increase in the air's $CO_2$ concentration. As the atmosphere's $CO_2$ concentration continues to rise, forests likely will respond by exhibiting significant increases in biomass production, and thus they likely will grow more robustly and significantly expand their ranges, as is already being documented in many parts of the world.

- Where tropical forests have not been decimated by the targeted and direct destructive actions of people, such as the felling and burning of trees, forest productivity has been growing with the passing of time, rising with the increasing $CO_2$ content of the air. It has been doing so despite changes in atmospheric, soil, and water chemistry, including twentieth century global warming, which IPCC claims to have been unprecedented over the past one to two millennia.

- In contrast to frequently stated assumptions, old-growth forests can be significant carbon sinks, and their capacity to sequester carbon in the future will be enhanced as the atmospheric $CO_2$ content rises.

- Future increases in air temperature likely will have a positive effect on carbon storage in forests and their associated soils.

- As the air's $CO_2$ concentration increases, the productivity of grassland species will increase, even under unfavorable growing conditions characterized by less-than-adequate soil moisture, inadequate soil nutrition, elevated air temperature, and physical stress imposed by herbivory.

- In contrast to IPCC projections, the thawing of permafrost caused by increases in air temperature and $CO_2$ will not likely transform peatlands from carbon-sink to carbon-source ecosystems. Instead, as permafrost thaws, plants and trees can begin to grow again on these lands and in so doing, they sequester carbon.

- Rising atmospheric $CO_2$ likely will enhance the productivity and carbon sequestering ability of wetlands. In addition, elevated $CO_2$ may assist some coastal wetlands in counterbalancing the negative impacts of rising seas.

- Rising atmospheric $CO_2$ concentrations likely will allow greater numbers of beneficial bacteria, which help sequester carbon and nitrogen, to exist within soils and anaerobic water environments, a two-pronged phenomenon benefiting both terrestrial and aquatic ecosystems.

- The aerial fertilization effect of atmospheric $CO_2$ enrichment likely will result in greater soil carbon stores due to increased carbon-input into soils, even in nutrient-poor soils and in spite of predicted increases in temperature. In addition, the soil-carbon-sequestering capability of Earth's vegetation likely will act as a significant brake on the rate-of-rise of the air's $CO_2$ content and thereby help to mute the magnitude of any $CO_2$-induced global warming.

- The historical increase in the atmosphere's $CO_2$ concentration has significantly reduced erosion of valuable topsoil over the past several decades, and the continuing increase in atmospheric $CO_2$ can maintain this trend, and perhaps even accelerate it, throughout the foreseeable future.

## Introduction

The United Nations' Intergovernmental International Panel on Climate Change (IPCC) insists that rising $CO_2$ levels, accompanied by even modest warming, will have harmful effects on plant life. In a draft of its Summary for Policymakers (SPM) to accompany its 2014 report, Working Group II says, "Without adaptation, local temperature increases of 1°C or more above preindustrial levels are projected to negatively impact yields for the major crops (wheat, rice, maize) in tropical and temperate regions, although individual locations may benefit (*medium confidence*). With or without adaptation, climate change will reduce median yields by 0 to 2% per decade for the rest of the century, as compared to a baseline without climate change" (IPCC 2014, p. 10).

These claims are at odds with the preponderance of research in this area dating as far back as the early 1900s (Demoussy, 1902–1904; Cummings and Jones, 1918) and as recent as 2013 (Isbell et al., 2013; Zhou *et al.*, 2013). Two previous volumes in the *Climate Change Reconsidered* series (Idso and Singer, 2009; Idso, Carter, and Singer, 2011) contained extensive literature reviews that also contradict IPCC's conclusions, suggesting once again IPCC is ignoring research appearing in peer-reviewed journals that contradicts its preferred narrative.

The current chapter begins with an analysis, in Section 1.1, of basic plant productivity responses to elevated $CO_2$. It references a tabular presentation of more than 5,000 individual plant photosynthetic and biomass responses appearing in Appendices 3 and 4. Section 1.2 surveys the literature on the effects of $CO_2$ on various eco-systems including forests, grasslands, peatlands, wetlands, and soils, finding in each case the beneficial effects of rising atmospheric concentrations of $CO_2$ more than offset any negative effects.

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## 1.1 Plant Responses to Atmospheric $CO_2$ Enrichment

### 1.1.1 Dry Weight (Biomass)

- Results from 3,586 separate experimental conditions conducted on 549 plant species reveal nearly all plants will experience increases in dry weight or biomass in response to atmospheric $CO_2$ enrichment.

Perhaps the best-known consequence of an increase in the air's $CO_2$ content is its stimulation of plant productivity (dry matter content or biomass). This growth enhancement occurs because carbon dioxide is the primary raw material utilized by plants to produce the organic matter out of which they construct their tissues. Consequently, the more $CO_2$ there is in the air, the bigger and better plants grow.

Table 1.1.1 in Appendix 3 reports the results of hundreds of peer-reviewed scientific studies indicating the biomass growth response of plants to a standardized 300 ppm increase in atmospheric $CO_2$ concentration. Plants are listed by common and/or scientific names, followed by the number of experimental studies conducted on each plant, the mean biomass response to a 300 ppm increase in the air's $CO_2$ content, and the standard error of that mean. Whenever the $CO_2$ increase for a given study was not exactly 300 ppm, a linear adjustment was computed. For example, if the $CO_2$ increase was 350 ppm and the growth response was a 60% enhancement, the adjusted 300 ppm $CO_2$ growth response was calculated as (300/350) x 60% = 51%.

The data in the table are printed by permission of the Center for the Study of Carbon Dioxide and Global Change and were taken from its Plant Growth database on 1 January 2014. The table summarizes $CO_2$ enrichment results from 3,586 separate experimental conditions conducted on 549 plant species. The responses are overwhelmingly positive. New data are added to the database at approximately weekly intervals and can be accessed free of charge at the center's website at http://www.co2science.org/data/plant_growth/dry/dry_subject.php. This online database also archives information pertaining to the experimental conditions under which each plant growth experiment was conducted, as well as the complete reference to the journal article from which the experimental results were obtained. The center's online database also lists percent increases in plant biomass for 600 and/or 900 ppm increases in the air's $CO_2$ concentration.

### 1.1.2 Plant Photosynthesis (Net $CO_2$ Exchange Rate)

- Results from 2,094 separate experimental conditions conducted on 472 plant species reveal nearly all plants will experience increases in photosynthesis in response to atmospheric $CO_2$ enrichment.

Table 1.1.2 in Appendix 4 reports the results of peer-reviewed scientific studies measuring the photosynthetic growth response of plants to a 300 ppm increase in atmospheric $CO_2$ concentration. Plants are listed by common and/or scientific names, followed by the number of experimental studies conducted on each plant, the mean photosynthetic response to a 300 ppm increase in the air's $CO_2$ content, and the standard error of that mean. Whenever the $CO_2$ increase for a given study was not exactly 300 ppm, a linear adjustment was computed. For example, if the $CO_2$ increase was 350 ppm and the growth response was a 60% enhancement, the adjusted 300 ppm $CO_2$ growth response was calculated as (300/350) x 60% = 51%.

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### 1.1.3 Long-Term Studies

One of the more commonly voiced concerns about atmospheric $CO_2$ enrichment is whether the plant growth enhancements observed in short-term laboratory and field studies will persist over the lifespan of plants. The subsections below investigate this topic with respect to both woody and non-woody plants, leaving no doubt as to the sustained response of plants to elevated atmospheric $CO_2$.

#### *1.1.3.1 Non-Woody Plants*

- Several long-term studies of various non-woody plants reveal sustained beneficial responses to elevated concentrations of atmospheric $CO_2$ over periods of many years.

In Switzerland, Niklaus *et al.* (2001) exposed a species-rich but nutrient-poor and water-limited, calcareous grassland dominated by *Bromus erectus* (which accounted for approximately half of the ecosystem's aboveground vegetative biomass) to atmospheric $CO_2$ concentrations of approximately 360 and 600 ppm for six years, using screen-aided $CO_2$ control (SACC) technology. $CO_2$-induced increases in biomass production in years one through six of the experiment were, respectively, 5%, 20%, 22%, 27%, 31%, and 18%, for an average of 23.6% over the last five years of the study (Niklaus and Körner, 2004). This biomass increase ultimately increased carbon stocks in plant shoots and roots by 17 and 24%, respectively, and enhanced carbon stocks in vegetative litter by 34%. The net effect of these increases was an initial air-to-soil carbon flux of 210 g C $m^{-2}$ $year^{-1}$. After six years of treatment, however, the $CO_2$-enriched soils held only about 44% of the carbon expected from this influx rate, due to the low soil residence time of the newly input carbon. Nevertheless, the study showed atmospheric $CO_2$ enrichment can in fact enhance plant growth and carbon sequestration in low-nutrient and water-limited soils.

In Italy, Bettarini *et al.* (1998) measured the stomatal densities and conductances of the leaves of 17 species of plants growing in the vicinity of a natural $CO_2$-emitting spring that has produced twice-ambient atmospheric $CO_2$ concentrations for at least two centuries, while making similar measurements on plants of the same species located further from the spring, where normal $CO_2$ concentrations prevail. The elevated $CO_2$ decreased leaf stomatal conductances in all but one of the species by 19 to 73%. These reductions, however, were not accompanied by decreases in stomatal density, which remained unaffected by long-term atmospheric $CO_2$ enrichment in all but three species. Consequently, life-long exposure to elevated $CO_2$ reduced plant water use primarily by controlling leaf stomatal function, not by changing leaf anatomical features (i.e., the number of stomata per unit leaf area).

These findings are encouraging, but it has been suggested they cannot persist indefinitely in all situations. The productivity of Earth's temperate grasslands, for example, is often limited by the availability of soil nitrogen (Vitousek and Howarth, 1991), and both empirical and modeling studies have suggested the magnitude and duration of grassland growth responses to rising levels of atmospheric $CO_2$ may be constrained by inadequate supplies of soil nitrogen (Rastetter *et al.*, 1997; Luo and Reynolds, 1999; Thornley and Cannell, 2000).

In light of this mix of real-world observations and theoretical calculations, it would seem only natural to hypothesize, as Richter *et al.* (2003) do, "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 that this phenomenon would lead ultimately to a reduction in the size of the growth-promoting effect of elevated atmospheric $CO_2$ that is manifest in short-term $CO_2$ enrichment experiments and at the start of long-term studies.

To test this 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 $CO_2$ at high and low rates of soil nitrogen addition for seven years in the Swiss free-air $CO_2$ enrichment (FACE) study conducted near Zurich. After seven years of treatment, they report, "gross mineralization, $NH_4^+$ consumption and N immobilization in both the *L. perenne* and the *T. repens* swards did not show significant differences." In addition, the size of the microbial N pool and immobilization of applied mineral $^{15}N$ were not significantly affected by the elevated $CO_2$.

Richter *et al.* note the results of their study "did not support the initial hypothesis and indicate that below-ground turnover of N, as well as N availability, measured in short-term experiments are not strongly affected by long-term exposure to elevated $CO_2$." They conclude "differences in plant N demand and not changes in soil N mineralization/immobilization are the driving factors for N dynamics in these meadow grassland systems."

Thus, as also found in the woody plant studies of Finzi and Schlesinger (2003) and Schafer *et al.* (2003) conducted in the Duke Forest FACE experiment, Richter *et al.*'s work provides no evidence the growth responses of Earth's grasslands to atmospheric $CO_2$ enrichment will ever be significantly reduced from what is suggested by moderate-term studies of a few to several years' duration.

In a study of the same *L. perenne* and *T. repens* ecosystems that helps to explain some of these observations, Gamper *et al.* (2004) analyzed the effects of elevated $CO_2$ and N fertilization (14 vs. 56 g N $m^{-2}$) on arbuscular mycorrhizal fungi. They report, "at elevated $CO_2$ and under both 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." In addition, they found an increase in non-AMF root colonization under elevated $CO_2$. As a result, they "hypothesize that AMF provide non-P-nutritional benefits under the phosphorus-rich soil conditions of our field experiment" and these benefits "may include improved N nutrition and increased protection against pathogens and/or herbivores."

In another long-term study conducted in Switzerland, Ainsworth *et al.* (2003b) analyzed data from what has become the longest-running FACE experiment ever conducted anywhere in the world. The impetus for their analysis was the speculation that, in their words, "elevated $CO_2$ may partition resources away from leaves and, through increased production, sequester nutrients into organic matter causing deficiencies which indirectly cause decreased photosynthetic capacity." In this regard, they cite the theoretical study of these considerations conducted by Luo and Reynolds (1999), who "predicted that the initial stimulation of photosynthetic production in grasslands would be lost within nine years of a step increase in $CO_2$, as imposed in FACE experiments."

With real-world data obtained over nearly a decade of experimentation with white clover (*Trifolium repens*) grown in monoculture in the Swiss FACE array, Ainsworth *et al.* (2003b) characterized the photosynthetic responses of the plants to the extra 240 ppm of $CO_2$ delivered to them in the spring and autumn of the eighth year of the experiment. They determined there was no acclimation or down-regulation of photosynthetic capacity in the spring of the year. In the autumn, however, there was a down-regulation of approximately 20%, but it occurred "late in the growing season, when the 24-hour mean temperature had dropped below 10°C, and nightly frosts were occurring," under which conditions "shoot growth is limited and the sink for carbohydrate is small, and acclimation of photosynthesis to elevated $CO_2$ would be expected."

In spite of that acclimation and the stress of those cold conditions, the average photosynthetic rate of the $CO_2$-enriched plants at that time of year was still 37% greater than the ambient-treatment plants. Therefore, the five scientists conclude their results "do not support the prediction that the response of grassland species to elevated $CO_2$ will be short-lived as the demand for nutrients increases." This conclusion clearly contradicts the claim of Luo and Reynolds and others' similar claims, for as Ainsworth *et al.* reiterate in the concluding sentence of their paper, "contrary to the belief that the response of grassland species to elevated $CO_2$ will be short-lived, stimulation of photosynthesis in *T. repens* remained after eight years of exposure to elevated $CO_2$."

In another report on this longest FACE study ever conducted on a grassland species, Ainsworth *et al.* (2003a) note "photosynthesis is commonly stimulated in grasslands with experimental increases in atmospheric $CO_2$ concentration, a physiological response that could significantly alter the future carbon cycle if it persists in the long term." However, they also note "an acclimation of photosynthetic capacity suggested by theoretical models and short-term experiments could completely remove this effect of $CO_2$." This suggests, in their words, "perennial systems will respond to elevated $CO_2$ in the short term, but the response for grasslands will be short-lived (Roumet *et al.*, 2000)," and they cite Luo and Reynolds (1999) as suggesting an effective $CO_2$-induced stimulatory period of less than 10 years for both high- and low-productivity grasslands.

The only way to resolve the issue is to conduct a long-term experiment—such as the sour orange tree study of Idso and Kimball (2001)—which is exactly what the eight-member Ainsworth *et al.* (2003a) team of American, British, Italian, and Swiss scientists did in its ten-year study of perennial ryegrass (*Lolium perenne*).

The study was conducted in Switzerland within three replicate blocks of two 18-m-diameter FACE rings maintained at either 360 or 600 ppm $CO_2$ throughout each growing season of the entire 10-year period. The experimental plots, established in 1993 on a field of perennial ryegrass planted in August 1992, were further subdivided into low and high nitrogen fertilization treatments, and the plants grown within them were periodically harvested several times a year. In addition, the authors write, "more than 3,000 measurements characterized the response of leaf photosynthesis and stomatal conductance to elevated $CO_2$ across each growing season for the duration of the experiment."

Ainsworth *et al.* (2003a) report, "over the 10 years as a whole, growth at elevated $CO_2$ resulted in a 43% higher rate of light-saturated leaf photosynthesis and a 36% increase in daily integral of leaf $CO_2$ uptake." The 36% increase in daily $CO_2$ uptake was, in their words, "almost identical to the 38% increase seen on the first day of measurements in August 1993 and the 39% stimulation on the last day of measurements in May 2002."

The researchers also reported a seasonal trend in the $CO_2$-induced increase in the daily integral of $CO_2$ fixation, which ranged from 25% in the spring to 41% in the summer and 48% in the fall. The scientists say this finding "is consistent with theoretical expectation, where because of the differing sensitivities of Rubisco oxygenase and carboxylase activity, the proportionate stimulation of photosynthesis by a given increase in $CO_2$ will rise with temperature (Long, 1991)." This phenomenon has also been observed in a number of other plants.

Ainsworth *et al.* (2003a) additionally note "the percentage increase in photosynthetic carbon uptake in the first 20 days following a harvest (45%) was nearly double the percentage increase later in the regrowth cycle (23%)." This finding indicates $CO_2$-induced growth stimulation is greatest when the plant source:sink ratio is small; i.e., when there are few photosynthesizing leaves and many photosynthate-storing roots, so the $CO_2$-induced enhancement of photosynthesis need not immediately decline for lack of a sufficient repository to deposit the fruits of its labors, so to speak.

Summing up, the international team of scientists says the $CO_2$-induced photosynthetic stimulation "was maximal following harvest, at the warmest times of year and with a high supply of nitrogen." They concluded, "this open-air field experiment provides no support for the prediction that stimulation of photosynthesis under elevated $CO_2$ is a transient phenomenon," or as they phrase it in the abstract of their paper, "in contrast with theoretical expectations and the results of shorter duration experiments, the present results provide no [evidence of] significant change in photosynthetic stimulation across a 10-year period, nor greater acclimation ... in the latter years in either nitrogen treatment."

The ultimate plant response is biomass production, which was studied in the same experiment by Schneider *et al.* (2004), who state, "in 1993, the $CO_2$ response of harvested biomass was 7.2%, increasing to 32% in 2002." At low N, they report the $CO_2$ response "varied annually." Nevertheless, it too exhibited a slowly increasing (though non-significant) trend, suggesting, given enough time, it might have gained statistical significance as well.

In addition, Schneider *et al.* report, "at high N supply, more N was mobilized from the soil after long-term exposure to elevated $CO_2$ than after ambient $CO_2$," in contrast to the suggestion of Hungate *et al.* (2003) that just the opposite likely would occur. At low N, the Swiss team writes, "the reduced availability of N constantly limited the harvestable biomass to elevated $CO_2$ throughout the experiment," more in harmony with Hungate *et al.*'s suggestion. This limitation may have been slightly reduced over the course of the 10-year study, and a still longer experiment may be needed to resolve the issue in the case of low-N soils.

Rasse *et al*. (2005) evaluated 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*, in a long-term *in situ* elevated $CO_2$ experiment at the Smithsonian Environmental Research Center on the USA's Chesapeake Bay. They found, in every one of the 17 years of the experiment's duration to the time of their analysis, 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 all greater than among the plants growing in ambient air. The extra $CO_2$ boosted the net $CO_2$ exchange rate 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, but whereas 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 do not appear to be leveling off.

Net $CO_2$ exchange, shoot density, and shoot biomass were closely correlated with bay water salinity in this study: the higher the salinity, the more detrimental were its effects on these variables. Nevertheless, even at the highest levels of salinity reported, atmospheric $CO_2$ enrichment was able to produce a positive, albeit reduced, stimulatory effect on 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*. note, "circumstantial evidence suggesting that salinity stress increased the stimulation of shoot density by elevated atmospheric $CO_2$ concentration."

This experiment demonstrated several important findings. 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, since 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, much more long-term research needs to be carried out in order to ascertain the full and correct impacts of atmospheric $CO_2$ enrichment on plants. In the case of the wetland sedge of this study, for example, it took ten years before an increasing trend in the shoot density could be recognized clearly. Finally, there is the authors' "most important finding": "that a species response to elevated atmospheric $CO_2$ concentration can continually increase when [it] is under stress and declining in its natural environment."

Gifford (2004) describes the findings of an international FACE workshop on *Short- and Long-Term Effects of Elevated Atmospheric $CO_2$ on Managed Ecosystems*, concentrating on a few key aspects of the aerial fertilization effect of atmospheric $CO_2$ enrichment and how it likely will be expressed in the real world as the air's $CO_2$ content rises.

He begins by noting Kimball *et al*. (2002) compared what was learned about elevated $CO_2$ effects on 11 different crops from recent FACE experiments with what had been learned from prior chamber studies, including open-top chambers. He reports Kimball *et al*. determined the FACE experiments confirmed, under longer-term field conditions and with but a couple exceptions, "all the prior quantitative chamber findings on crops grown and measured in elevated $CO_2$ concentration compared with ambient $CO_2$ concentration."

Next, Gifford notes the subsequent study of Long *et al*. (2004) confirms, "with greater statistical rigor and for a much wider range of species including crops, pasture species and trees, most of the conclusions of the evaluation by Kimball *et al*. (2002)." He reports Long presented an elegant exposition of how plants optimize "the deployment of N from photosynthetic machinery to growth organs such that a balance between C-source and C-sinks is maintained in the plant under elevated $CO_2$ concentration—a response that generally increases nitrogen use efficiency (Wolfe *et al*., 1998)." In addition, he reports, several FACE studies demonstrate an increased abundance of legumes in $CO_2$-enriched plots, and this observation "is supportive of the notion that, in the long run, elevated $CO_2$ concentration may cause N-fixation to entrain more atmospheric $N_2$ into the ecosystem, leading ultimately to fuller expression of the increased growth and standing biomass potential that the elevated $CO_2$ provides (Gifford, 1992)."

Next, in an update of the analysis of Hendry *et al*. (1997), which focused on the effects of the rapidly fluctuating atmospheric $CO_2$ concentrations characteristic of FACE experiments, the technique's primary developer (George Hendry) concluded, according to

Gifford, plant photosynthesis rates "can be decreased by 17% or more for the mean concentration reported when that mean is of large $CO_2$ fluctuations on the order of half the mean, and the deviations from the mean occur over a minute or longer." In light of this finding, Gifford writes, "FACE technology might be systematically understating the effect of globally elevated $CO_2$ on ecosystem productivity."

Gifford sums up the consensus of the participants at the FACE workshop with respect to "the $CO_2$ fertilizing effect," stating, "the evidence for its existence in the real world continues to consolidate."

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## *1.1.3.2 Woody Plants*

The aerial fertilization effect of atmospheric $CO_2$ enrichment will continue to benefit woody plants significantly.

### *1.1.3.2.1 Oak*

- Multiple-year studies point to the likelihood oak trees of all species will grow ever more productively as the air's $CO_2$ content climbs higher, and they will be better able to withstand droughty conditions and more effectively sequester carbon in the years and decades ahead.

After burning to the ground a natural scrub-oak ecosystem comprised of *Quercus myrtifolia*, *Q. chapmanii*, and *Q. geminata*, located on an island just off the coast of central Florida, USA, Ainsworth *et al.* (2002) erected 16 open-top chambers on the site and fumigated them with air of either 380 or 700 ppm $CO_2$. In the third and fourth years of the experiment, they report, the extra $CO_2$ increased photosynthetic rates in regenerating *Q. myrtifolia* and *Q. chapmanii* trees by as much as 150% without inducing any degree of photosynthetic acclimation or down-regulation. *Q. geminata* did exhibit signs of acclimation, but after three years of exposure to elevated $CO_2$, the three species still exhibited an average increase of 53% in their combined mean rate of photosynthesis.

In a subsequent analysis of other data from the same experiment, Dijkstra *et al.* (2002) evaluated the effects of elevated $CO_2$ on the growth of the three oak species by means of allometric relationships between stem diameter and aboveground biomass (AGB), which they derived from destructive measurements made on trees growing on an adjacent site. They found, in their words, "increased AGB in elevated $CO_2$ was apparent after eight months (44%), and the relative stimulation increased over time, from 55% at the end of 1997, 66% at the end of 1998, to 75% at the end of 1999." They also report at the time of the last measurement, the AGB of the dominant *Q. myrtifolia* had increased by 73%, the AGB of the subdominant *Q. geminata* had increased by only 23%, and the AGB of the subdominant *Q. chapmanni* had risen by more than 150%. With respect to individual years, they note even though the mean increase in AGB during the drought year of 1998 was 51% lower than it was during 1997 and 54% lower than in 1999, "elevated $CO_2$ significantly increased annual increment in AGB by 122% during the drought year 1998, compared to a 65% increase in 1997 and a 116% increase in 1999."

In another study of the Florida scrub-oak ecosystem, Hymus *et al.* (2003) report the extra $CO_2$ supplied to the $CO_2$-enriched chambers in their experiment increased maximum net ecosystem exchange of $CO_2$ (NEE) and the apparent quantum yield of NEE during the photoperiod. They also state 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. Hymus *et al.* additionally note their study was the largest to show "the effects of elevated $CO_2$ on NEE measured *in situ*, and is the first to be carried out in a woody ecosystem," where the beneficial effects of atmospheric $CO_2$ enrichment are "still evident after 6 years regeneration in the elevated $CO_2$."

Another way of studying the long-term effects of atmospheric $CO_2$ enrichment on trees and shrubs was pioneered by researchers in Italy, where many natural springs emit copious quantities of $CO_2$ into the air, raising atmospheric $CO_2$ concentrations over modest tracts of land by various amounts. By measuring the air's $CO_2$ content at different places around these "$CO_2$ springs" over the course of long-term experiments conducted there, mean canopy-level atmospheric $CO_2$ concentrations can be determined, and woody plants growing at those locations are typically assumed to have lived their entire lives at the measured $CO_2$ concentrations.

In a study of *Quercus ilex* trees, some growing close to, and others distant from, certain of these $CO_2$ springs, Paoletti *et al.* (1998) found, in moving from an atmospheric $CO_2$ concentration of 350 ppm to 750 ppm, leaf stomatal frequency dropped by a factor of nearly 1.5, but there were no further reductions in this parameter as the air's $CO_2$ concentration rose as high as 2,600 ppm. They also note the amount of wax comprising the leaf cuticle increased nearly threefold between 750 and 2,600 ppm $CO_2$, but between 350 and 750 ppm $CO_2$ there was no difference in this leaf property. The net effect of these several responses was thus a continuous decline in water loss from the trees as the air's $CO_2$ content continuously rose, which led to a concomitant continuous increase in their water use efficiencies.

In another study conducted in Italy in the vicinity of natural $CO_2$ springs, Stylinski *et al.* (2000) worked with *Quercus pubescens* trees grown in ambient air and at an atmospheric $CO_2$ concentration of approximately 700 ppm throughout the entire 40 to 50 years of their existence. The $CO_2$-enriched trees exhibited photosynthetic rates 36–77% greater than those of the trees growing in ambient air; and the researchers did not detect signs of any photosynthetic down-regulation in the $CO_2$-enriched trees. In fact, they found no differences between the $CO_2$-enriched and ambient-treatment trees in terms of rubisco activity and content, total nitrogen content, chlorophyll content, and carotenoid content. As a result, they conclude "enhanced leaf photosynthetic rates at the $CO_2$ springs could increase carbon sequestrating and productivity of whole tree canopies" and "higher carbon acquisition by *Q. pubescens* and other species could slow the rise in atmospheric $CO_2$."

Blaschke *et al.* (2001) also studied gas exchange in mature *Q. pubescens* and *Q. ilex* trees exposed to atmospheric $CO_2$ concentrations of approximately 370 and 700 ppm for their entire lives. The average net photosynthetic rates of the $CO_2$-enriched trees were, respectively, 69% and 26% greater than those of the trees growing in ambient air. In addition, the stomatal conductances of the $CO_2$-enriched *Q. pubescens* trees were approximately 23% lower than those of trees of the same species growing in ambient air, and the $CO_2$-enriched *Q. ilex* trees displayed no stomatal response to elevated $CO_2$. Nevertheless, both species exhibited significant $CO_2$-induced increases in water use efficiency.

One less-than-ideal aspect of the Italian $CO_2$ springs is that they emit higher-than-normal concentrations of the phytotoxic air pollutants $H_2S$ and $SO_2$ (Schulte *et al.*, 1999). This fact, however, makes the springs perfect settings in which to study the relative strengths of two competing phenomena: the growth-promoting effect of elevated $CO_2$ and the growth-retarding effect of elevated $H_2S$ and $SO_2$.

Grill *et al.* (2004) analyzed various properties of leaves and acorns produced on *Q. ilex* and *Q. pubescens* trees growing at double-to-triple normal atmospheric $CO_2$ concentrations near the $CO_2$ springs, as well as the same characteristics of leaves and acorns growing on similar trees located some distance away in ambient-$CO_2$ air. In addition, they 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 sulphur-regime have negative consequences for seedlings."

In reporting their findings, Grill *et al.* say "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 affected by the $H_2S$ and $SO_2$ contained in the air in the vicinity of the $CO_2$ springs. They also report *Q. ilex* seedlings grown from $CO_2$-spring acorns showed elevated rates of chromosomal aberrations in their root tips, suggesting the presence of a permanent pollution-induced stress. Nevertheless, as demonstrated by the results of several other studies conducted near the springs, the $CO_2$-enriched air—even in the presence of phytotoxic $H_2S$ and $SO_2$—significantly enhanced the trees' photosynthetic prowess: by 26–69% in the study of Blaschke *et al.* (2001), by 36–77% in the study of Stylinski *et al.* (2000), and by 175–510% in the study of Tognetti *et al.* (1998).

In a study in Italy that did not make use of natural $CO_2$ springs, Marek *et al.* (2001) constructed open-top chambers around 30-year-old *Q. ilex* trees growing in perennial evergreen stands and continuously exposed them to atmospheric $CO_2$ concentrations of 350 and 700 ppm for five more years. Throughout this period, the extra $CO_2$ increased rates of net photosynthesis in Sun and shade leaves by 68% and 59%, respectively, and photosynthetic acclimation was not apparent in any of the $CO_2$-enriched trees' leaves. In addition, the light compensation point—the light intensity at which photosynthetic carbon uptake is equivalent to respiratory carbon loss—was 24% and 30% lower in the Sun and shade leaves of the $CO_2$-enriched trees than in the corresponding leaves of trees growing in ambient air. These findings suggest *Q. ilex* trees growing in $CO_2$-enriched air should exhibit net carbon gains earlier in the morning and maintain them later into the evening than trees exposed to ambient air. Together with the stimulatory effect of higher $CO_2$ concentrations on photosynthesis, this observation further suggests carbon sequestration by this tree species will likely be much greater in a higher-$CO_2$ world of the future.

Although all of the reports described above imply the ongoing rise in the air's $CO_2$ content will do only good to the long-term growth and health of oak trees, Gartner *et al*. (2003) were concerned the wood of the trees might be more vulnerable to embolism in a $CO_2$-enriched atmosphere. They investigated this question with *Quercus ilex* seedlings grown for more than a year in climate-controlled greenhouses in either ambient air or air enriched to twice the ambient concentration of $CO_2$. Contrary to their hypothesis, they found the "plants grown in elevated $CO_2$ did not differ significantly in vulnerability to embolism or kS [specific conductivity] from plants grown in ambient $CO_2$." In addition, they report "Tognetti *et al*. (1999) found no significant effect of elevated $CO_2$ on vulnerability to embolism or kS of branch samples from *Q. ilex* trees growing near $CO_2$ vents compared with trees growing at normal ambient $CO_2$."

In one final study conducted under entirely natural, real-world conditions, Waterhouse *et al*. (2004) determined the intrinsic water use efficiency (IWUE) responses of three tree species growing across northern Europe—one of which was pedunculate oak (*Quercus robur*) growing at three sites in England and two sites in Finland—to the increase in atmospheric $CO_2$ concentration experienced between 1895 and 1994, using parameters derived from measurements of stable carbon isotope ratios of tree-ring cellulose. They report "all species at all the sites show a long-term increase in their values of IWUE during the past century," noting "the main cause of this common behavior is likely to be the increase in atmospheric $CO_2$ concentration."

Linearly extrapolating these responses (which occurred over a period of time when the air's $CO_2$ concentration rose by approximately 65 ppm) to what would be expected for the more common 300 ppm increase employed in the majority of atmospheric $CO_2$ enrichment experiments, the IWUE increase Waterhouse *et al*. observed for *Q. robur* amounted to 158 ± 14%, as best as can be determined from the graphs of their results. A response of this magnitude is probably not due to rising $CO_2$ alone, but instead to the positive synergism that occurs when atmospheric $CO_2$ and temperature rise together (see Section 3.13, Temperature Stress, in Chapter 3), as these parameters have done over the past century or so, clearly demonstrating high temperatures and high $CO_2$ concentrations benefit plants.

The findings of the several papers reviewed above point to the likelihood oak trees of all species will grow more productively as the air's $CO_2$ content climbs higher, will likely be better able to withstand droughty conditions, and will more effectively sequester carbon in the years and decades ahead.

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### *1.1.3.2.2 Pine*

It is important to know how Earth's trees will respond to the ongoing rise in the air's $CO_2$ content over the long-term; the only way to obtain such knowledge is to enrich the air in which they grow in long-term experiments. The following subsections review what has been learned in this regard with respect to various pine tree species.

#### 1.1.3.2.2.1 Loblolly

- The "aerial fertilization effect" of atmospheric $CO_2$ enrichment will continue to significantly benefit Earth's loblolly pine forests as the atmosphere's $CO_2$ concentration rises.

In what was originally considered a long-term study, Tissue *et al.* (1997) grew loblolly pine seedlings for four years in open-top chambers maintained at atmospheric $CO_2$ concentrations of 350 and 650 ppm. Throughout the summers of this experiment, the seedlings in the $CO_2$-enriched chambers displayed photosynthetic rates 60 to 130% greater than those of the seedlings growing in ambient air, and during the colder winter months, they exhibited photosynthetic rates 14 to 44% greater. These persistent increases in the rate of net carbon uptake increased biomass accumulation rates in the $CO_2$-enriched seedlings by fully 90%, prompting the scientists conducting the study to declare loblolly pines growing in a $CO_2$-enriched world of the future "could be a large sink for fossil fuel carbon emitted to the atmosphere."

In another study of the same trees, Telewski *et al.* (1999) report elevated $CO_2$ did not significantly affect anatomical features of xylem cells, including their cell wall to cell interior ratio, resin canal area, and resin canal density, but it did significantly increase annual growth-ring widths by 93, 29, 15, and 37% during the four consecutive years of the study. Also, although not significantly so, the extra $CO_2$ increased average ring density in the same four years by 60, 4, 3, and 5%, leading the researchers to state, "projected increases in the atmospheric content of $CO_2$ may result in increased wood production without a loss in structural strength." The tendency for wood density to increase in $CO_2$-enriched air portends the possibility of increased structural strength in the years ahead.

By far the longest study of loblolly pines was the free-air $CO_2$ enrichment (FACE) experiment conducted at Duke Forest in the Piedmont region of North Carolina, USA, where in August 1996 three 30m-diameter $CO_2$ delivery rings began to enrich the air around the 13-year-old trees they encircled to 200 ppm above the atmosphere's ambient $CO_2$ concentration, and three other FACE rings served as ambient-air control plots, as described by Hendrey *et al.* (1999).

In this study, LaDeau and Clark (2001) report, by the fall 1999 the $CO_2$-enriched trees "were twice as likely to be reproductively mature and produced three times more cones per tree." Similarly, the trees growing in the $CO_2$-enriched air produced 2.4 times more cones in fall 2000. From August 1999 through July 2000, the two scientists also collected three times as many seeds in the $CO_2$-enriched FACE rings as they did in the ambient-air control rings.

LaDeau and Clark note naturally regenerated loblolly pine stands of the southeastern United States "are profoundly seed-limited for at least 25 years." Thus, as the air's $CO_2$ content rises, the researchers state, "this period of seed limitation may be reduced," which is more good news about this highly prized tree, in addition to the fact, according to William Schlesinger, codirector of the Duke project (Tangley, 2001), "trees in the high-$CO_2$ plots grew 25% faster than controls did during the first three growing seasons of the experiment."

One year later, Finzi *et al.* (2002) report over the first four years of differential $CO_2$ exposure in this study, the trees in the $CO_2$-enriched plots maintained average yearly rates of dry matter production 32% greater than the trees growing in ambient air. The average uptake of nitrogen from the soil was enhanced by 28% in the $CO_2$-enriched plots, and the $CO_2$-enriched trees displayed a 10% increase in nitrogen-use efficiency.

Several other papers dealing with various aspects of the experiment were published about the same time. As recounted by Luo *et al.* (2003), these analyses reveal the existence of a $CO_2$-induced "sustained photosynthetic stimulation at leaf and canopy levels [Myers *et al.*, 1999; Ellsworth, 2000; Luo *et al.*, 2001; Lai *et al.*, 2002], which resulted in sustained stimulation of wood biomass increment [Hamilton *et al.*, 2002] and a larger carbon accumulation in the forest floor at elevated $CO_2$ than at ambient $CO_2$ [Schlesinger and Lichter, 2001]." Based upon these findings and what they imply about rates of carbon removal from the atmosphere and its different residence times in plant, litter, and soil carbon pools, Luo *et al.* (2003) developed a model for studying the sustainability of carbon sequestration in forests. Applying this model to a situation where the atmospheric $CO_2$ concentration gradually rises from a value of 378 ppm in 2000 to a value of 710 ppm in 2100, they calculated the carbon sequestration rate of the Duke Forest would rise from an initial value of 69 g $m^{-2}$ $yr^{-1}$ to a final value of 201 g $m^{-2}$ $yr^{-1}$.

Schafer *et al.* (2003) linked a leaf-level $CO_2$ assimilation model (Katul *et al.*, 2000) with a light attenuation model (Campbell and Norman, 1998; Stenberg, 1998) and measurements of sap-flux-based canopy conductance (Kostner *et al.*, 1992; Ewers and Oren, 2000) to create what they call a canopy conductance-constrained $CO_2$ assimilation model, which they tested with measurements of net ecosystem exchange and net ecosystem production in the ambient and $CO_2$-erniched plots of the Duke Forest FACE study. They then used it to assess the effects of elevated $CO_2$ on carbon uptake and allocation to different components of the forest's carbon budget under ambient and $CO_2$-enriched conditions. They report during the third and fourth years of the study, the extra 200 ppm of $CO_2$ supplied to the $CO_2$-enriched FACE plots increased the uptake of $CO_2$ by 39% in the dominant *Pinus taeda* L. trees.

These results were most impressive. However, many scientists at that time questioned whether the productivity gains associated with $CO_2$ enrichment would persist in the long term. Even Schafer *et al.* suggested "if nutrient limitation imposes a constraint on future productivity," as was widely believed would be the case, "it is likely that carbon allocation to the production of wood will decrease in favor of the allocation to fine root production, rhizodeposition, and mycorrhizal symbionts," citing Norby *et al.* (1992, 2001). They further suggested this decrease could "result in a rapid return of fixed carbon to the atmosphere (Merbach *et al.*, 1999)," and thus, "high rates of carbon fixation under elevated $CO_2$ will result in an acceleration of the carbon cycle through the forest ecosystem with little of the carbon remaining in long-term storage pools."

Indeed, it was well-accepted that the productivity of Earth's temperate forests was limited by the availability of soil nitrogen (Vitousek and Howarth, 1991). This was especially believed to be the case in the southeastern United States, where pine-hardwood forests often remove so much nitrogen from the soils in which they grow that they induce what Finzi and Schlesinger (2003) describe as "a state of acute nutrient deficiency that can only be reversed with fertilization." It would seem only natural, therefore, to presume (as they hypothesized in the early stages of the Duke Forest FACE study) "the increase in carbon fluxes to the microbial community under elevated $CO_2$ would increase the rate of nitrogen immobilization over mineralization," which would ultimately lead to a decline in—and perhaps the total negation of—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).

To test this hypothesis, Finzi and Schlesinger (2003) measured and analyzed the 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 in the Duke Forest FACE study, where half the plots were fumigated to maintain a mean $CO_2$ concentration 200 ppm above ambient. They report the extra $CO_2$ "significantly increased the input of carbon and nitrogen to the forest floor and the mineral soil." Nevertheless, the researchers state "there was no statistically significant change in the cycling rate of nitrogen derived from soil organic matter under elevated $CO_2$." Indeed, "neither the rate of net nitrogen mineralization nor gross $^{15}NH_4^+$ dynamics were significantly altered by elevated $CO_2$." In addition, they acknowledge "there was no statistically significant difference in the concentration or net flux of organic and inorganic nitrogen in the forest floor and top 30-cm of mineral soil after five years of $CO_2$ fumigation," concluding "microbial biomass was not a larger sink for nitrogen."

On the basis of these results from the first five years of the Duke Forest FACE study, Finzi and Schlesinger rejected their original hypothesis that elevated levels of atmospheric $CO_2$ would significantly increase the rate of nitrogen immobilization by the microbial community, although they contend "elevated $CO_2$ will only increase the productivity of this forest during the initial stages of stand development, with nitrogen limitation constraining additional carbon sequestration under elevated $CO_2$ well before this stand reaches its equilibrium biomass."

Crous and Ellsworth (2004) measured the photosynthetic rates of different-age needles at different crown positions on the loblolly pine trees at the Duke Forest FACE facility in the sixth year of the study, and then compared their results with the results of similar measurements made over the prior five years. Although they report there was "some evidence of moderate photosynthetic down-regulation ... in 1-year-old needles across the fifth to sixth year of $CO_2$ exposure," the two researchers state "strong photosynthetic enhancement in response to elevated $CO_2$ (e.g., +60% across age classes and canopy locations) was observed across the years."

Also at the conclusion of the sixth year of the study, Lichter *et al.* (2005) reviewed what had been learned about the effects of the extra $CO_2$ on the soil carbon dynamics of Duke Forest. Their work revealed, since the beginning of the study, organic carbon accumulated in the forest floor of the elevated $CO_2$ plots at a rate $52 \pm 16$ g C $m^{-2}$ $yr^{-1}$ greater than expected during reforestation under ambient $CO_2$ conditions, as represented by the rate of carbon accumulation in the forest floor of the ambient $CO_2$ plots. This additional carbon sink, in the words of the researchers, "resulted from increased carbon inputs of $50 \pm 30$ g C $m^{-2}$ $yr^{-1}$ to the forest floor in response to $CO_2$ enhancement of primary production." And since there was "no evidence that the overall rate of decomposition of the forest floor decreased under the elevated $CO_2$ treatment," they conclude "the additional carbon sink in the forest floor of the elevated $CO_2$ treatment ... is wholly dependent on the net primary production enhancement and increased carbon inputs," which after a total of six years had increased the forest floor's organic carbon content by approximately 27%, as best as can be determined from their plotted data. In addition, the data gave no indication this trend was on the verge of declining anytime soon.

With respect to the underlying mineral soil, Lichter *et al.* said they could detect no statistically significant treatment effects on the carbon content of the bulk mineral soil or the intra-aggregate particulate organic matter and mineral-associated organic matter fractions after six years of $CO_2$ enrichment. Nevertheless, there was a nearly statistically significant ($P = 0.11$) increase of 18.5% in the free light fraction of the organic matter in the top 15 cm of the soil profile, as well as a 3.9% increase in the total intra-aggregate particulate organic matter there. The sum of the organic carbon in these two different categories plus the mineral-associated organic carbon was 11.5% greater in the $CO_2$-enriched plots than in the ambient treatment plots.

Although the scientists remained pessimistic and continued to assert "forest soils are unlikely to sequester significant additional quantities of atmospheric carbon associated with $CO_2$ fertilization because of the low rates of carbon input to refractory and protected soil organic matter pools," the $CO_2$-enriched trees of their study continued to demonstrate a large and unabated growth advantage over the ambient-$CO_2$ trees. In addition, both the forest floor and the surface soil horizon beneath the $CO_2$-enriched trees continued to accumulate more organic carbon than the forest floor and surface soil horizon beneath the ambient-$CO_2$ trees.

LaDeau and Clark (2006) determined the reproductive responses (cone and seed production) of the loblolly pine trees at the Duke Forest FACE site to atmospheric $CO_2$ enrichment. They state, "carbon dioxide enrichment affected mean cone production both through early maturation and increased fecundity," such that "trees in the elevated $CO_2$ plots produced twice as many cones between 1998 and 2004 as trees in the ambient plots." They also report trees grown in elevated $CO_2$ "made the transition to reproductive maturation at smaller [trunk] diameters," and they "not only reached reproductive maturation at smaller diameters, but also at younger ages." By 2004, for example, "roughly 50% of ambient trees and 75% of fumigated trees [had] produced cones." In addition, they observe, "22% of the trees in high $CO_2$ produced between 40 and 100 cones during the study, compared with only 9% of ambient trees."

The two scientists say their findings indicate their previously documented "short-term responses indeed persist," contradicting the opinions of those who downplay the biological benefits of atmospheric $CO_2$ enrichment. Furthermore, noting "*P. taeda* trees that produce large seed crops early in their life span tend to continue to be prolific producers (Schultz, 1997)," they conclude "individual responses seen in this young forest may be sustained over their life span."

At the eight-year point of the long-term FACE experiment, Moore *et al.* (2006) conducted a study that represented a turning point in most scientists' thinking about what had come to be known as the Progressive Nitrogen Limitation hypothesis. They analyzed measurements of the basal areas of the trees' trunks at approximately 1.4 m above ground level made at monthly intervals since the inception of the experiment. This work revealed, in response to the 50% increase in atmospheric $CO_2$ concentration employed in the Duke Forest FACE study, there was "a sustained increase in basal area increment over the first 8 years of the experiment" that varied between 13 and 27% with variations in weather and the timing of growth. In addition, the six scientists found "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 amazed many researchers (including several who were working on the experiment themselves), considering the low-fertility state of the soil in which the experiment was being conducted. Nevertheless, and despite many researchers' presumptions the $CO_2$-induced growth stimulation of long-lived woody plants would gradually (and drastically) decline over time, there was no evidence that was occurring in the Duke Forest FACE study. The trees kept growing at a significantly elevated rate, even when nutrient limitations would have been expected to have kept them from doing so.

Two years later, Pritchard *et al.* (2008a) used minirhizotrons to characterize the fine root development of the trees from autumn 1998 through autumn 2004. Averaged over all six years of the study, they found the extra 200 ppm of $CO_2$ increased average fine-root standing crop by 23%, in good agreement with the stimulation of the forest's net primary productivity of 18–24% observed over the period 1996–2002.

The nine researchers write, "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)," providing once again no hint of progressive nitrogen limitation of the stimulatory effect of atmospheric $CO_2$ enrichment in a situation where one might have expected to have encountered it. In partial explanation of this finding, Pritchard *et al.* note 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." Nearly all evidence obtained to date suggests trees can indeed sustain a significant $CO_2$-induced increase in net primary productivity over the long term, and the reason they can do so may reside in the $CO_2$-induced stimulation of the growth of their important fine-root tips, as suggested by Pritchard *et al.*

In a related contemporaneous paper, Pritchard *et al.* (2008b) state data from long-term FACE experiments "have yet to provide convincing evidence in support of the progressive nitrogen limitation hypothesis." They report exposure to elevated concentrations of atmospheric $CO_2$ had increased net primary productivity by 59%, 24%, 23%, and 30% at the Rhinelander, Wisconsin (USA), Oak Ridge National Laboratory (USA), Tuscania (Italy), and Duke, North Carolina (USA) FACE sites, respectively, "with little evidence to indicate a diminished response through time," citing Finzi *et al.* (2007).

The leading hypothesis to explain these sustained high growth responses had been that atmospheric $CO_2$ enrichment leads to greater fine-root production and increased allocation of carbon to ectomycorrhizal fungi living in symbiotic association with plant roots, a dual phenomenon that leads to (1) the exploration of a greater volume of soil by plants in search of much-needed nitrogen, and (2) a more thorough search of each unit volume of soil. Consequently, Pritchard *et al.* (2008b) focused their attention on the role played by ectomycorrhizal fungi for five years in the Duke Forest FACE study.

Summed across all years of the study, the five researchers found the extra 200 ppm of $CO_2$ enjoyed by 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. In addition, the production of soil rhizomorph length was 27% greater in $CO_2$-enriched plots than in the ambient-air plots.

In discussing their findings, Pritchard *et al.* note 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 study amounts to approximately 12 g N per $m^2$ per year and is well above estimated rates of N acquisition by the combined phenomena of N deposition, heterotrophic N fixation, and net N mineralization, which range from 3.4 to 6.0 g N per $m^2$ per year, as per Finzi *et al.* (2006, 2007), Hofmockel and Schlesinger (2007), and Hofmockel *et al.* (2007). Consequently, in concluding their commentary on the results of their work, Pritchard *et al.* 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 nitrogen-limited ecosystems more than previously expected."

Jackson *et al.* (2009) describe belowground data they obtained at the Duke Forest FACE site, then present a synthesis of these and other results obtained for the years 1996 through 2008, to determine "which, if any, variables show evidence for a decrease in their response to atmospheric $CO_2$ during that time frame." Their analyses indicate, among many other things, "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 $CO_2$." In terms of coarse roots having 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 $CO_2$." From the graphical representation of their results, it can be calculated the coarse-root biomass was fully 130% greater, which is astounding, particularly since 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. In the concluding sentence of their paper's abstract, Jackson *et al.* state, "overall, the effect of elevated $CO_2$ belowground shows no sign of diminishing."

In discussing their findings, the four researchers write, "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 "in fact 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," even "after more than a decade of manipulation" of the air's $CO_2$ content, citing—with respect to the latter portion of their statement—Finzi *et al.* (2007).

These most recent findings, plus all that preceded them, indicate there are many extremely well-documented observational—as opposed to theoretical—reasons to conclude the "aerial fertilization effect" of atmospheric $CO_2$ enrichment will significantly benefit Earth's forests as the atmosphere's $CO_2$ concentration rises.

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### 1.1.3.2.2.2 Scots

- Evidence gleaned from multiyear studies suggests the historical rise in the atmosphere's $CO_2$ concentration has significantly enhanced the growth and well-being of Scots pine trees over the past century or more and will likely do the same for them in decades yet to come.

Researchers planted three-year-old pot-grown Scots pine (*Pinus sylvestris* L.) seedlings in the ground in four open-top chambers at the University of Antwerp in Belgium on 21 March 1996, and they continuously maintained them at atmospheric $CO_2$ concentrations of either 350 or 750 ppm, to determine the long-term effects of elevated $CO_2$ on various aspects of the growth and development of this important timber species, as described by Jach and Ceulemans (1999). To make the experimental results as representative as possible of the natural world, no nutrients or irrigation waters were applied to the soils during the entire period of the investigation.

During the second year of the study, Jach and Ceulemans (2000a) discovered the photosynthetic rates of current and one-year-old $CO_2$-enriched needles were 62 and 65% greater, respectively, than the photosynthetic rates of comparable needles on seedlings growing in ambient air. Simultaneously, Jach and Ceulemans (2000b) found dark respiration rates expressed on a needle-mass basis were 27 and 33% lower in current-year and one-year-old needles, respectively, on the $CO_2$-enriched trees than on the ambient-treatment trees. After three years of differential $CO_2$ exposure, Jach *et al.* (2000) determined the extra $CO_2$ of the study had increased total seedling biomass production by 55%, even though the experimental soils were relatively nutrient-poor.

Possibly to compensate for this deficiency of nutrients, Jach *et al.* found the elevated $CO_2$ had increased root biomass by more than 150%, which would likely have enhanced the ability of the $CO_2$-enriched seedlings to explore a greater volume of soil for the nutrients they required to sustain their augmented growth and development. The three researchers conclude, "it is likely that on nutrient-poor forest sites valuable gains to the timber industry may be achieved under future climatic conditions, since increased root production may enhance both nutrient availability, and hence timber production, as well as increase wind stability."

At the three-year point of the study, Gielen *et al.* (2000) determined elevated $CO_2$ did not significantly impact the photochemical quantum efficiency of photosystem II, nor did it affect any parameters associated with chlorophyll fluorescence, suggesting atmospheric $CO_2$ enrichment did not modify the light-dependent reactions of photosynthesis. They did find, however, elevated $CO_2$ reduced needle nitrogen and chlorophyll contents by 33 and 26%, respectively, although these reductions were statistically insignificant. Nonetheless, these latter observations suggest the light-independent reactions of photosynthesis were being modified by long-term exposure to elevated $CO_2$ in a manner indicating photosynthetic acclimation that allows for the redistribution of limiting resources, such as nitrogen, to other areas of the tree where they may be more needed.

At the four-year point of the study, Lin *et al.* (2001) found elevated $CO_2$ reduced needle stomatal density by an average of 7.4% while increasing needle thickness, mesophyll tissue area, and total cross-sectional area by 6.4, 5.7, and 10.4%, respectively. In addition, atmospheric $CO_2$ enrichment increased the average relative area occupied by phloem cells by 4.4%. The first of these observations suggests Scots pine trees will be better able to conserve water and cope with periods of drought in a future high-$CO_2$ world. In addition, the increase in mesophyll tissue portends an increase in photosynthetic rates, and the increase in phloem cell area suggests a greater capacity for transport of photosynthetic sugars from needles to actively growing sink tissues.

Finally, Waterhouse *et al.* (2004) determined the intrinsic water use efficiency response of Scots pines growing in South Bedfordshire in England to the increase in the air's $CO_2$ content between 1895 and 1994, using parameters derived from measurements of stable carbon isotope ratios of tree-ring cellulose. The found there was a long-term increase in intrinsic water use efficiency during the prior century, and the main cause of this behavior was likely "the increase in atmospheric $CO_2$ concentration."

Linearly extrapolating the response (which occurred over a period of time when the air's $CO_2$ concentration rose by approximately 65 ppm) to what would be expected for a 300 ppm increase, the intrinsic water use efficiency increase they derived amounts to 195%, as best as can be determined from the graphs of their results. This substantial response is probably not due to the rising $CO_2$ alone but to the positive synergism that occurs when atmospheric $CO_2$ and temperature rise together.

The evidence gained from the last of these multiyear studies suggests the historical rise in the atmosphere's $CO_2$ concentration has significantly enhanced the growth and well-being of Earth's Scots pine trees over the past century or more, and the evidence of the other studies suggests the ongoing rise in atmospheric $CO_2$ (and possibly temperature as well) will likely do the same for decades yet to come.

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### 1.1.3.2.2.3 Other Pine Trees

- Aleppo and Shortleaf pines will likely experience greatly enhanced growth and development as the atmospheric $CO_2$ content continues its upward trajectory.

Clues to how Earth's trees will respond to future increases in atmospheric $CO_2$ concentration may be obtained from studies of how they have responded to historical increases in the air's $CO_2$ content. This section reviews what has been learned for two less-analyzed species of pine tree: Aleppo pine (*Pinus halepensis* Mill.) and Shortleaf pine (*Pinus echinata* Mill.).

Rathgeber *et al.* (2003) used tree-ring width and density chronologies (in both earlywood and latewood) from 21 stands of Aleppo pines in the Provence region of southeast France to calibrate the BIOME3 biogeochemistry model of forest productivity in terms of growth responses to known historical changes in atmospheric temperature, precipitation, and $CO_2$ concentration. They then used the calibrated model to calculate changes in the mean productivity of the same forest stands that could be expected to result from changes in these parameters driven by a doubling of the air's $CO_2$ content, as calculated by Meteo-France's ARPEGE atmospheric general circulation model when downscaled to that specific part of the country.

In response to the predicted changes in climate, forest productivity increased moderately for all stands (17% to 24%), and in response to the aerial fertilization effect of the doubling of the air's $CO_2$ content, it rose considerably more (72% to 86%). Even more impressively, when the climatic changes and atmospheric $CO_2$ increase were considered together, forest productivity increased still more (107% to 141%).

This latter response range is even greater than what is implied by the sum of the individual responses, due to the amplifying synergy of the atmospheric compositional and climatic factors on basic plant physiological processes. Therefore, the researchers conclude, "although the detected effects of global change during the 20th century were slight, acceleration of these changes is likely to lead to great changes in the future productivity of *P. halepensis* forests." Their study suggests a doubling of the air's $CO_2$ content could more than double the growth of Aleppo pine forests in southeast France.

Working with Shortleaf pine in the Ozark Mountains of Missouri, USA, Voelker *et al*. (2006) cross-dated a large number of increment cores and aligned the ring-width data by pith date for accurate age-constant assessments of growth over the past 150 years, thereby circumventing "changes in growth trend associated with differences in physiological functioning during development, as well as the need for statistical detrending that removes an unknown degree of long-term environmental signal, the so-called segment length curse that applies to standard dendrochronological investigations." In addition, they similarly analyzed previously acquired data for Shortleaf pine stretching back to nearly AD 1600. Since 1850, the stem growth of the trees rose "coincidently with increases in atmospheric $CO_2$," such that the overall trend in ring-width in recent years is "nearly two times that" experienced prior to 1850. In addition, "long-term increases in radial growth appear unrelated to historical disturbance levels for the region, to long-term changes in relevant climatic variables, or to productivity of sites sampled." Consequently, the four Department of Forestry researchers from the University of Missouri (USA) conclude the rising atmospheric $CO_2$ concentration—aided by continued nitrogen deposition—will likely "stimulate further increases in the rates of stand development and carbon storage."

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### *1.1.3.2.3 Sour Orange*

- The long-term equilibrium response of sour orange trees to a 75% increase in the air's $CO_2$ concentration after 17 years of study was a $CO_2$-enriched/ambient-treatment biomass ratio of 1.69 for all above-ground parts of the trees (other than fruit), 1.85 for the cumulative amount of biomass due to fruit production, and 1.07 for the vitamin C content of the fruit (though this latter ratio was based on samples from the fourth through the 12th years of the experiment only).

In July 1987, as described by U.S. Department of Agriculture researchers Idso and Kimball (2001), eight 30-cm-tall sour orange tree (*Citrus aurantium* L.) seedlings were planted directly into the ground at the Agricultural Research Service's U.S. Water Conservation Laboratory in Phoenix, Arizona, where they were enclosed in pairs within four clear-plastic-wall open-top chambers. In November of that year, the two scientists began to continuously pump ambient air through two of the chambers via perforated plastic tubes that lay upon the ground beneath the trees, and through the other two chambers they pumped air enriched with carbon dioxide to a concentration 300 ppm greater than the surrounding ambient air, which had an average $CO_2$ concentration of 400 ppm. Thus began one of the longest atmospheric $CO_2$ experiments ever conducted anywhere in the world.

Throughout the experiment, the Phoenix global-change research team irrigated and fertilized the trees according to standard agronomic practices in the area, to keep them as free as possible from water and nutrient stresses. They measured the circumferences of the trees' trunks at a height of 45 cm above the surface of the ground at the midpoint of every month. At the end of the second and third years of the study, they also determined the total trunk and branch volume of each tree from trunk and branch length and diameter measurements. From these data they developed a relationship between trunk cross-sectional area and trunk plus branch volume that applied equally well to the $CO_2$-enriched and ambient-treatment trees. Then they made numerous wood density measurements that allowed them to calculate the total aboveground woody biomass of each tree at the midpoint of every month. In addition, all the oranges produced by the trees were picked, counted, and weighed each year, and a large number of the fruit were dried in ovens to determine the amount of dry matter they contained. The two researchers thus developed a yearly record of total fruit biomass production to accompany their monthly record of wood biomass production.

As the experiment progressed, the $CO_2$-enriched/ambient-treatment ratio of cumulative aboveground wood biomass rose rapidly from an initial value of unity to a value slightly greater than 3.0 at the two-year point of the study, as shown in Figure 1.1.3.2.3.1, which depicts the changing ratio of the aboveground wood biomass of the $CO_2$-enriched trees to the ambient-treatment trees over the first two years of the study.

From the data of Figure 1.1.3.2.3.1, it could reasonably be assumed the $CO_2$-enriched/ambient-treatment wood biomass ratio might rise a little higher but would have to level off sometime soon. Hence, the researchers decided to continue collecting data to determine the long-term asymptotic growth response of the trees. After seven additional months, they obtained the results depicted in Figure 1.1.3.2.3.2.

To the researchers' surprise, the wood biomass ratio not only did not rise any higher, or even level out, it began a steep decline. Projecting forward in time, it appeared a continuation of the new trend could result in all the biomass advantage acquired by the $CO_2$-enriched trees possibly disappearing altogether over the next couple of years. To continue the experiment, they obtained the additional data depicted in Figure 1.1.3.2.3.3.

The results portrayed in Figure 1.1.3.2.3.3 were enlightening. They suggest, after an initial "overshoot" of the long-term response of the trees to atmospheric $CO_2$ enrichment, things finally settled down and a final answer was obtained: The ultimate equilibrium response of the trees was a 150% increase in wood biomass production in response to the 75% increase in the air's $CO_2$ concentration. The research team continued collecting data, only to be surprised once again as depicted in Figure 1.1.3.2.3.4.

The results portrayed in Figure 1.1.3.2.3.3 were enlightening. They suggest, after an initial "overshoot" of the long-term response of the trees to atmospheric $CO_2$ enrichment, things finally settled down and a final answer was obtained: The ultimate equilibrium response of the trees was a 150% increase in wood biomass production in response to the 75% increase in the air's $CO_2$ concentration. The research team continued collecting data, only to be surprised once again as depicted in Figure 1.1.3.2.3.4.

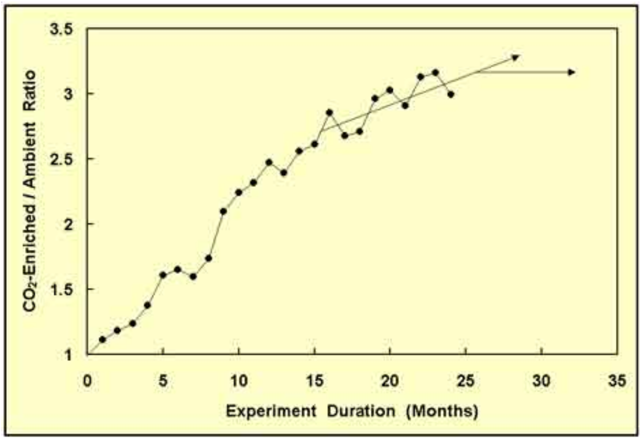

**Figure 1.1.3.2.3.1.** The $CO_2$-enriched/ambient-treatment ratio of total aboveground sour orange tree wood biomass plotted as a function of time since the start of the experiment, along with arrows that depict two logical projections of what might happen to this ratio if the experiment were continued beyond the last point shown. Adapted from Idso and Kimball (2001).

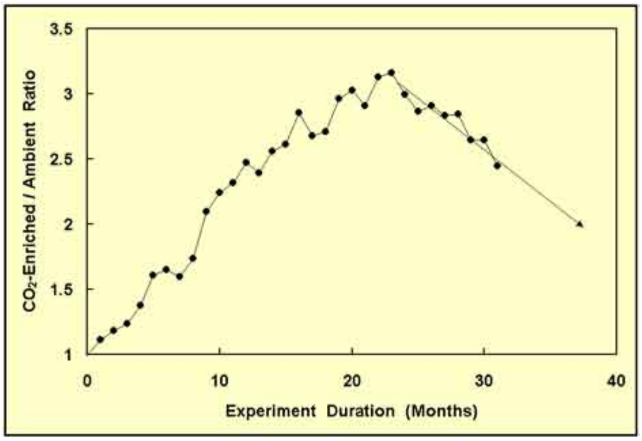

**Figure 1.1.3.2.3.2.** Same as Figure 1.1.3.2.3.1, but with seven additional months of data and a new forward projection of the $CO_2$-enriched/ambient-treatment wood biomass ratio. Adapted from Idso and Kimball (2001).

After having maintained a near-constant value for more than a year and a half, the wood biomass ratio began to decline again, as shown in Figure 1.1.3.2.3.4 not as rapidly as it had the first time, but at a still substantial rate. As it dropped ever-lower, the researchers decided to continue collecting data, which yielded the results depicted in Figure 1.1.3.2.3.5.

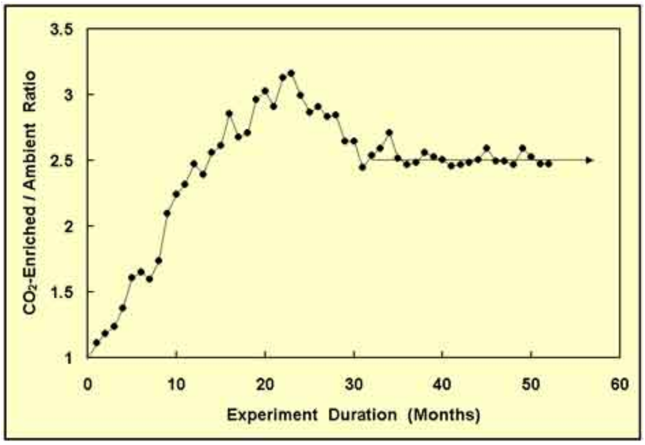

**Figure 1.1.3.2.3.3.** Same as Figure 1.1.3.2.3.2, but with 21 additional months of data and a new forward projection of the wood biomass ratio. Adapted from Idso and Kimball (2001).

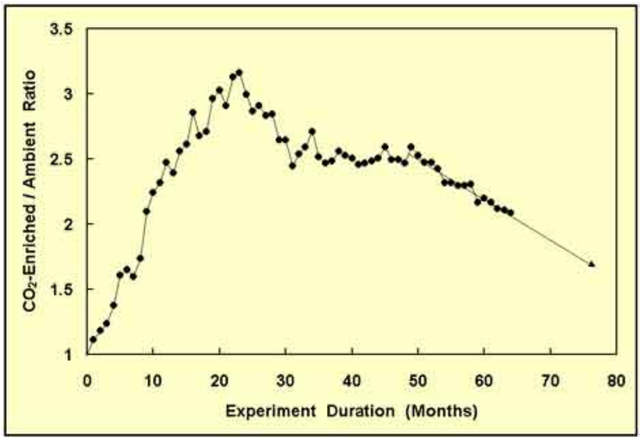

**Figure 1.1.3.2.3.4.** Same as Figure 1.1.3.2.3.3, but with 12 more months of data and yet another forward projection of the $CO_2$-enriched/ambient-treatment wood biomass ratio. Adapted from Idso and Kimball (2001).

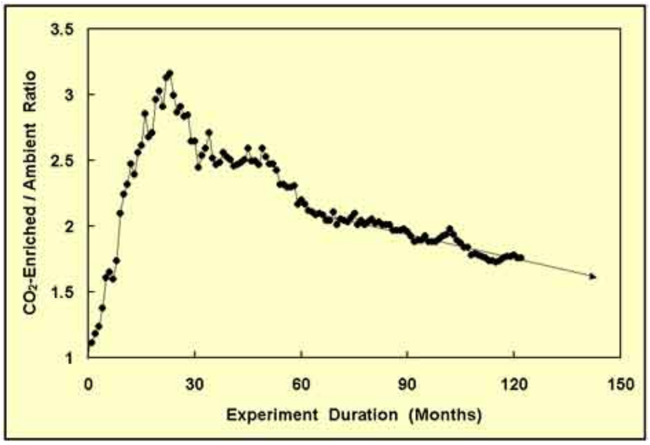

**Figure 1.1.3.2.3.5.** Same as Figure 1.1.3.2.3.4, but with 58 months of additional data and one more projection of the $CO_2$-enriched/ambient-treatment wood biomass ratio. Adapted from Idso and Kimball (2001).

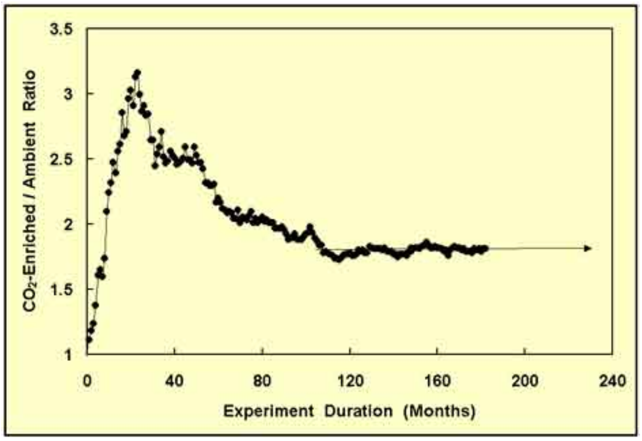

**Figure 1.1.3.2.3.6.** Same as Figure 1.1.3.2.3.5, but with 60-plus months of additional data and one last forward projection of the wood biomass ratio. Adapted from Idso and Kimball (2001).

This time, the change was to a reduced rate of decline in the wood biomass ratio, and it persisted for nearly five years. At this point, the experiment had passed the decade point, and it appeared the wood biomass ratio was going to continue to decline slowly and probably approach some asymptotic limit that might not be much greater than unity. As that possibility would be of extreme significance, Idso and Kimball continued collecting data, obtaining the results portrayed in Figure 1.1.3.2.3.6.

Finally, at the nine-year point of the study, the $CO_2$-enriched/ambient-treatment wood biomass ratio leveled out at 1.80, which the researchers concluded was the true long-term growth response of the trees to the 75% increase in atmospheric $CO_2$ concentration.

Providing additional support for this conclusion, fruit production began in the third year of the study, when the $CO_2$-enriched trees produced an average of 25 fruit per tree and the ambient-treatment trees produced an average of only one fruit per tree. Thereafter, the cumulative $CO_2$-enriched/ ambient-treatment fruit biomass ratio also dropped substantially, ultimately leveling out just a little above the 1.80 $CO_2$-enriched/ ambient-treatment wood biomass ratio. These findings, Idso and Kimball (2001) write, "are indicative of the likelihood that the $CO_2$-enriched trees may have reached an equilibrium condition with respect to the $CO_2$-induced enhancement of wood biomass and fruit production, and that they will not substantially depart from these steady-state responses over the remainder of their lifespan."

Giving added confidence to these conclusions was the ancillary study of Leavitt *et al.* (2003). They evaluated the intrinsic water use efficiencies of the trees via analyses of the stable carbon isotopes of leaves collected from each of them every two months throughout 1992, as well as on three occasions in 1994–95, plus wood samples extracted five years later from two cores that passed through the center of each tree's trunk at a height of 45 cm above the ground. The ultimate finding of this endeavor was an 80% increase in intrinsic water use efficiency in response to the 75% increase in atmospheric $CO_2$ concentration employed in the study. Since the earlier work of Idso *et al.* (1993) had demonstrated there was very little difference in leaf stomatal conductance between the two $CO_2$ treatments, nearly all this water use efficiency increase had to have resulted from the $CO_2$-induced increase in net primary productivity that led to the 80% increases in wood and fruit production.

This result may be typical of trees in general. In a massive review of the pertinent scientific literature, Saxe *et al.* (1998) observed "increasing numbers of experiments show a lack of stomatal sensitivity to $CO_2$," especially when the data come "from long-term experiments on larger trees rooted directly in the ground," as also may be deduced from Eamus (1996). And Feng (1999) reports, for 23 sets of trees in locations across western North America, the average stable-carbon-isotope-derived increase in intrinsic water use efficiency (iWUE) that occurred in response to the historical increase in the air's $CO_2$ concentration experienced over the period 1800–1985 yielded essentially the same value of iWUE/ $CO_2$ as derived from the sour orange tree study of Leavitt *et al.* In addition, even greater natural $CO_2$-induced increases in iWUE have been documented in various trees in Europe: by Bert *et al.* (1997) in the case of white fir, and by Hemming (1998) in the cases of beech, oak, and pine.

Perhaps the most convincing evidence for the validity of the long-term equilibrium response of the sour orange trees in the $CO_2$-enriched chambers came from the harvesting of the trees after 17 years of study at the conclusion of the experiment, in January 2005, as described by Kimball *et al.* (2007). The scientists found the final $CO_2$-enriched/ambient-treatment biomass ratio of all of the above-ground parts of the trees (other than fruit) was 1.69, and "the cumulative amount of biomass due to fruit production over the duration of the experiment was increased 85% due to elevated $CO_2$." In addition, they report, "the vitamin C content of the fruit was increased 7% based on samples taken from the fourth through the 12th years of the experiment," citing Idso *et al.* (2002). Many more oranges were produced by the trees in the $CO_2$-enriched chambers, and those oranges were of a higher quality as well.

In addition, Idso *et al.* (2001) discovered three soluble proteins in the leaves of the sour orange trees whose synthesis and transference from second- to first-year leaves in the early springtime of each year were influenced by the atmosphere's $CO_2$ concentration in ways likely to facilitate the trees' large positive photosynthetic and biomass responses to atmospheric $CO_2$ enrichment. The proteins appeared to function as vacuolar storage proteins, which may supply each year's first flush of new foliage with the large amounts of nitrogen needed to sustain the ultra-enhanced spring branch growth of the $CO_2$-enriched trees, which was four to six times more rapid than the trees growing in ambient air in their experiment (Idso *et al.*, 2000), and which likely provided the yearly initial impetus for the 70 to 80% long-term growth enhancement of the trees maintained throughout the remainder of each year of the last half of their long-term study.

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### *1.1.3.2.4 Spruce*

- Spruce trees have a good chance of indefinitely maintaining the long-term positive growth responses to the ongoing rise in the air's $CO_2$ content, even when growing on nutrient-deficient soils.

Spunda *et al.* (1998) grew 15-year-old Norway spruce (*Picea abies*) trees in open-top chambers maintained at atmospheric $CO_2$ concentrations of 350 and 700 ppm for four years. At the end of this period they found current-year shoots of the trees growing in the $CO_2$-enriched chambers displayed rates of net photosynthesis 78% greater than those exhibited by the current-year shoots of the trees growing in ambient air.

Spinnler *et al.* (2003) grew Norway spruce seedlings originating from eight different provenances for four full years on a nutrient-poor acidic soil and a nutrient-rich calcareous soil placed in lysimeters located within open-top chambers maintained at $CO_2$ concentrations of either 370 or 570 ppm. When growing in the nutrient-poor soil, total spruce biomass increased by 9 to 38% across the eight different provenances, and in the nutrient-rich soil it increased by 10 to 74%.

In an experiment that ran for five years and focused on Sitka spruce (*Picea sitchensis*), Liu *et al.* (2002) grew seedlings in open-top chambers maintained for five years at $CO_2$ concentrations of either 350 or 700 ppm. For the first three years, the seedlings were grown in well-watered and -fertilized pots placed within the chambers. They were then planted directly in native nutrient-deficient forest soil and maintained for two more years in larger open-top chambers, either with or without an extra supply of nitrogen (N).

After the first three years of growth in pots, the $CO_2$-enriched trees were found to possess 11.6% more total biomass than the ambient-treatment trees. At the end of the next two years of the study, the trees supplied with extra N possessed 15.6% more total biomass than their similarly treated ambient-air counterparts, and those receiving no extra N had 20.5% more total biomass than their ambient-air counterparts.

Liu *et al.* make a point of noting these $CO_2$-induced increases in growth occurred in spite of a down-regulation of photosynthesis and a reduction of foliar rubisco activity. In addition, they report "visual foliar N-deficiency symptoms (needle yellowing and chlorosis) were obvious on some of the saplings with no added N supply during the final year of the experiment." However, they further note "such N deficiency is common in many boreal forest sites, and therefore a growth response to rising atmospheric $CO_2$ can be expected to occur in such forests," in support of which they state, "growth responses to elevated $CO_2$ despite nutrient stress have been reported previously in Scots pine (Kellomaki and Wang, 1997), grass (Cannell and Thornley, 1998) and Sitka spruce (Centritto *et al.*, 1999; Murray *et al.*, 2000)."

These findings, plus those cited by Liu *et al.*, indicate spruce trees (and other species) have a good chance of indefinitely maintaining long-term positive growth responses to the ongoing rise in the air's $CO_2$ content, even on nutrient-deficient soils.

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#### *1.1.3.2.5 Sweetgum*

- Long-term FACE studies of mature sweetgum trees demonstrate significant increases in net primary production and give no evidence of decline.

In spring 1988, a single-species sweetgum (*Liquidambar styraciflua* L.) plantation was established in nutrient-rich soil at the Oak Ridge National Environmental Research Park in Roane County, Tennessee, USA, where a group of scientists constructed five circular FACE plots of 25 meters' diameter several years later. They began initial atmospheric $CO_2$ enrichment to a daytime average concentration of 533 ppm (as opposed to the ambient concentration of 394 ppm) in two of the plots in April 1998, well after the 1996 date at which the young forest's canopy had achieved closure and the trees had entered the stable linear growth phase in which annual growth increments are approximately the same each year (as opposed to the exponential growth that precedes this more mature state).

In April 1997 (a full year before the start of differential $CO_2$ treatments), the scientists began monthly bole circumference measurements at a height of 1.3 meters above the ground on every tree within 10 meters of the centers of the ambient and $CO_2$-enriched plots. Several of these trees were subsequently sacrificed to determine their aboveground biomass, and a relationship was developed between this parameter and the tree basal area derived from the bole circumference measurements. Based on these data, Norby *et al.* (2001) state, "there was no pretreatment bias to confound subsequent effects of $CO_2$ on growth."

Over the next two years of differential $CO_2$ exposure, they determined the increase in atmospheric $CO_2$ concentration employed in their study increased the biomass production of the trees by an average of 24% over the first two years of the experiment. That result indicated, they write, "large trees have the capacity to respond to elevated $CO_2$ just as much as younger trees that are in exponential growth," which had been highly conjectural until that time.

After three years of exposure to different $CO_2$ concentrations (reported at this subsequent time to be 360 and 550 ppm in the ambient and $CO_2$-enriched plots, respectively), Gunderson *et al.* (2002) found the 53% increase in the air's $CO_2$ concentration imposed on the trees was boosting rates of net photosynthesis by 46% in both upper- and mid-canopy foliage. In addition, they report there was no decline in photosynthetic enhancement over the preceding three years of their study.

Norby *et al.* (2002) state the elevated $CO_2$ increased ecosystem net primary productivity of the trees by 21% in all of the three preceding years, stating once again, "this experiment has provided the first evidence that $CO_2$ enrichment can increase productivity in a closed-canopy deciduous forest." After an additional year of measurements, Norby *et al.* (2003) determined net primary productivity was enhanced by an average of 22% over years 2–5 of the study, reaffirming their conclusions of the year before.

A second long-term FACE study of sweetgum trees was conducted at the Duke Forest in the Piedmont region of North Carolina, USA, where the soils are low in available nitrogen and phosphorus. In August 1996, three 30m-diameter $CO_2$ delivery rings began to enrich the air around the then-13-year-old trees they encircled—including loblolly pine (1733 stems per ha), sweetgum (620 stems per ha), and yellow poplar (68 stems per ha)—to 190 ppm above the ambient $CO_2$ concentration, and three other FACE rings were used as ambient-air control plots.

In the initial stages of this study, Herrick and Thomas (1999) found elevated $CO_2$ significantly increased photosynthetic rates in both Sun and shade leaves, with the greatest $CO_2$-induced photosynthetic stimulation occurring in August, when the mean maximum air temperature was 4°C higher and monthly rainfall was 66% lower than in June. In June, the extra $CO_2$ increased photosynthetic rates of Sun and shade leaves by 92 and 54%, respectively, whereas in August corresponding increases were 166 and 68%.

Two years later, Herrick and Thomas (2001) observed mean photosynthetic enhancements of 63 and 48% in Sun and shade leaves during the middle portion of the study's third full growing season, indicating little to no down-regulation of photosynthesis over the first three years of the experiment. After two more years, Herrick and Thomas (2003) found there were still large increases in the net photosynthetic rates of the leaves of the $CO_2$-enriched trees: 51 to 96% in Sun leaves and 23 to 51% in shade leaves.

These two long-term FACE studies of mature sweetgum trees demonstrate significant increases in net primary production and give no evidence of decline.

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## 1.1.4 Lifetime Exposure to Elevated $CO_2$

- Trees and shrubs growing for multiple generations in $CO_2$-enriched air near $CO_2$-emitting springs and vents provide a unique opportunity for evaluating the effects of permanently elevated atmospheric $CO_2$ concentrations on their physiology and growth. Such effects indicate a doubling, tripling, or even greater enhancement of the atmosphere's $CO_2$ concentration will only further improve the productivity and water use efficiency of woody plants.

A number of woody plants, including shrubs and trees, have been growing for multiple generations in $CO_2$-enriched air near $CO_2$-emitting springs and vents at various locations around the world. These circumstances provide unique settings for evaluating the effects of permanently elevated atmospheric $CO_2$ concentrations on their physiology and productivity.

Taking advantage of one of these natural situations—$CO_2$-emitting springs near Pisa, Italy—Tognetti *et al*. (2000a) studied the water relations of three woody shrubs (*Erica arborea*, *Myrtus communis,* and *Juniperus communis*) growing at small distances from the springs, where atmospheric $CO_2$ concentrations of approximately 700 ppm prevailed, as well as at greater distances from the springs, where normal concentrations of 360 ppm prevailed at the time of their study. Two common responses were evident in all the shrubs: The $CO_2$-enriched air reduced leaf stomatal conductances and increased leaf water potentials (making them less negative and, therefore, less stressful). The group of five scientists conclude the $CO_2$-induced adjustments in the shrubs' internal water relations would likely allow them "to endure severe periodic drought."

In an analysis of other aspects of the same study, Tognetti *et al*. (2000b) report the plants growing in the $CO_2$-enriched air closer to the springs experienced increased leaf turgor pressure, particularly during the warmer summer months, which is also indicative of better plant water relations. And in another study at that location, Tognetti *et al.* (2002) found elevated $CO_2$ altered the elastic cell-wall properties of all three shrubs in such a way as to endow the shrubs with greater capacities for water uptake from the soil than by control plants growing in ambient air. In addition, the $CO_2$-enriched shrubs displayed greater relative water content than did ambiently grown plants as leaf water potentials declined with available soil moisture.

Bartak *et al.* (1999) studied various physiological processes of mature *Arbutus unedo* trees growing in the general vicinity of $CO_2$-emitting vents located in central Italy. At different distances from the vents, physiological measurements were made on trees exposed to average atmospheric $CO_2$ concentrations of approximately 355 ppm (ambient) and 465 ppm ($CO_2$-enriched) over 30 years. Bartak *et al.* determined this modest 30% increase in atmospheric $CO_2$ concentration boosted net photosynthetic rates in the perennial evergreen species by 110 to 140%, depending on light intensity. They also found the $CO_2$-enriched trees experienced no photosynthetic acclimation to the extra vent-derived $CO_2$ to which they were continuously exposed.

At the high end of the $CO_2$ concentration spectrum, Fernandez *et al.* (1998) studied a number of the effects of very high $CO_2$ levels produced by natural $CO_2$ springs on an indigenous tree during the rainy and dry seasons in Venezuela. They found the ultra-high $CO_2$ concentrations—some as much as 100 times the current global mean—were in no way detrimental to the trees. Instead, photosynthesis was stimulated by the high $CO_2$ in all seasons and in spite of the likely presence of toxic hydrocarbons and sulfur gases typically released to the air along with $CO_2$ in such situations. During the dry season, in fact, trees growing away from the springs at ambient $CO_2$ levels displayed net losses of carbon from their leaves, whereas trees growing near the springs at elevated $CO_2$ concentrations exhibited net carbon gains. In addition, the high $CO_2$ concentrations reduced leaf stomatal densities by about 70%, causing the water use efficiency of the trees to rise twofold and 19-fold, respectively, during the rainy and dry seasons, when measured at a $CO_2$ concentration of 1,000 ppm compared to an ambient concentration of 350 ppm, which represents less than a tripling of the air's $CO_2$ content.

Consequently, and because of the trees' long-term exposure to these high $CO_2$ concentrations under totally natural conditions, Fernandez *et al.* conclude their work provides "a positive answer to the question of whether increases in carbon assimilation will be sustained throughout the growing season and over multiple seasons" in a high-$CO_2$ world of the future.

Schwanz *et al.* (1998) measured various parameters in leaves of mature holm and white oak trees growing near natural $CO_2$ springs in central Italy for 30 to 50 years in order to determine the effects of elevated $CO_2$ on their antioxidative systems. They report elevated $CO_2$ decreased the activities of superoxide dismutase, which detoxifies highly reactive oxygen species, by approximately 30 and 47% in leaves of holm and white oak trees, respectively, when compared with activities measured in leaves of trees growing some distance away from the $CO_2$-emitting springs. Trees of both species growing near the springs also exhibited lower activities of catalase and other enzymes involved in the degradation of hydrogen peroxide ($H_2O_2$), which is produced during photorespiration. Thus, atmospheric $CO_2$ enrichment generally decreased the activities of protective enzymes that reduce oxidative stress brought about by unfavorable environmental factors such as drought, high light intensity, high air temperature, and aerial pollutants.

To determine whether the $CO_2$-induced decreases in the antioxidative machinery of the $CO_2$-enriched trees increased their susceptibility to oxidative damage, the authors evaluated the degree of lipid peroxidation within the leaves. They report trees growing near the $CO_2$-emitting springs did not display increased levels of lipid peroxidation in their leaves, and in some cases they exhibited significant reductions in their amounts of lipid peroxidation. Thus, as the $CO_2$ content of the air increases, most plants will likely experience an amelioration of unfavorable environmental growing conditions that often lead to oxidative stresses within leaves.

This study was the first to identify changes in leaf physiology that have persisted for decades in response to elevated $CO_2$. Specifically, it shows reductions in antioxidative enzymes, which have been observed in seedlings, can persist indefinitely as trees mature. Furthermore, because these enzymes remove reactive compounds that can cause cellular damage, their reduced activities at high $CO_2$ implies plants experience less intrinsic oxidative stress and produce fewer harmful oxidants as the amount of $CO_2$ in the air increases. Thus this beneficial consequence of atmospheric $CO_2$ enrichment should allow plants to increase their productivity, growth, and yield as the air's $CO_2$ content climbs.

Rapparini *et al.* (2004) measured isoprenoid emissions over two consecutive years from two species of mature oak trees—the deciduous downy oak (*Quercus pubescens* Willd.) and the evergreen holm oak (*Quercus ilex* L.)—growing close to a natural $CO_2$ spring in central Italy, where atmospheric $CO_2$ concentrations averaged about 1,000 ppm, and at a nearby control site where the air's $CO_2$ content was unaffected by the spring. Rapparini *et al.* report long-term exposure to high levels of atmospheric $CO_2$ did not significantly affect actual isoprenoid emissions from the trees—emissions experienced under prevailing environmental conditions at the time of measurement. However, they report, "when leaves of plants grown in the control site were exposed for a short period to an elevated $CO_2$ level by rapidly switching the $CO_2$ concentration in the gas-exchange cuvette, both isoprene and monoterpene basal emissions were clearly inhibited," where basal emissions are defined as those that occur at standard measuring conditions of 30°C air temperature and 1,000 $\mu$mol $m^{-2}$ $s^{-1}$ light intensity.

In commenting on these findings, the authors say "these results generally confirm the inhibitory effect of elevated $CO_2$ on isoprenoid emission." In addition, they note the absence of a $CO_2$ effect on actual emissions might indicate "an interaction with multiple stresses," such as the "recurrent droughts" that are typical of the Mediterranean climate in which the experiment was conducted, and these stresses are known to enhance isoprenoid emissions. Thus, evidence continues to mount for the beneficial phenomenon of $CO_2$-induced decreases in isoprene emissions.

Paoletti *et al.* (2007) measured rates of net photosynthesis during a two-week period in June 2002 "at the end of the spring rains," when midday air temperatures rose above 40°C, in upper, sunlit leaves of mature holm oak (*Quercus ilex* L.) trees growing close to (5 m) and further away from (130 m) a natural $CO_2$-emitting spring near Laiatico (Pisa, Italy), where the trees had experienced lifetime exposure to atmospheric $CO_2$ concentrations of approximately 1,500 and 400 ppm, respectively.

At the midpoint of the 14-day measurement period, the net photosynthetic rates of the leaves on the trees growing closest to the $CO_2$ spring were approximately 250% greater than those of the leaves on the trees growing 125 meters further away, where the air's $CO_2$ concentration was 1,100 ppm less. The four Italian researchers say "the considerable photosynthetic stimulation at the very high $CO_2$ site suggests no photosynthetic down-regulation over long-term $CO_2$ enrichment."

Polle *et al.* (2001) collected acorns from mature holm oak (*Quercus ilex* L.) trees growing naturally for their entire lifetimes at ambient and twice-ambient atmospheric $CO_2$ concentrations due to their different distances from a $CO_2$-emitting spring in central Italy. After germinating the acorns, the resulting seedlings were grown for eight months at both atmospheric $CO_2$ concentrations to determine whether atmospheric $CO_2$ enrichment of parent trees had any effect on seedling response to atmospheric $CO_2$ enrichment.

The results reveal elevated $CO_2$ increased whole-plant biomass by 158% and 246% in seedlings derived from acorns produced in ambient and twice-ambient atmospheric $CO_2$ concentrations, respectively, so the final biomass of the $CO_2$-enriched seedlings derived from acorns produced in the $CO_2$-enriched air was 25% greater than the $CO_2$-enriched seedlings derived from acorns produced in ambient air. In addition, gas exchange measurements indicate $CO_2$-enriched seedlings derived from acorns produced on $CO_2$-enriched trees exhibited less-pronounced photosynthetic acclimation to elevated $CO_2$ concentrations than $CO_2$-enriched seedlings derived from acorns produced on trees exposed to ambient air.

Onoda *et al.* (2009) state the ongoing rise in the air's $CO_2$ content "is likely to act as a selective agent" among Earth's plants, citing Woodward *et al.* (1991), Thomas and Jasienski (1996), Ward *et al.* (2000), Kohut (2003), Ward and Kelly (2004), and Lau *et al.* (2007). They report, "evolutionary responses have been found in selection experiments with short-lived organisms, such as *Arabidopsis thaliana* (e.g. development rate and biomass production; Ward *et al.*, 2000) and *Chlamydomonas reinhardtii* (e.g. photosynthesis and cell size; Collins and Bell, 2004)." They hasten to add, however, "the evolutionary response of wild plants (especially long-lived plants) is, in general, difficult to evaluate using growth experiments," because of the long time spans needed to evaluate the phenomenon properly.

They avoid this problem in their study by utilizing plants growing around natural $CO_2$ springs where they "have been exposed to a $CO_2$-enriched atmosphere over many generations," which provides what they call "a unique opportunity to explore the micro-evolutionary response of wild plants to elevated $CO_2$."

The three researchers write, "the adaptation of leaf photosynthesis to elevated $CO_2$ was tested by a common garden experiment with herbaceous species originating from three different natural $CO_2$ springs in Japan: Nibu, Ryuzin-numa and Yuno-kawa," where "several genotypes were collected from each high-$CO_2$ area (spring population) and nearby control areas (control population), and each genotype was propagated or divided into two ramets, and grown in pots at 370 and 700 ppm $CO_2$." The researchers assessed the plants' photosynthetic nitrogen use efficiency (PNUE), water use efficiency (WUE), and degree of carbohydrate accumulation in the plants' leaves, which if too large can lead to the down-regulation of photosynthesis.

Onoda *et al*. report "high $CO_2$ concentration directly and greatly increased PNUE and WUE, suggesting that plants will show higher growth rates at a given resource availability." They also found "a significant reduction in stomatal conductance, which contributed to higher WUE, and a trend of reduced down-regulation of photosynthesis with a lower starch accumulation," and they note these results suggest "there is substantial room for plant evolution in high-$CO_2$ environments." Further to this point, they say a still-to-be-published molecular study "also found relatively large genetic differentiation across the $CO_2$ gradient in these plants." Consequently, as a result of their own work and "the increasing number of studies on $CO_2$ springs (e.g. Fordham *et al.*, 1997; Polle *et al.*, 2001; Schulte *et al.* 2002) and selection experiments (Ward *et al.*, 2000; Collins and Bell, 2004)," Onoda *et al*. conclude, "high $CO_2$ will act as a selection agent" as the air's $CO_2$ content rises. This phenomenon should enable plants to fare even better in the $CO_2$-enriched air of the future than they do currently.

The several observations above suggest a doubling, tripling, or even greater enhancement of the atmosphere's $CO_2$ concentration will only further improve the productivity and water use efficiencies of woody plants.

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### 1.1.5 Growth Response to Very High $CO_2$ Concentrations

- Several studies indicate plants are not harmed by super-elevated atmospheric $CO_2$ concentrations an order of magnitude or more greater than the globe's current mean. Positive growth responses are reported in all instances. Thus it is likely most plants will display enhanced rates of photosynthesis and biomass production as the atmosphere's $CO_2$ concentration rises.

Terrestrial plants grown in elevated atmospheric $CO_2$ typically exhibit increased rates of photosynthesis and biomass production. Most of the studies establishing this fact have historically utilized $CO_2$ concentration increases on the order of 300 to 400 ppm, which represents an approximate doubling of the atmosphere's current $CO_2$ concentration. This section examines the growth response of plants when the air's $CO_2$ content is *super*-enriched, to a concentration an order of magnitude or more larger.

Louche-Tessandier *et al.* (1999) grew potato plantlets inoculated with an arbuscular mycorrhizal fungus at ambient and super-elevated (10,000 ppm) $CO_2$ for one month at a number of different light intensities. They report the high $CO_2$ treatment stimulated root colonization by the fungus, but biomass production in the $CO_2$-enriched inoculated plantlets increased significantly only when they were grown at high light intensity.

Also studying potatoes, Teixeira da Silva *et al.* (2005) grew single-node explants of sweet potato (*Ipomoea batatas* cv. Naruto Kintok) for five weeks *in vitro* within special culture vessels supplied with a 3% sugar-containing agar, during which time the vessels were maintained at atmospheric $CO_2$ concentrations of either 400 ppm (ambient) or 1,000, 2,000, or 3,000 ppm The plants were then transplanted into soil and grown *ex vitro* for three additional weeks. Relative to the plants exposed to ambient air, those exposed to air of 1,000, 2,000, and 3,000 ppm $CO_2$ produced 20%, 20%, and 65% more total biomass, respectively, after having been grown for five weeks *in vitro*, and they produced 20%, 32%, and 82% more biomass, respectively, after having been grown for three additional weeks *ex vitro*. Thus, for sweet potato plants, a several-fold increase in the atmosphere's $CO_2$ concentration appears to pose no problem to the plants' growth and development.

Dempster *et al.* (2009) grew a mixture of cowpeas, pinto beans, and wheat for three months, measuring the net fixation rate of carbon by the entire three-crop system during the greater portion of this "growing season." Relative to a $CO_2$ concentration of 385 ppm, net photosynthesis at 1,000 ppm, 2,000 ppm, and 2,800 ppm were 150%, 275%, and 355% greater, respectively. The authors note the "high productivity from these crops and the increase of fixation rates with elevated $CO_2$ concentration supports the concept that enhanced $CO_2$ can be a useful strategy for remote life support systems," presumably on long manned space flights or outposts on other planets or moons.

Schubert and Jahren (2011) grew radishes (*Raphanus sativus*) from seed to maturity (four months) in standard potting soil within eight growth chambers maintained at optimum temperature, humidity, and soil water and fertility conditions in air of eight different $CO_2$ concentrations (348, 388, 413, 426, 760, 1,090, 1,425, and 1,791 ppm). They then harvested the plants and determined their above- and below-ground biomass, both of which they found to be well described by a two-parameter rectangular hyperbola, "employing the method used by Hunt *et al.* (1991, 1993) for assessing the trajectory of the biomass response for 36 herbaceous species grown under $CO_2$ levels ranging from 365 to 812 ppm."

Going from the lowest to the highest $CO_2$ concentration employed in their study, the two U.S. researchers state above-ground biomass rose by a modest 58%, but below-ground biomass rose by a phenomenal 279%, the trajectory of which "greatly exceeded a trajectory based on extrapolation of previous experiments for plants grown at $CO_2 < 800$ ppm." Commenting on these findings, Schubert and Jahren state, "if the below-ground biomass enhancement that we have quantified for *R. sativus* represents a generalized root-crop response that can be extrapolated to agricultural systems, below-ground fertilization under very high $CO_2$ levels could dramatically augment crop production in some of the poorest nations of the world." They continue, "needless to say, a doubling or tripling of below-ground crop tissue due to $CO_2$ fertilization would be welcome on both a nutritional and economic basis."

Gouk *et al.* (1999) grew orchid plantlets at ambient and super-elevated (10,000 ppm) $CO_2$ for three months. In their study, the extra $CO_2$ more than doubled plant dry weight, stimulated the induction of new roots, increased the total chlorophyll contents of both roots and leaves, and boosted tissue starch contents nearly 20-fold, all without any disruption of or damage to chloroplasts.

Also working with orchids were Norikane *et al.* (2010), who grew *Cymbidium* (Music Hour 'Maria') shoots in air augmented with either 0, 3,000, or 10,000 ppm $CO_2$ under photosynthetic photon flux densities of either 45 or 75 $\mu$mol $m^{-1}$ $s^{-1}$ provided by cold cathode fluorescent lamps for 90 days. The plants then were transferred to *ex vitro* culture for an additional 30 days. Relative to plants grown *in vitro* in ambient air, the percentage increases in shoot and root dry weight due to enriching the air in which the plants grew by 3,000 ppm $CO_2$ were, respectively, 216% and 1,956% under the low light regime and 249% and 1,591% under the high light regime. Corresponding increases for the plants grown in air enriched with an extra 10,000 ppm $CO_2$ were 244% and 2,578% under the low light regime and 310% and 1,879% under the high light regime.

In the *ex vitro* experiment, percentage increases in shoot and root dry weight due to enriching the air in which the plants grew by 3,000 ppm $CO_2$ were, respectively, 223% and 436% under the low light regime and 279% and 469% under the high light regime. Corresponding increases for the plants grown in air enriched with an extra 10,000 ppm $CO_2$ were 271% and 537% under the low light regime and 332% and 631% under the high light regime. The four Japanese researchers conclude "super-elevated $CO_2$ enrichment of in vitro-cultured *Cymbidium* could positively affect the efficiency and quality of commercial production of clonal orchid plantlets."

Hew *et al.* (1995) grew orchids at ambient and 10,000 ppm $CO_2$ and found the elevated $CO_2$ boosted dry weights by 28 to 37%. Likewise, Tisserat *et al.* (2002) fumigated mint and thyme with air containing 10,000 ppm $CO_2$ and determined the super-$CO_2$-enrichment increased the fresh weights of the two species by 3.1- and 5.8-fold, respectively.

In a study of an epiphytic fern, Ong *et al.* (1998) grew the seedless vascular species *Pyrrosia piloselloides* (which is less adapted to terrestrial habitats than its seed-producing relatives) from spores in small containers maintained at atmospheric $CO_2$ concentrations of 350, 515, and 3,360 ppm to study the effects of elevated $CO_2$ on the fern's photosynthesis and growth. Forty days after germination, light-saturated rates of net photosynthesis were 22% and 114% greater at 515 and 3,360 ppm, respectively, than they were at 350 ppm. Over time, the elevated $CO_2$ induced photosynthetic acclimation in the plants, but in a concentration-dependent manner. After 100 days of exposure to elevated $CO_2$, for example, the photosynthetic stimulation of plants grown at 515 ppm $CO_2$ had dropped to 10%, representing a 50% decline from their original stimulation, but the photosynthetic adjustment was much less at the super-enriched $CO_2$ concentration of 3,360 ppm—plants in this treatment reduced their original photosynthetic enhancement by only 10%.

As part of their acclimation response to elevated $CO_2$, gametophytes exposed to 515 and 3,360 ppm $CO_2$ reallocated limiting resources away from their photosynthetic apparatus, as indicated by respective 11 and 28% reductions in their tissue chlorophyll contents. Despite these reductions, resulting from an optimization of resources at elevated $CO_2$ concentrations, total gametophytic dry mass at 515 and 3,360 ppm was still 43 and 214% greater, respectively, than at ambient $CO_2$, at physiological maturity (100 and 80 days for plants grown at 515 and 3,360 ppm $CO_2$, respectively).

These findings suggest Earth's rising atmospheric $CO_2$ content likely will promote the photosynthesis and growth of ferns, which are considered more primitive forms of terrestrial plant life than the planet's more-numerous seed-bearing plants. Thus, ferns should continue to maintain their presence in many ecosystems across the globe. Ong *et al.* conclude, the "sum responses of *Pyrrosia piloselloides* gametophytes to elevated $CO_2$ concentration suggest greater success against competitors in the future environment, enabling this fern to continue to establish itself in a future world with high atmospheric $CO_2$."

Teixeira Da Silva *et al.* (2006) grew ornamental *Spathiphyllum* cv. Merry plantlets for five weeks in novel culture vessels on a sugar-free liquid medium at low light intensity in controlled-environment chambers maintained at atmospheric $CO_2$ concentrations of 375, 1,000, 2,000, or 3,000 ppm. Relative to the growth experienced by the plantlets exposed to ambient air of 375 ppm $CO_2$, the plantlets exposed to 1,000, 2,000, and 3,000 ppm $CO_2$ produced 39%, 81%, and 129% more shoot dry weight, respectively, plus 316%, 639%, and 813% more root dry weight, respectively, for corresponding total $CO_2$-induced biomass enhancements of 61%, 127%, and 185%.

Ali *et al*. (2005) worked with the ginseng plant (*Panax ginseng*), which is widely cultivated in China, South Korea, and Japan, the roots of which have been used for medicinal purposes since Greek and Roman times and are well known for their anti-inflammatory, diuretic, and sedative properties and are also acknowledged to be effective healing agents (Gillis, 1997; Ali *et al*., 2005). Ginseng roots normally require four to six years to accumulate the amounts of the various phenolic compounds needed to produce their health-promoting effects. In an important step toward developing an efficient culture system for the commercial production of ginseng roots, Ali *et al*. investigated the effects of growing them in suspension culture in bioreactors maintained in equilibrium with air enriched to $CO_2$ concentrations of 10,000 ppm, 25,000 ppm, and 50,000 ppm for periods of up to 45 days.

Of most immediate concern in such an experiment would be the effects of the ultra-high $CO_2$ concentrations on root growth. Would they be toxic and lead to biomass reductions or even root death? The answer was a resounding no. After 45 days of growth at 10,000 ppm $CO_2$, for example, root dry weight was increased by 37% relative to the dry weight of roots produced in bioreactors in equilibrium with normal ambient air. Root dry mass was increased by 27% after 45 days at 25,000 ppm $CO_2$, and by 9% after 45 days at 50,000 ppm $CO_2$. Thus, although the optimum $CO_2$ concentration for ginseng root growth likely resided at some value lower than 10,000 ppm in this study, the concentration at which root growth rate was reduced below that characteristic of ambient air was somewhere significantly above 50,000 ppm, for even at that extremely high $CO_2$ concentration, ginseng root growth was greater than in ambient air.

Almost everything else measured by Ali *et al*. was even more dramatically enhanced by the ultra-high $CO_2$ concentrations employed in their experiment. After 45 days of treatment, total root phenolic concentrations were 58% higher at 10,000 ppm $CO_2$ than at ambient $CO_2$, 153% higher at 25,000 ppm $CO_2$, and 105% higher at 50,000 ppm $CO_2$, as best as can be determined from the bar graphs of their results. Likewise, total root flavonoid concentrations were enhanced by 228%, 383%, and 232%, respectively, at the same ultra-high $CO_2$ concentrations. Total protein contents rose by 14%, 22%, and 30%; non-protein thiol contents by 12%, 43%, and 62%; and cysteine contents by 27%, 65%, and 100% under the identical respective set of conditions. There were equally large $CO_2$-induced increases in the activities of a large number of phenol biosynthetic enzymes.

Discussing the implications of their results, Ali *et al*. write, "the consumption of foodstuffs containing antioxidant phytonutrients such as flavonoids, polyphenolics, ascorbate, cysteine and non-protein thiol is advantageous for human health," citing Cervato *et al*. (2000) and Noctor and Foyer (1998). They thus conclude their technique for the culture of ginseng roots in $CO_2$-enriched bioreactors could be used for the large-scale production of an important health-promoting product that could be provided to the public in much greater quantities than is currently possible.

Levine *et al*. (2008) grew well-watered and well-fertilized wheat plants (*Triticum aestivum*, cv Yocoro roho) from seed in custom-designed root modules—"consisting of a porous tube embedded in Turface (1–2 mm particle size) substrate containing 5 g Osmocote time release fertilizer per liter"— housed in Plexiglas chambers maintained at atmospheric $CO_2$ concentrations of 400, 1,500, or 10,000 ppm for periods of 14, 21, and 28 days. They measured a number of plant metabolic properties, among which were the leaf concentrations of several flavonoids capable of scavenging reactive oxygen species (ROS).

They found "elevated $CO_2$ promoted the accumulation of secondary metabolites (flavonoids) progressively to a greater extent as plants became mature." As best as can be determined from the bar graphs of their results, for example, the percentage increase in total wheat leaf flavonoid concentration in going from an atmospheric $CO_2$ concentration of 400 to 1,500 ppm was 22%, 38%, and 27% (the one exception to this general rule) at 14, 21, and 28 days after planting, respectively. In going from a $CO_2$ concentration of 400 to 10,000 ppm, the percentage increase in total flavonoid concentration was 38%, 56%, and 86%, respectively, at 14, 21, and 28 days after planting. In addition, they report "both elevated $CO_2$ levels resulted in an overall 25% increase in biomass over the control plants."

With respect to the cultivation of trees, Tisserat (2005) notes "vitrified shoots are characterized as being small, succulent (i.e., 'glassy' or 'wet' in appearance) and immature, but [are] capable of readily proliferating additional axillary shoots." However, he also notes vitrified shoots of the type that are cultured *in vitro* "do not transfer readily into soil well." Consequently, because there is a need for literally millions of sweetgum seedlings to be planted annually (Lin *et al*., 1995), it would be advantageous if a technique could be developed to increase the success of transferring tissue-culture-produced vitrified shoots to *ex vitro* growth in soil.

In searching for a technique to accomplish this feat, Tisserat first produced sweetgum shoots in an automated plant culture system in which ten times more shoots developed than in prior plant culture systems, and where vitrification was observed in fully 80% of the shoots. He then studied the effects of ultra-high atmospheric $CO_2$ concentrations on the vitrified shoots when they were transferred to soil and grown in air enriched with $CO_2$ to concentrations as high as 30,000 ppm. After four weeks of growth at atmospheric $CO_2$ concentrations of 350, 1,500, 3,000, 10,000, and 30,000 ppm, survival percentages of 1cm-long explants were found to be 48.6, 56.5, 65.7, 93.1, and 67.1%, respectively, and corresponding survival percentages of 2cm-long explants were 61.2, 64.1, 69.2, 93.9, and 64.3%. For these same $CO_2$ concentrations, the numbers of leaves produced per shoot were 4.17, 5.38, 5.85, 6.14, and 4.83, and the numbers of roots produced per shoot were 5.35, 8.58, 9.19, 9.66, and 9.82. Also, leaf and shoot lengths were similarly enhanced by the suite of increased $CO_2$ concentrations.

Tisserat concludes the procedures he developed should "minimize the time and labor involved in sweetgum micropropagation" and "can be readily adapted to the micropropagation of other woody and non-woody plants." Tisserat's results suggest anthropogenic emissions will never raise the air's $CO_2$ concentration so high as to retard the growth and development of sweetgum trees and, by implication, many (if not most) other plants. Even in those cases where plant growth responses did decline between 10,000 and 30,000 ppm in Tisserat's study, for example, the responses at 30,000 ppm $CO_2$ were still greater than those observed at 350 ppm.

Tisserat and Vaughn (2003) grew four-week-old loblolly pine seedlings for 30 days at the same suite of atmospheric $CO_2$ concentrations within 17.6-liter transparent containers, where the seedlings were watered three times per week but not fertilized. Three repetitions of this procedure revealed seedling fresh weight, needle number, root number, and shoot length increased 341%, 200%, 74%, and 75%, respectively, after 30 days of growth at 10,000 ppm $CO_2$. There were no further increases—or decreases—when going to an atmospheric $CO_2$ concentration of 30,000 ppm. Also, associated with increased growth and morphogenesis, the researchers found a corresponding increase in secondary metabolites (more than 99% of which were a- and ß-pinene) in the ultra-high $CO_2$ environments, and they note "high a- and ß-pinene levels may confer an additional positive survival advantage" on the seedlings, because these substances "have fungicidal and insecticidal activity (Harbone, 1982; Klepzig *et al*., 1995)."

In a field study, Fernandez *et al*. (1998) investigated the effects of even higher $CO_2$ concentrations (some as great as 35,000 ppm) on an herb and a tree growing in the vicinity of natural $CO_2$ springs in Venezuela. These high $CO_2$ concentrations stimulated the photosynthetic rates of both plants in all seasons of the year. In the dry season, this effect was particularly important: Plants exposed to elevated $CO_2$ continued to maintain positive net photosynthetic rates, whereas those exposed to ambient air a few tens of meters away exhibited negative rates, which if prolonged, would be expected to lead to their eventual demise. The researchers thus note their work provides "a positive answer to the question of whether increases in carbon assimilation will be sustained throughout the growing season and over multiple seasons." It also demonstrates very high atmospheric $CO_2$ concentrations—some as much as two orders of magnitude greater than the current global mean—are not detrimental to but in fact helped the plants they investigated.

Garcia *et al*. (1994) grew two Eldarica pine (*Pinus eldarica* L.) seedlings out-of-doors in a field of Avondale loam at Phoenix, Arizona (USA) within transparent open-top enclosures. They maintained one for 15 months at a mean atmospheric $CO_2$ concentration of 402 ppm and one at 788 ppm. They then measured short-term whole-tree net photosynthetic rates (one-hour averages) at a number of different $CO_2$ concentrations (changed at 1.5-hour intervals) ranging from ambient (360 ppm) to 3,000 ppm.

Garcia *et al*. report "the two trees responded identically to short-term atmospheric $CO_2$ enrichment to about a tripling of the ambient $CO_2$ concentration." As the $CO_2$ content of the air was increased further, they write, "the net $CO_2$ assimilation responses of the two trees diverged: the photosynthetic response curve of the low-$CO_2$-grown tree exhibited the classical form of a rate-limiting rectangular hyperbola, while that of the high-$CO_2$-grown tree maintained its linearity to the highest $CO_2$ concentration investigated." At this latter $CO_2$ concentration (3,000 ppm), the photosynthetic rate of the low-$CO_2$-grown tree had long since plateaued at a value approximately five times its value at 360 ppm, whereas the photosynthetic rate of the high-$CO_2$-grown tree was still rising linearly at a value approximately ten times greater than what it had exhibited at 360 ppm. The three researchers conclude, "atmospheric $CO_2$ enrichment produces a type of up-regulation of carbon assimilation in Eldarica pine trees, as long-term exposure to elevated $CO_2$ enabled the high-$CO_2$-grown tree to continue to respond to further increases in the $CO_2$ content of the air while the photosynthetic rate of the tree grown in ambient air reached an asymptotic limit." This observation suggests plants may continuously adapt to—and thereby continuously profit from—the ongoing increase of the air's $CO_2$ content.

Tisserat *et al*. (2008) grew three types of well-watered two-week-old *Cuphea viscosissima* x *C. lanceolata* L. (McCoy GT #1, Morton GT #1, and Morris heavy) seedlings within 162-L transparent containers maintained for 30 days at atmospheric $CO_2$ concentrations of either 350, 1,500, 3,000, 10,000, or 30,000 ppm $CO_2$, after which they were harvested and assessed for a number of measures of growth. The authors report the "fresh weight of seedlings, leaves per seedling, roots per seedling, and seedling length in cuphea Morris heavy seedlings increased 607%, 184%, 784%, and 175%, respectively, after 30-day exposure to 10,000 ppm $CO_2$ over those obtained from seedlings grown on ambient [350 ppm] $CO_2$ levels," with a leveling off of growth stimulation between 10,000 and 30,000 ppm $CO_2$. They further note the other two cuphea varieties "showed similar response trends."

The three USDA Agricultural Research Service scientists say their data suggest "ultrahigh $CO_2$ treatments may be effective for enhancing cuphea growth and benefit breeding treatments." In addition, their data indicate large increases in the air's $CO_2$ concentration can lead to huge increases in plant growth and development.

The results of the several studies reviewed above indicate plants are not harmed by super-elevated atmospheric $CO_2$ concentrations an order of magnitude or more greater than the globe's current mean. The studies all report positive growth responses, with some being particularly large, even huge. Most plants should display enhanced rates of photosynthesis and biomass production as the atmosphere's $CO_2$ concentration rises.

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## 1.2 Ecosystem Responses to $CO_2$ Enrichment

### 1.2.1 Forests

Forests contain perennial trees that remove $CO_2$ from the atmosphere during the process of photosynthesis and store its carbon within their woody tissues for decades to periods of sometimes more than a thousand years. It is important to understand how increases in the air's $CO_2$ content affect forest productivity and carbon sequestration, which has a great impact on the rate of rise of the air's $CO_2$ concentration. The subsections below review scientific publications pertaining to these subjects.

#### *1.2.1.1 Tropical*

- Where tropical forests have not been decimated by the targeted and direct destructive actions of human society, such as the felling and burning of trees, forest productivity has been growing ever-greater with the passing of time, rising with the increasing $CO_2$ content of the air. This has occurred despite all concomitant changes in atmospheric, soil, and water chemistry, including twentieth century global warming, which IPCC claims to have been unprecedented over the past one to two millennia.

Perhaps the most striking evidence for the significant growth enhancement of Earth's forests being driven by the historical increase in the air's $CO_2$ concentration was provided by Phillips and Gentry (1994). Noting turnover rates of mature tropical forests correlate well with measures of net productivity (Weaver and Murphy, 1990), the two scientists assessed the turnover rates of 40 tropical forests around the world in order to test the hypothesis that global forest productivity was increasing, *in situ*. They found the turnover rates of these highly productive forests had indeed been rising since at least 1960, with an apparent pan-tropical acceleration since 1980. In discussing what might have been causing this phenomenon, they state, "the accelerating increase in turnover coincides with an accelerating buildup of $CO_2$." As Pimm and Sugden (1994) state in a companion article, it was "the consistency and simultaneity of the changes on several continents that [led] Phillips and Gentry to their conclusion that enhanced productivity induced by increased $CO_2$ is the most plausible candidate for the cause of the increased turnover."

Four years later, Phillips *et al.* (1998) reported another impressive finding. Working with data on tree basal area (a surrogate for tropical forest biomass) for the period 1958–1996, which they obtained from several hundred plots of mature tropical trees around the world, they found the average forest biomass for the tropics as a whole had increased substantially. They calculate the increase amounted to approximately 40% of the missing terrestrial carbon sink of the entire globe. Hence, they suggest, "intact forests may be helping to buffer the rate of increase in atmospheric $CO_2$, thereby reducing the impacts of global climate change," as Idso (1991a,b) had earlier suggested. Phillips *et al.* also identified the aerial fertilization effect of the increasing $CO_2$ concentration of the atmosphere as one of the primary factors responsible for this phenomenon. Other contemporary studies (Grace *et al*., 1995; Malhi *et al*., 1998) support their findings, verifying the fact neotropical forests were indeed accumulating ever-more carbon at ever-increasing rates. Phillips *et al.* (2002) subsequently suggested this phenomenon was occurring "possibly in response to the increasing atmospheric concentrations of carbon dioxide (Prentice *et al*., 2001; Malhi and Grace, 2000)."

Lin *et al.* (1998) measured the ecosystem carbon exchange rate of a 1,700-$m^3$ synthetic rainforest mesocosm alternately maintained at atmospheric $CO_2$ concentrations of either 430 or 740 ppm. This enormous study site, managed by Columbia University, was located in the 1.25 ha naturally lit Biosphere 2 research "dome," which contained several large synthetic ecosystems enclosed by stainless steel sheets and glass. After the dome's air was stabilized at a treatment $CO_2$ level for about a week, the rainforest mesocosm was isolated from the rest of the dome for one to three days so its carbon exchange rate could be measured. This work revealed the 72% increase in atmospheric $CO_2$ concentration increased the daytime net ecosystem carbon exchange rate of the synthetic rainforest by 79%, without affecting the amount of carbon respired from the soil, indicating the increased carbon uptake in the $CO_2$-enhanced ecosystem was primarily caused by increased canopy net photosynthesis, as the elevated $CO_2$ had no significant effect on soil respiration.

Wurth *et al.* (1998) enclosed upper-canopy leaves of four species of trees located in a semi-deciduous tropical forest near Panama City, Republic of Panama, in small transparent cups enriched with $CO_2$ to about twice the current ambient concentration, to determine the effects of elevated $CO_2$ on sugar and starch production in the trees' leaves. "Against expectation," they write, they determined the elevated $CO_2$ caused 30 and 100% increases in leaf sugar and starch concentrations, respectively, for all four of the tropical tree species, regardless of whether they were sampled in the morning or evening or under high or low light intensities. This finding demonstrates atmospheric $CO_2$ enrichment can significantly stimulate individual-leaf total nonstructural carbohydrate contents in tropical tree species, even when there is a very large "sink" (the rest of the tree) to which the carbohydrates readily could be exported.

Working concurrently in Panama, Lovelock *et al.* (1998) grew ten tropical tree species in open-top chambers on the edge of a tropical forest for six months at both ambient and twice-ambient atmospheric $CO_2$ concentrations, to determine the effects of elevated $CO_2$ on them. They found the leaf starch concentrations of the trees approximately doubled in the doubled-$CO_2$ environment.

Lovelock *et al.* (1999b) enclosed branchlets of 30m-tall *Luehea seemannii* trees in small open-top chambers suspended within their upper canopies, and exposed them to atmospheric $CO_2$ concentrations of 360 or 750 ppm for nearly 40 weeks, to study the effects of elevated $CO_2$ on photosynthesis, growth, and reproduction in this deciduous tropical tree. They found the leaves of branchlets grown in elevated $CO_2$ had net photosynthetic rates approximately 30% greater than those in leaves of ambiently grown branchlets. However, the extra carbohydrates produced by this phenomenon were not used by $CO_2$-enriched branchlets to increase leaf growth or reproductive efforts. Instead, they were stored away in terminal woody tissues, which led the four researchers to speculate the enhanced carbohydrate storage in terminal branchlets may facilitate greater first-flush leaf growth the following year.

Breaking from experimental work to conduct a mini-review of the scientific literature dealing with subtropical and tropical fruit tree responses to atmospheric $CO_2$ enrichment to that point in time, Schaffer *et al*. (1999) found exposure to elevated $CO_2$ concentrations significantly enhanced photosynthesis in leaves of avocado, banana, citrus, mango, and mangosteen trees. After being exposed to an atmospheric $CO_2$ concentration of 800 ppm for one year, for example, the leaves of mangosteen trees displayed photosynthetic rates 40 to 60% greater than rates observed in ambiently grown leaves.

In addition, atmospheric $CO_2$ enrichment increased biomass accumulation in each of these species, and in macadamia trees as well. In most cases, elevated $CO_2$ also increased total yield and fruit weight. However, when it did not immediately increase yield in avocado, mango, and macadamia, plants showed a preferential allocation of carbon belowground to their roots, suggesting "increasing water and nutrient uptake resulting from increased root mass would eventually increase assimilate partitioning to the aboveground organs," ultimately enhancing yield.

Sheu and Lin (1999) grew 50-day-old seedlings of the subtropical tree *Schima superba* for six additional months in pots placed within glass chambers maintained at atmospheric $CO_2$ concentrations of 360 and 720 ppm. In addition, at each $CO_2$ concentration half of the seedlings were grown at an optimal day/night temperature regime of 25/20°C, and the other half were subjected to a higher temperature treatment of 30/25°C. The $CO_2$-enriched seedlings exhibited photosynthetic rates 20% greater than those displayed by ambiently grown trees at the original "optimal" day/night temperatures, and their photosynthetic rates were fully 40% greater than those displayed by the ambiently grown trees in the elevated temperature regime, demonstrating the optimal growth temperature for this species had to have increased with the increasing $CO_2$ concentration. As a result, the $CO_2$-enriched seedlings displayed total dry weights 14 and 49% greater than control seedlings at the lower and higher set of growth temperatures, respectively.

Lovelock *et al*. (1999a) 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. After 14 days of differential $CO_2$ exposure, half the seedlings in each treatment were subjected to mechanical defoliation, which removed about 40% of their leaf area and enabled the three researchers to study the influence of simulated herbivory on the $CO_2$ growth response of this species.

During the experiment, the seedlings grown in the elevated $CO_2$ treatment displayed rates of net photosynthesis between 50 and 100% greater than those of plants grown in ambient $CO_2$, regardless of defoliation, which had little to no impact on photosynthesis in either $CO_2$ treatment. Mechanical defoliation did, however, temporarily reduce seedling leaf area and leaf relative growth rates in both $CO_2$ environments. But by the end of the experiment, leaf relative growth rates had recovered, and there were no differences between defoliated and undefoliated seedlings in either $CO_2$ treatment. In contrast, the leaf area of defoliated seedlings never recovered to match undefoliated controls in either $CO_2$ treatment. But defoliated seedlings grown at ambient $CO_2$ ultimately attained leaf areas 77% of their un-defoliated controls, and those exposed to elevated $CO_2$ attained leaf areas 67% of their respective controls.

Despite that difference, the defoliated seedlings grown in elevated $CO_2$ still possessed about 20% more leaf area than the defoliated plants grown in ambient $CO_2$. In addition, final plant dry weight, which better represents the total impact of any stress upon a plant and indicates how well a plant is able to deal with a stress, was 15% greater in defoliated seedlings exposed to elevated $CO_2$ than in defoliated seedlings growing in ambient $CO_2$. Therefore, even with leaf destruction resulting from herbivory, *Copaifera aromatica* seedlings likely will exhibit increased photosynthetic rates and greater biomass accumulation as the air's $CO_2$ content rises.

Hoffmann *et al*. (2000) germinated and grew specimens of a tree common to the Brazilian savannah (*Keilmeyera coriacea*) in controlled-environment chambers maintained at combinations of ambient (350 ppm) and elevated (700 ppm) atmospheric $CO_2$ concentration and low- and high-strength soil nutrient solutions. At 10 weeks post-germination, they clipped to the ground half of the seedlings in each treatment, to simulate burning and allow the five researchers to study the interactive effects of elevated $CO_2$ and soil nutrients on seedling growth and regrowth with and without the presence of a simulated burning event.

Among the uncut seedlings, the doubled atmospheric $CO_2$ treatment increased total dry weight by about 50%, and the high nutrient solution increased it by 22%, with no significant interactions between the two factors. In seedlings subjected to the simulated burning, elevated $CO_2$ had a significant impact on regrowth, but only in the presence of high soil nutrient availability, when it stimulated regrowth by nearly 300%. This observation, coupled with the knowledge that large pulses of nutrients typically become available in soils following burning events, led Hoffmann *et al*. to conclude, "under elevated $CO_2$, enhanced growth following fire will reduce the time required for individuals to regain the pre-burn size, minimizing the negative effect of fire on population growth." As a result, they write, "greater growth rates and higher capacities of regeneration under elevated $CO_2$ are expected to increase the ability of woody plants to withstand the high fire frequencies currently prevalent in moist savannahs throughout the tropics."

Aidar *et al*. (2002) note the leguminous *Hymenaea courbaril* L. tree—which is commonly known as jatoba and grows to a height of 20 to 30 meters with a trunk diameter of 200 cm—is "a late secondary/climax species that is one of the most important trees in mature tropical forests of the Americas." It occurs "in more than 30% of 43 inventories made in the extra-Amazonian riparian forests (Rodrigues and Nave, 2000)," they write, and it shows "wide distribution in [the] neotropics, from the Caribbean isles, Mexico and Peru to Southeastern Brazil (Allen and Allen, 1981)."

The six scientists sprouted and grew jatoba seedlings in pots placed in small open-top chambers maintained at atmospheric $CO_2$ concentrations of 360 and 720 ppm in a shaded glasshouse (to simulate the low light regime at the forest floor where the seeds typically germinate) for 70 days. During that time they measured rates of net photosynthesis in seedlings with and without cotyledons, which they removed from half of the plants.

These efforts revealed a persistent doubling of photosynthesis both with and without cotyledons, when the seedlings were exposed to elevated $CO_2$. In addition, the scientists observed a 35% increase in the water use efficiency of the seedlings. As a result, Aidar *et al*. state, "under the climatic conditions forecasted on the basis of the present carbon dioxide emissions, *Hymenaea courbaril* should establish faster in its natural environment and might also serve as an efficient mechanism of carbon sequestration within the forest." They also opine the $CO_2$-induced increase in water use efficiency may enable jatoba "to tolerate dryer and more open environments, which should allow them to better cope with drought stress or a more seasonal climate." Finally, they state the jatoba tree likely would exhibit similar positive responses to even greater emissions of $CO_2$ because light-saturated photosynthesis in jatoba seedlings continued to rise in response to increasing atmospheric $CO_2$ concentrations well above 1,000 ppm. In addition, they report they "have measured the saturation level of some other tropical trees from the rain forest (*Caesalpinia echinata*, *Piptadenia gonoacantha*, *Tibouchina granulose*, *T. pulchra*) and all of them [also] saturate at relatively high $CO_2$ concentrations." It is thus quite likely neotropical forests in general are suited to much higher-than-present atmospheric $CO_2$ concentrations and would fare far better than they do today in a $CO_2$-enriched world of the future.

Laurance *et al*. (2004a) reported accelerated growth in the 1990s relative to the 1980s for the large majority (87%) of tree genera in 18 one-hectare plots spanning an area of about 300 $km^2$ in central Amazonia, and Laurance *et al*. (2004b) observed similarly accelerated tree community dynamics in the 1990s relative to the 1980s. And in Laurance *et al*. (2005), the scientists once again suggest these "pervasive changes in central Amazonian tree communities were most likely caused by global- or regional-scale drivers, such as increasing atmospheric $CO_2$ concentrations (Laurance *et al*., 2004a,b)."

Expanding upon this theme, Laurance *et al*. (2005) interpret the observed changes as "being consistent with an ecological 'signature' expected from increasing forest productivity (cf., Phillips and Gentry, 1994; Lewis *et al*. 2004a,b; Phillips *et al*., 2004)." However, they note Nelson (2005) had challenged this conclusion, so Laurance *et al*. went on to consider his arguments in some detail, methodically dismantling them one by one.

Others questioned the findings of Phillips *et al*. (Sheil, 1995; Sheil and May, 1996; Condit, 1997; Clark, 2002; Clark *et al*., 2003), and in response to these challenges, Phillips and 17 other researchers (Lewis *et al*., 2005), including one scientist who had earlier criticized the group's conclusions, published a new analysis vindicating their earlier results.

One of the primary criticisms of Phillips *et al*.'s findings was their meta-analyses included sites with a wide range of tree census intervals (2–38 years), which critics contended could be confounding. In their detailed study of this potential problem, however, Lewis *et al*. (2005) found a re-analysis of Phillips *et al*.'s published results shows the pan-tropical increase in turnover rates over the late twentieth century "cannot be attributed to combining data with differing census intervals." Or as they state in another place, "the conclusion that turnover rates have increased in tropical forests over the late 20th century is robust to the charge that this is an artifact due to the combination of data that vary in census interval (cf. Sheil, 1995)."

Lewis *et al*. additionally note “Sheil’s (1995) original critique of the evidence for increasing turnover over the late 20th century also suggests that the apparent increase could be explained by a single event, the 1982–83 El Niño Southern Oscillation (ENSO), as many of the recent data spanned this event.” However, Lewis *et al*. report “recent analyses from Amazonia have shown that growth, recruitment and mortality rates have simultaneously increased within the same plots over the 1980s and 1990s, as has net above-ground biomass, both in areas largely unaffected, and in those strongly affected, by ENSO events (Baker *et al*., 2004a; Lewis *et al*., 2004a; Phillips *et al*., 2004).” These developments further support the view there has been an increase in forest growth rates throughout the world that has gradually accelerated over the years in concert with the historical increase in the air’s $CO_2$ concentration.

In another analysis of the subject, Lewis (2006) reports, over the prior two decades, intact tropical forests had exhibited “concerted changes in their ecology, becoming, on average, faster growing—more productive—and more dynamic, and showing a net increase in above-ground biomass,” and the rates of increase of all these factors were greater than the previously documented increases. In addition, Lewis notes “preliminary analyses also suggest the African and Australian forests are showing structural changes similar to South American forests.”

As for what had been causing this suite of concerted changes, Lewis writes, “the results appear to show a coherent fingerprint of increasing net primary productivity across tropical South America, caused by a long-term increase in resource availability (Lewis *et al*., 2004a,b).”

As to what “resources” might have been involved, Lewis postulates four possibilities: increases in solar radiation, air temperature, nutrient deposition, and atmospheric $CO_2$ concentration. After analyzing each of them in detail, he concludes, “the most parsimonious explanation is the increase in atmospheric $CO_2$, because of the undisputed long-term historical increase in $CO_2$ concentrations, the key role of $CO_2$ in photosynthesis, and the demonstrated positive effects of $CO_2$ fertilization on plant growth rates including experiments on whole temperate-forest stands (Ainsworth and Long, 2005).” As he states in another place in his review, the explanation resides in “the anthropogenic increase in atmospheric carbon dioxide concentrations, increasing forest net primary productivity leading to accelerated forest growth and dynamics.”

In light of the voluminous and undeniable real-world observations Lewis reported, it is clear that where tropical forests have not been damaged by the felling and burning of trees, forest productivity has been growing ever-greater with the passing of time, rising with the increasing $CO_2$ content of the air. Research published since 2004 suggests this view is widely shared in the scientific community.

Working in a primary rain forest in Ariuana, Brazil, Hietz *et al*. (2005) collected samples of wood from 37 tropical cedar (*Cedrela odorata* L.) trees between 11 and 151 years old in 2001 and from 16 big-leaf mahogany (*Swietenia macrophylla* King) trees between 48 and 126 years old at that time. They then measured wood cellulose $\delta^{13}C$ in 10-year growth increments. They found cellulose $\delta^{13}C$ decreased by 1.3 per mil in *Cedrela* and by 1.1 per mill in *Swietenia* over the past century, with the largest changes occurring during the past 50 years. Based on these data and known trends in atmospheric $CO_2$ and $\delta^{13}CO_2$, they calculated the intrinsic water use efficiency of the trees increased by 34% in *Cedrela* and by 52% in *Swietenia* over this period, which they say is about the same as what was deduced from similar measurements of the wood of temperate trees (Freyer, 1979; Bert *et al*., 1997; Feng, 1999). And because “water is probably not a strong limiting factor in tropical rain forest trees,” they conclude “the gain in water use efficiency translates mostly to increased carbon assimilation, which may explain the observed increase in tree growth and turnover (Phillips, 1996; Laurance *et al*., 2004),”

Three years later, Phillips *et al*. (2008) synthesized recent observational results from the network of Amazon-forest researchers known as RAINFOR (*Red Amazonica de Inventarios Forestales*), which represents the combined long-term ecological monitoring efforts of 35 institutions from around the world, with plots spanning Amazonia “from the driest southeast to the wettest northwest and the least fertile east to the most fertile west.” The team of five researchers report finding evidence for “concerted changes in the structure, dynamics and composition of old-growth Amazonian forests in the late twentieth century,” noting “in the 1980s and 1990s, mature forests gained biomass and underwent accelerated growth and dynamics, all consistent with a widespread, long-acting stimulation of growth” that was “normally distributed” and “occurred across regions and environmental gradients and through time,” indicating “continued biomass sink strength through to the end of the century.”

In numerical terms, they state, “in the late twentieth century, biomass of trees of more than

10cm diameter increased by 0.62 t C $ha^{-1}$ $yr^{-1}$ averaged across the basin," which implies "a carbon sink in Neotropical old-growth forest of at least 0.49 Pg C $yr^{-1}$." They add, "if other biomass and necromass components are increased proportionally, then the old-growth forest sink here has been 0.79 Pg C $yr^{-1}$, even before allowing for any gains in soil carbon stocks." This finding, they write, is "consistent with the evidence from recent global inversions of atmospheric $CO_2$ measurements and local aircraft measurements of atmospheric $CO_2$ profiles, showing that the tropics are either carbon-neutral or sink regions, despite widespread deforestation."

As to what has been driving these changes, the five researchers state "the simplest explanation for the ensemble result—more biomass, more stems, faster recruitment, faster mortality, faster growth and more lianas—is that improved resource availability has increased net primary productivity, in turn increasing growth rates." They conclude "the only change for which there is unambiguous evidence that the driver has widely changed and that such a change should accelerate forest growth is the increase in atmospheric $CO_2$," because of "the undisputed long-term increase in concentrations, the key role of $CO_2$ in photosynthesis, and the demonstrated effects of $CO_2$ fertilization on plant growth rates."

Lloyd and Farquhar (2008)—as part of an international workshop held at Oriel College, Oxford, UK, in March 2007—reviewed the effects of rising temperatures and atmospheric $CO_2$ concentrations on the productivity of tropical forest trees. Based on their examination of the pertinent scientific literature, and using a mixture of observations and climate model outputs together with a simple parameterization of leaf-level photosynthesis incorporating known temperature sensitivities, they could find "no evidence for tropical forests currently existing 'dangerously close' to their optimum temperature range." Quite to the contrary, they state increases in photosynthetic rates associated with increases in ambient $CO_2$ over forthcoming decades should "more than offset" any decline in photosynthetic productivity due to higher leaf temperatures, leaf-to-air vapor pressure deficits, or autotrophic respiration rates. And they affirm "the magnitude and pattern of increases in forest dynamics across Amazonia observed over the last few decades are consistent with a $CO_2$-induced stimulation of tree growth." Thus not only have past increases in the atmosphere's $CO_2$ content and temperature apparently been a boon to the productivity of Amazonia's tropical forests—as well as the world's other tropical forests—the materials reviewed by these two highly regarded scientists, as well as their own original research, indicate the productivity of Earth's tropical forests will likely rise even higher in response to predicted future increases in the atmosphere's temperature and $CO_2$ concentration.

A subsequent report by Oliver L. Phillips of the UK's University of Leeds and 65 coauthors (Phillips *et al.*, 2009) suggests a similar conclusion. The scientists note, over the prior quarter-century of intensive region-wide measurements, the productivity of the Amazon rainforest—even in its extreme old age—has been "increasing with time," in support of which they cite the comprehensive observational studies of Phillips *et al.* (1998), Nemani *et al.* (2003), Baker *et al.* (2004a), Lewis *et al.* (2004), and Ichii *et al.* (2005). In their own new study, they find, although extremely severe drought conditions can indeed bring a halt to biomass accumulation in old growth tropical forests—and sometimes even lead to minor reductions in biomass due to selective tree mortality—the vast majority of the aged trees are able to regain their photosynthetic capability and add to their prior store of biomass once the moisture stress subsides, thanks in large measure to the enhanced growth and water use efficiency experienced by nearly all woody plants as the air's $CO_2$ content rises.

Lewis *et al.* (2009) documented changes in aboveground carbon storage in 79 permanent sample plots spanning 40 years (1968–2007), located in closed-canopy moist forest, spanning West, Central, and Eastern Africa, based on data regarding more than 70,000 individual trees spread across ten countries. They found "aboveground carbon storage in live trees increased by 0.63 Mg C $ha^{-1}$ $year^{-1}$ between 1968 and 2007," and "extrapolation to unmeasured forest components (live roots, small trees, necromass) and scaling to the continent implies a total increase in carbon storage in African tropical forest trees of 0.34 Pg C $year^{-1}$."

The 33 researchers say the observed changes in carbon storage "are similar to those reported for Amazonian forests per unit area, providing evidence that increasing carbon storage in old-growth forests is a pan-tropical phenomenon," and "combining all standardized inventory data from this study and from tropical America and Asia together yields a comparable figure of 0.49 Mg C $ha^{-1}$ $year^{-1}$," which equates to "a carbon sink of 1.3 Pg C $year^{-1}$ across all tropical forests during recent decades" and could account for roughly half of the so-called missing carbon sink.

As for the identity of the driving force that seemed to have breathed new life into old trees, Lewis *et al*. write, in the concluding sentence of the abstract of their paper, "taxon-specific analyses of African inventory and other data suggest that widespread changes in resource availability, such as increasing atmospheric carbon dioxide concentrations, may be the cause of the increase in carbon stocks, as some theory (Lloyd and Farquhar, 1996) and models (Friedlingstein *et al*., 2006; Stephens *et al*., 2007; Ciais *et al*., 2008) predict."

Laurance *et al*. (2009) report what they learned while working within 20 one-hectare plots in approximately 300 $km^2$ of intact rainforests in the Amazon, where they evaluated forest dynamics over the period 1981–2003, based on data for 21,667 individual trees. Their "large-scale, long-term study appears to illustrate two contrasting patterns: (1) long-term trends in which tree mortality, recruitment, turnover, and basal area are progressively increasing over time in most (80–100%) of our study plots; and (2) shorter-term fluctuations in which strong pulses of tree mortality and poor growth have more transitory impacts on forest dynamics."

With respect to the first of these findings, Laurance *et al*. note "the increasing forest dynamics, growth and basal area observed are broadly consistent with the $CO_2$ fertilization hypothesis." With respect to the second finding, they state "tree mortality peaked, and tree recruitment and growth declined during atypically wet periods," and "tree growth was fastest during dry periods, when reduced cloudiness might have increased available solar radiation." These findings indicate the historical increase in the atmosphere's $CO_2$ concentration, driven by the burning of fossil fuels, has been good for the Amazon's trees and very likely for the rest of the region's plants and animals, even in the face of a local warming of 0.26°C per decade reported for the region since the mid-1970s.

In assessing this latter suggestion, Lapola *et al*. (2009) used a potential vegetation model (CPTEC-PVM2) "to analyze biome distribution in tropical South America under a range of climate projections," while taking into consideration the aerial fertilization and transpiration-reducing effects of atmospheric $CO_2$ enrichment. The Brazilian and German researchers say their modeling work revealed, "if the $CO_2$ 'fertilization effect' indeed takes place and is maintained in the long term in tropical forests, then it will avoid biome shifts in Amazonia in most of the climate scenarios, even if the effect of $CO_2$ fertilization is halved." They state the $CO_2$ fertilization effect, "when fully or half considered, overwhelms the impacts arising from temperature (in agreement with Lloyd and Farquhar, 2008) and even some of the precipitation changes projected by most of the global climate models, resulting in higher net primary production by the end of the century."

Gloor *et al*. (2009) write, "analysis of earlier tropical plot data has suggested that large-scale changes in forest dynamics are currently occurring in Amazonia (Phillips and Gentry, 1994; Phillips *et al*., 2004), and that an increase in aboveground biomass has occurred, with increases in mortality tending to lag increases in growth (Phillips *et al*., 1998; Baker *et al*., 2004a,b; Lewis *et al*., 2004)." However, they state this conclusion has been challenged recently by what they call an overzealous application of the "Slow in, Rapid out" dictum. This concept is based on the fact forest growth is a slow process, whereas mortality can be dramatic and singular in time, such that sampling over relatively short observation periods may miss these more severe events, leading to positively biased estimates of aboveground biomass trends, when either no trend or negative trends actually exist.

In evaluating this claim, Gloor *et al*. statistically characterize "the disturbance process in Amazon old-growth forests as recorded in 135 forest plots of the RAINFOR network up to 2006," as well as other independent research programs; and they "explored the consequences of sampling artifacts using a data-based stochastic simulator." The researchers say this work revealed, "over the observed range of annual aboveground biomass losses, standard statistical tests show that the distribution of biomass losses through mortality follow an exponential or near-identical Weibull probability distribution and not a power law as assumed by others." In addition, they write, "the simulator was parameterized using both an exponential disturbance probability distribution as well as a mixed exponential-power law distribution to account for potential large-scale blow-down events," and "in both cases, sampling biases turn out to be too small to explain the gains detected by the extended RAINFOR plot network." In light of these findings, Gloor *et al*. conclude their results lend "further support to the notion that currently observed biomass gains for intact forests across the Amazon are actually occurring over large scales at the current time, presumably as a response to climate change," which many of their earlier papers explicitly state as including the aerial fertilization effect of the historical increase in the air's $CO_2$ content.

Lewis *et al*. (2009) set out to evaluate tropical forest inventory data, plant physiology experiments, ecosystem flux observations, Earth observations, atmospheric measurements, and dynamic global vegetation models, which, "taken together," they write, "provide new opportunities to cross-validate results." The five researchers confirm both theory and experiments suggest, over the past several decades, "plant photosynthesis should have increased in response to increasing $CO_2$ concentrations, causing increased plant growth and forest biomass." Also in this regard, they report, "long-term plot data collectively indicate an increase in carbon storage, as well as significant increases in tree growth, mortality, recruitment, and forest dynamism." In addition, they confirm satellite measurements "indicate increases in productivity and forest dynamism," and "five Dynamic Global Vegetation Models, incorporating plant physiology, competition, and dynamics, all predict increasing gross primary productivity, net primary productivity, and carbon storage when forced using late-twentieth century climate and atmospheric $CO_2$ concentration data." In addition, they state "the predicted increases in carbon storage via the differing methods are all of similar magnitude (0.2% to 0.5% per year)."

"Collectively," therefore, Lewis *et al.* conclude, "these results point toward a widespread shift in the ecology of tropical forests, characterized by increased tree growth and accelerating forest dynamism, with forests, on average, getting bigger (increasing biomass and carbon storage)"—results just the opposite of what IPCC predicted.

Friend (2010) worked with the Hybrid6.5 model of terrestrial primary production, which simulates the carbon, nitrogen, phosphorus, water and energy fluxes, and structural changes in terrestrial ecosystems at hourly to decadal timescales and at spatial scales ranging from individual plants to the whole Earth, while employing the climate change anomalies predicted by the GISS-AOM GCM under the A1B emissions scenario for the 2090s relative to observed modern climate. With atmospheric $CO_2$ increased from 375.7 ppm to 720 ppm—a 92% increase—Friend calculated the percentage changes in terrestrial plant production that would occur throughout the world in response to (1) the projected climate changes alone and (2) the projected concurrent changes in climate and atmospheric $CO_2$ concentration.

In response to the projected climate changes alone between 2001–2010 and 2091–2100, the net primary production (NPP) of the entire planet was reduced by 2.5%, with the largest negative impacts occurring over southern Africa, central Australia, northern Mexico, and the Mediterranean region, where reductions of more than 20% were common. At the other extreme, climatic impacts were modestly positive throughout most of the world's boreal forests, as might have been expected when these colder regions received an influx of welcome heat.

But when both climate and atmospheric $CO_2$ concentrations were changed concurrently, the story was vastly different, with a mean increase in global NPP of 37.3%, driven by mean increases of 43.9–52.9% among $C_3$ plants and 5.9% among $C_4$ species. In this case of concurrent increases in the globe's air temperature and $CO_2$ concentration, the largest increases occurred in tropical rainforests and $C_3$ grass and croplands.

Jaramillo *et al.* (2010) looked back in time—way back in time—to the days of the Paleocene-Eocene Thermal Maximum (PETM) of some 56 million years ago, which they note "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 driven, as they describe it, 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)." During this period of warming, according to many scientists, Earth's tropical ecosystems "suffered extensively because mean temperatures are surmised to have exceeded the ecosystems' heat tolerance (Huber, 2008)."

In an attempt to discover whether that warming did major damage to 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. Their work reveals—contrary to the prevailing wisdom of the recent past—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." And they report this increase in biodiversity "was permanent and not transient."

In discussing their findings, Jaramillo *et al.* write, "today, most tropical rainforests are found at mean annual temperatures below 27.5°C," and they note several scientists have argued "higher temperatures could be deleterious to the health of tropical ecosystems," citing Huber (2008, 2009) and Tewksbury *et al.* (2008) in this regard. They report tropical warming during the PETM was postulated to have produced intolerable conditions for tropical ecosystems. Nevertheless, they reiterate, at the sites they studied, "tropical forests were maintained during the warmth of the PETM (~31° to 34°C)," concluding "it is possible that higher Paleocene $CO_2$ levels (Royer, 2010) contributed to their success."

Rasineni *et al.* (2011a) introduce their study by explaining "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 "plants grown in tropical climates usually experience significantly high irradiance leading to the strong midday depression of photosynthesis (Hymus *et al.*, 2001)."

To investigate how this problem might be overcome, the authors conducted an experiment utilizing two open-top chambers in the Botanical Gardens of the University of Hyderabad, India. Each chamber contained four six-month-old specimens of the fast-growing tropical *Gmelina arborea* tree, which they maintained at optimum moisture and nutrient levels. During the course of their experiment the three scientists measured several plant physiological properties and processes related to leaf photosynthesis and photosystem II (PSII) photochemistry and photoinhibition 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."

Their work revealed no significant differences in $CO_2$ assimilation rates between the ambient- and elevated $CO_2$-grown plants during early morning hours; but thereafter, they report, "photosynthesis 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%. For the more standard $CO_2$ enrichment of 300 ppm, that would be roughly equivalent to an enhancement of 180%. Subsequently, during the following midday period of 1100–1300 hours, the rate of net photosynthesis 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 which 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.

Bonal *et al.* (2011) introduce their work by writing, "an increase in tree radial growth increment over recent decades in Amazonian tropical rainforests has been observed, leading to increased above-ground biomass at most study sites," citing Phillips *et al.* (1998, 2009) and Malhi *et al.* (2004), noting "the stimulating impact on photosynthesis of increased $CO_2$ concentrations in the air ($C_a$) could explain these growth patterns (Lloyd and Farquhar, 2008)." Further investigating this phenomenon, the 11 researchers assessed the impacts of historical environmental changes on several leaf morphological and physiological traits of two tropical rainforest species (*Dicorynia guianensis*; *Humiria balsamifera*) abundant in the Guiana shield (Northern Amazonia), working with leaf samples from different international herbariums that covered a 200-year time period (AD 1790–2004).

Bonal *et al.* state their results revealed "a clear response of leaf physiological characteristics to increasing $C_a$ for both species," consistent with previous studies "from different ecosystems (Penuelas and Azcon-Bieto, 1992; Beerling *et al.*, 1993; Van de Water *et al.*, 1994; Pedicino *et al.*, 2002; Penuelas *et al.*, 2008), and with data from tree rings in Europe (Bert *et al.*, 1997; Duquesnay *et al.*, 1998; Saurer *et al.*, 2004), Africa (Gebrekirstos *et al.*, 2009) and in tropical rainforests (Hietz *et al.*, 2005; Silva *et al.*, 2009; Nock *et al.*, 2011)." More specifically, they say their results point to "an increase in water use efficiency over recent decades of about 23.1 and 26.6% for *Humiria* and *Dicorynia*, respectively," driven mostly by increases in leaf photosynthesis. And they state "the range of change in water use efficiency for these two species was consistent with many results observed not only in tropical forests (Hietz *et al.*, 2005; Nock *et al.*, 2011), but in boreal (Saurer *et al.*, 2004) and temperate forests (Francey and Farquhar, 1982; Penuelas and Azcon-Bieto, 1992; Bert *et al.*, 1997; Duquesnay *et al.*, 1998)." Bonal *et al.* conclude the responses of the two tree species they studied to increasing $C_a$ appear to be "simply related to the availability of $CO_2$ in the air (fertilization effect)," and "this trend seems to be consistent with recent tree growth patterns in the Amazonian region."

Rasineni *et al.* (2011b) describe growing well-watered and -fertilized five-week-old fast-growing

*Gmelina arborea* trees out-of-doors at the University of Hyderabad, India, in open-top chambers maintained at ambient and ambient+100 ppm atmospheric $CO_2$ concentrations throughout the 120 days of that region's spring and summer seasons, while they periodically made numerous measurements of the trees' physical properties and physiological prowess. The trees in the modestly elevated $CO_2$ chambers exhibited net photosynthetic rates 38% greater than the trees growing in ambient air. Also, aided by a significant $CO_2$-induced reduction in leaf transpiration rates, the mean instantaneous water use efficiency of the leaves of the $CO_2$-enriched trees was 87% greater than the ambient-treatment trees. As a result of these $CO_2$-induced plant physiological benefits, the above-ground biomass of the $CO_2$-enriched trees at the end of the growing season was 45% greater than the trees growing in ambient air, and their total biomass (above and below ground) was 53% higher.

In discussing their findings, Rasineni *et al*. note elevated atmospheric $CO_2$ "persistently enhanced all the growth characteristics in *Gmelina*, including plant height, number of branches, internodes, internodal distance, aerial biomass and total plant biomass." They suggest "high sink demand and better growth dynamics" are what led to the huge sustained increase in carbon sequestration in the tropical deciduous tree. They conclude their findings indicate "there are management options for creating short-rotation deciduous tree plantations to achieve increased sequestration of carbon in a future elevated $CO_2$ environment."

Dick *et al*. (2012) introduce the final study we review here by noting, "tropical rain forest has been a persistent feature in South America for at least 55 million years" and "at times in the past, Amazon surface air temperatures have been higher than those today," citing Feely and Silman (2010), Hoorn *et al*. (2010), Jaramilo *et al*. (2010), and Haywood *et al*. (2011). They also report "experiments show that tropical plants can photosynthesize and maintain a positive carbon balance under higher temperatures than those occurring today (Krause *et al*., 2010; Way and Oren, 2010)." So the question naturally arises: How high can Amazon temperatures rise and its trees still survive?

Dick *et al*. hypothesize "the older the age of a species prior to the Pleistocene, the warmer the climate it has previously survived," noting Pliocene and late-Miocene air temperatures of 2.6 to 5 million years ago (Ma) and late-Miocene air temperatures of 8 to 10 Ma across Amazonia were "similar to AD 2100 temperature projections under low and high carbon emission scenarios, respectively." They note "some 56.3 Ma during the Paleocene-Eocene Thermal Maximum (PETM), global mean temperature increased by 5–6°C over a period of <= 20 ka," citing Haywood *et al*. (2011). And they affirm "fossil pollen from the PETM showed an increase in tree diversity in three South American rainforest sites with abundant rainfall (Jaramillo *et al*., 2010)." Thus they used comparative phylogeographic analyses to determine the age of the tropical tree *species* currently found in Amazonia. The four researchers report, "9 of 12 widespread Amazon tree species have Pliocene or earlier lineages (>2.6 Ma), with seven dating from the Miocene (>5.6 Ma) and three >8 Ma."

Based on these findings, Dick *et al*. conclude "the remarkably old age of these species suggests that Amazon forests passed through warmth similar to AD 2100 levels [predicted by climate models] and that in the absence of other major environmental changes, near-term high temperature-induced mass species extinction is unlikely."

These and the many other positive findings of the studies reviewed above indicate rising atmospheric $CO_2$ concentrations probably will enhance the rates of photosynthesis and biomass production of tropical and sub-tropical trees, even under conditions of herbivory, water stress, and elevated air temperature. That, in turn, likely will allow greater sequestration of carbon in Earth's tropical and sub-tropical forests.

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### *1.2.1.2 Other Forest Observations*

- Forest growth rates throughout the world have gradually accelerated over the years in concert with, and in response to, the historical increase in the air's $CO_2$ concentration. As the atmosphere's $CO_2$ concentration rises, forests likely will respond by exhibiting significant increases in biomass production, and thus likely will grow much more robustly and significantly expand their ranges, as is already being documented in many parts of the world.

In a small booklet published by the University of Minnesota (USA) nearly two decades ago, Idso (1995) laid out the evidence for a worldwide increase in the growth rates of Earth's forests coeval with the progression of the Industrial Revolution and the rising $CO_2$ content of the atmosphere. The development of this concept began with LaMarche *et al*. (1984), who analyzed annual growth rings of two species of pine tree growing near the timberline in California, Colorado, Nevada, and New Mexico, and in doing so discovered large increases in growth rate between 1859 and 1983, which exceeded what might have been expected from climatic trends but were consistent with the global trend of atmospheric $CO_2$.

The next stage of the research was inspired by a study of ring-width measurements of Douglas fir trees in British Columbia, Canada, which also revealed a marked increase in the growth rates of the trees in later decades (Parker *et al*., 1987). This finding led the principal investigator of the project to state "environmental influences other than increased $CO_2$ have not been found that would explain this [phenomenon]." West (1988) reports much the same thing with respect to long-leaf pines in Georgia—their annual growth increments had begun to rise at an unusual rate about 1920, increasing by approximately 30% by the mid-1980s. He states, "the increased growth cannot be explained by trends in precipitation, temperature, or Palmer Drought Severity Index," leaving the rising $CO_2$ content of the atmosphere as the likely cause of the observed increase in productivity.

Contemporaneously, stands of Scots pines in northern Finland were found to have experienced growth increases ranging from 15 to 43% between 1950 and 1983 (Hari *et al*., 1984; Hari and Arovaara, 1988). As for the cause of this phenomenon, the researchers involved in the work state "$CO_2$ seems to be the only environmental factor that has been changing systematically during this century in the remote area under study," and it was thus to this factor that they looked for an explanation of their observations.

A few years later, Graybill and Idso (1993) reported very long ring-width chronologies (some stretching back nearly 1,800 years) of high-altitude, long-lived bristlecone, foxtail, and limber pine trees in Arizona, California, Colorado, and Nevada all showed an unprecedented upward growth trend beginning in the 1850s that continued as far toward the present as the records extended. Comparisons of the chronologies with temperature and precipitation records ruled out the possibility either of these variables played a significant role in enhancing the trees' growth rates, strongly implicating the historical rise in the air's $CO_2$ concentration as the factor responsible for their ever-increasing productivity over the prior century and a half.

Duquesnay *et al*. (1998) analyzed the relative amounts of $^{12}C$ and $^{13}C$ present in yearly growth rings of beech trees raised in silviculture regimes in northeastern France. They discovered the trees' intrinsic water-use efficiencies rose by approximately 33% during the prior century, as the atmosphere's $CO_2$ concentration rose from approximately 280 to 360 ppm. Rathgeber *et al.* (2000) used tree-ring density data to create a historical productivity baseline for forest stands of *Pinus halepensis* in southeastern France, from which they determined the net productivity of such forests likely would increase by 8 to 55% with a doubling of the air's $CO_2$ content.

Running a forest growth model based on empirical observations reported in the literature, Lloyd (1999) determined the rise in the atmospheric $CO_2$ concentration since the onset of the Industrial Revolution likely increased the net primary productivity of mature temperate deciduous forests by about 7%. In addition, he determined a proportional increase in anthropogenic nitrogen deposition likely increased forest net primary productivity by 25%. When he combined the two effects, the net primary productivity stimulation rose to 40%, which, as a result of synergetic interactions, was actually more than the sum of the growth enhancements resulting from the individual increases in $CO_2$ and nitrogen acting by themselves.

Medlyn *et al.* (1999) conducted a meta-analysis of data from 15 atmospheric $CO_2$ enrichment studies of European forest species growing in field environments to determine their overall photosynthetic response to elevated (approximately doubled) atmospheric $CO_2$ concentrations. The resulting meta-analysis by the 21 researchers revealed the twice-ambient $CO_2$ concentrations stimulated the trees' net photosynthetic rates by an average of 51%.

In 1996, circular Free-Air $CO_2$ Enrichment (FACE) plots (30m diameter) maintained at atmospheric $CO_2$ concentrations of 360 and 560 ppm were established in a 15-year-old loblolly pine (*Pinus taeda*) plantation in North Carolina, USA, to study the effects of elevated $CO_2$ on the growth and productivity of this particular forest community, which also had several hardwood species present in its understory. Based on some of the first sets of data to come out of this endeavor, Hymus *et al.* (1999) report net photosynthetic rates of the $CO_2$-enriched loblolly pines trees were 65% greater than rates observed in control trees exposed to ambient air. These greater rates of carbon fixation contributed to the 24% greater growth rates observed in the $CO_2$-enriched pine trees in the first year of this long-term study, according to Naidu and DeLucia (1999). In addition, DeLucia and Thomas (2000) report the elevated $CO_2$ increased rates of net photosynthesis by 50 to 160% in four subdominant hardwood species present in the forest understory. Moreover, for one species—sweetgum (*Liquidambar styraciflua*)—the extra $CO_2$ enhanced the rates of net photosynthesis in Sun and shade leaves by 166 and 68%, respectively, even when the trees were naturally subjected to summer seasonal stresses imposed by high temperature and low soil water availability, as Herrick and Thomas (1999) report. After two years of atmospheric $CO_2$ enrichment, total ecosystem net primary productivity in the $CO_2$-enriched plots was found to be 25% greater than what was measured in control plots fumigated with ambient air.

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

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

Near the turn of the century, therefore, it was becoming quite clear that as the atmosphere's $CO_2$ concentration continued to rise, forests likely would respond by exhibiting significant increases in biomass production, with the result that they likely would grow much more robustly and significantly expand their ranges, as was already being documented in many parts of the world, including Kansas, USA (Knight *et al*., 1994) and the Budal and Sjodal valleys of Norway (Olsson *et al*., 2000).

In the first of these cases, aerial photographs taken over a 46-year period were used to analyze the dynamics and spatial extent of gallery forest on the Konza Prairie Research Natural Area (KPRNA) in Kansas, USA, between 1939 and 1985. Over the 46-year period of study, total gallery forest area increased from 157 hectares to 241 hectares. Looking further back in time and studying additional historical information obtained from the Original Land Office Surveys of KPRNA, the scientists found total forest area in the region increased fully 97% between 1859 and 1939, leading Knight *et al*. to conclude there was "no question that the absolute amount of forested areas has increased."

Taking an even longer view of the subject, the explorer Coronado in 1541 stated, in reference to the Great Plains of America, "there is not any kind of wood in all these plains, away from the gullies and rivers, which are very few." Clearly, therefore, a dramatic increase in forest growth has occurred in this region since that time, and especially over the last century and a half. One of the reasons for this increase is certainly the historical increase in Earth's atmospheric $CO_2$ concentration. Rising from a value of 265 ppm at the time of Coronado, to a value of 370 ppm in 1994, the increased $CO_2$ likely had a pronounced positive impact on the photosynthesis and growth of woody species on every continent of the globe where trees are found, as has been further elucidated by Idso (1995).

In Norway, domestic livestock have been raised on mountains for the past 4,000 years, but especially since the sixteenth century, which saw the development of the summer farming system there. Olsson *et al*. (2000) thus speculated this activity originally reduced forested areas, and changes in farming practices more recently allowed the forests to return. Investigating this hypothesis, they studied two valleys—Budal and Sjodal—in mid-Norway, which they say were representative of core areas of the Norwegian summer farming ecosystems "shaped by human activities rooted in pre-history." Specifically, they analyzed changes in land use and landscape patterns in the two areas over the period 1960–1993. This work revealed grasslands and heathlands that had long dominated the mountain slopes of the two study areas were, in their words, "today decreasing due to forest invasion," which they say is characterized by "the spread of subalpine woodlands, and a raised treeline."

Olsson *et al*. conclude the expansion of the subalpine Norwegian woodlands was "primarily related to changes in the human use of those areas," which in their estimation were "much more influential than possible effects of climate change." However, it is also possible the concurrent rise in the atmosphere's $CO_2$ concentration may have played a role in the forests' comeback. In any event, the ongoing increase in the presence of forests in the mountain valleys of Norway is but one more manifestation of the spreading of woody species over the face of the planet, which is helping to slow the rate of rise of the atmosphere's $CO_2$ concentration.

Walker *et al*. (2000) grew ponderosa pine (*Pinus ponderosa* Dougl.) seedlings for five years in open-top chambers having atmospheric $CO_2$ concentrations of 350, 525, and 700 ppm on soils of low, medium, and high nitrogen content, to determine the interactive effects of these two variables on the long-term growth response of this particular tree species. They found the moderate level of atmospheric $CO_2$ enrichment (525 ppm) had the greatest effect on tree height and trunk diameter in the first three years of the experiment. By years four and five, trees grown at 700 ppm $CO_2$ exhibited the greatest growth responses to elevated $CO_2$. At final harvest, the trees exposed to 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 levels of soil nitrogen, respectively. Similarly, trunk diameters of trees fumigated with 700 ppm $CO_2$ for five years were 24, 73, and 20% greater than trunk diameters of ambiently grown trees exposed to high, medium, and low levels of soil nitrogen.

Naumburg and Ellsworth (2000) measured photosynthetic rates in leaves of four hardwood saplings growing beneath the canopy of a *Pinus taeda* forest, several portions of which were exposed to either ambient or enriched (ambient + 200 ppm) atmospheric $CO_2$ concentrations in a FACE study spanning two years. The measurements were made under conditions of both low and high light intensity, which commonly exist beneath maturing forest canopies because of shading and intermittent illumination by sunflecks, respectively. Thus the two researchers studied the effects of elevated $CO_2$ on sapling performance under the variable light conditions prevailing beneath the canopies of real-world forests.

The data indicate elevated $CO_2$ increased the mean photosynthetic rates of four hardwood understory saplings by 60 and 40% under high and low light conditions, respectively. Also, in going from shaded to lighted conditions, elevated $CO_2$ had no effect on photosynthetic induction, with ambient and $CO_2$-enriched species both reaching 90% of their maximal transient photosynthetic rates at approximately the same time. However, in going from lighted to shaded conditions, elevated $CO_2$ extended the time during which maximal rates of photosynthesis were maintained. Thus, elevated $CO_2$ slowed the rate of photosynthetic decline caused by the onset of shading, and as a result, the shaded leaves of $CO_2$-enriched saplings maintained greater rates of photosynthesis for longer periods of time than did shaded leaves of saplings growing in ambient air, which allowed the $CO_2$-enriched leaves to sequester greater amounts of carbon than was expected from photosynthetic measurements made under steady-state conditions.

As the air's $CO_2$ content rises, therefore, saplings growing beneath the canopies of larger trees will likely increase their rates of photosynthesis under both high and low light conditions characteristic of intermittent shading and illumination by sunflecks. Moreover, because elevated $CO_2$ concentrations allow saplings to maintain higher rates of photosynthesis for longer periods of time when going from lighted to shaded conditions, such trees should be able to sequester greater quantities of carbon than they do now. So powerful is this phenomenon, in fact, the two researchers state current estimates of the enhancement of long-term carbon gains by forests under conditions of elevated atmospheric $CO_2$ "could be underestimated by steady-state photosynthetic measures."

Hamilton *et al.* (2001) investigated the short- and long-term respiratory responses of loblolly pine (*Pinus taeda*) and sweetgum (*Liquidambar styraciflua*) trees to the ambient and elevated atmospheric $CO_2$ concentrations (360 and 560 ppm) of the 30-meter-diameter FACE plots of the long-running loblolly pine plantation experiment in North Carolina, USA, where the deciduous trees had naturally established themselves beneath the primarily coniferous canopy. They report the modest 200 ppm increase in atmospheric $CO_2$ concentration resulted in no significant short-term suppression of dark respiration rates in needles of loblolly pine. It did, however, reduce rates of dark respiration in sweetgum leaves by an average of 10%. The long-term exposure to elevated $CO_2$ also did not appear to alter maintenance respiration, which is the amount of $CO_2$ needed to maintain existing tissue, in either of the tested species. But growth respiration, the amount of $CO_2$ respired when constructing new tissues, was reduced by 21% in loblolly pine and 39% in sweetgum leaves that reached the top of the canopy. Thus, as the air's $CO_2$ content rises, it is likely these two forest species will exhibit increased rates of photosynthesis that will provide them with more of the raw materials required for constructing new and greater amounts of biomass, and the costs of respiration during the synthesis of new tissues likely will be reduced, thus allowing greater amounts of carbon to be retained in the trees and thereby helping to reduce the rate of rise of the atmosphere's $CO_2$ concentration.

Working at the same location, Hussain *et al.* (2001) collected seeds from trees exposed to both atmospheric $CO_2$ concentrations to study the effects of elevated $CO_2$ on seed characteristics, germination success, and early seedling growth. Seeds collected from $CO_2$-enriched trees were 91% heavier than seeds collected from trees growing in ambient air. In addition, the $CO_2$-enriched seeds had a lipid content 265% greater than that observed in seeds produced on the ambient-treatment trees, and the germination success for seeds developed under atmospheric $CO_2$ enrichment was more than three times greater than control seeds developed at ambient $CO_2$, regardless of germination $CO_2$ concentration. Also, the seeds from the $CO_2$-enriched trees germinated approximately five days earlier than their ambiently produced counterparts, again regardless of germination $CO_2$ concentration. And seedlings developing from seeds collected from $CO_2$-enriched trees displayed significantly greater root lengths and needle numbers than those developing from trees exposed to ambient air, also regardless of current growth $CO_2$ concentration. Thus, as the $CO_2$ content of the air increases, loblolly pine trees likely will display significant increases in their photosynthetic rates, and the enhanced carbohydrate supplies resulting from this phenomenon likely will be used to increase seed weight and lipid content. These seeds consequently should exhibit significant increases in germination success, and their enhanced lipid content likely will lead to greater root lengths and needle numbers in developing seedlings. Thus, when these seedlings become photosynthetically active, they likely will photosynthesize and produce biomass at greater rates than those currently exhibited by seedlings growing under ambient $CO_2$ concentrations, in a positive cycle that keeps repeating.

Kellomaki and Wang (2001) grew birch seedlings (*Betula pendula* Roth.) for approximately five months in enclosed environmental chambers maintained at atmospheric $CO_2$ concentrations of 350 and 700 ppm. The seedlings were simultaneously exposed to ambient or elevated (ambient plus 3°C) air temperatures to study the interactive effects of elevated $CO_2$ and temperature on the growth of this common boreal forest species. During the most rapid phase of growth observed in the study, elevated $CO_2$ increased rates of net photosynthesis by 21 and 28% at the ambient and elevated air temperatures, respectively. These increases in carbon uptake led to corresponding biomass increases of 17 and 18%, which suggest boreal forests likely will increase their carbon-sequestering abilities, locking up increasing amounts of carbon within their woody tissues as the air's $CO_2$ content increases.

Hamilton *et al.* (2002) report what they learned from the Duke Forest FACE Experiment over four years. This ecosystem—a predominantly loblolly pine (*Pinus taeda* L.) forest with sweetgum (*Liquidambar styraciflua* L.) and yellow poplar (*Liriodendron tulipifera* L.) trees as sub-dominants, together with numerous other trees, shrubs, and vines—was established in 1983 following the clear-cutting of a regenerating forest in 1979. The experiment was begun in August 1996, when three 30-meter-diameter FACE plots were enriched with $CO_2$ to atmospheric concentrations 200 ppm above ambient, and three similar plots were maintained at ambient conditions as controls. Based on the standing pool of ecosystem biomass in 1998 and more recent measurements of various carbon fluxes, Hamilton *et al.* calculated a complete carbon budget for the forest for that particular year. They found the extra $CO_2$ supplied to the FACE plots stimulated net ecosystem productivity (NEP) by 41%, and for a 300 ppm increase in atmospheric $CO_2$ concentration—the most common increment of $CO_2$ enrichment employed in $CO_2$ enrichment experiments over the years—this result translates into a $CO_2$-induced NEP increase on the order of 60%. That improvement represents a significant stimulation of biological carbon sequestration, especially for trees growing on a soil the researchers described as being of "low nitrogen and phosphorus availability."

Norby *et al.* (2002) describe a FACE study established in a ten-year-old stand of sweetgum (*Liquidambar styraciflua* L.) trees growing in a forest plantation on nutrient-rich soils in Tennessee, USA, where the trees were exposed to atmospheric $CO_2$ concentrations of 360 and 550 ppm. In response to that $CO_2$ increase, ecosystem net primary productivity rose by 21% in all three years of their study; aboveground woody biomass rose by 33% in the first year, 15% in the second year, and 7% in the third year; and net primary productivity remained unchanged. The biomass drop occurred because an increasing amount of newly fixed carbon in the $CO_2$-enriched trees was being utilized to increase fine-root and leaf production in each progressive year. Over the three-year period of their study, however, 77% of the additional fixed carbon was nevertheless allocated to aboveground woody biomass, leading the 11 researchers to conclude, "this experiment has provided the first evidence that $CO_2$ enrichment can increase productivity in a closed-canopy deciduous forest."

Rathgeber *et al.* (2003) used tree-ring width and density chronologies (both earlywood and latewood) from 21 stands of Aleppo pine (*Pinus halepensis* Mill.) in the Provence region of southeast France to calibrate the BIOME3 biogeochemistry model of forest productivity in terms of growth responses to known historical changes in atmospheric temperature, precipitation, and $CO_2$ concentration. They then used the BIOME3 model to calculate changes in the mean productivity of the same forest stands expected to result from changes in these parameters driven by a doubling of the air's $CO_2$ content, as calculated by Meteo-France's ARPEGE atmospheric general circulation model when downscaled to that specific part of the country. In response to the predicted changes in climate, forest productivity increased moderately for all stands (17% to 24%); in response to the aerial fertilization effect of the doubling of the atmosphere's $CO_2$ concentration, it increased considerably more (72% to 86%). Even more impressively, when the climatic changes and atmospheric $CO_2$ increase were considered together, forest productivity increased still more (107% to 141%). That response was greater than that provided by the sum of their individual contributions, as a result of the amplifying synergy among these factors with respect to their combined impact on basic plant physiological processes.

Bergh *et al.* (2003) used a boreal version of a process-based simulation model (BIOMASS) to quantify the individual and combined effects of elevated air temperature (2 and 4°C above ambient) and $CO_2$ concentration (350 ppm above ambient) on the net primary production (NPP) of both coniferous (*Pinus sylvestris*, *Picea abies*) and deciduous broad-leaf (*Fagus sylvatica*, *Populus trichocarpa*) forests growing in Denmark, Finland, Iceland, Norway, and

Sweden. For three of the four species (*P. sylvestris*, *P. abies*, *P. trichocarpa*), air temperature increases of 2 and 4°C led to mean NPP increases of 11 and 20%, respectively. For the other species (*F. sylvatica*), there were corresponding 21 and 48% decreases in NPP. When the atmosphere's $CO_2$ concentration was simultaneously increased from 350 to 700 ppm, the corresponding mean NPP increases of the three-species group rose to 41 and 55%, and the NPP of *F. sylvatica* jumped from -21 and -48% to +37 and +10%. Finally, when the atmosphere's $CO_2$ content was doubled at the prevailing ambient air temperature, the mean NPP value of the three-species group rose by 27%, and *F. sylvatica* rose by 58%. Consequently, as the air's $CO_2$ content climbs higher, the major tree species of Denmark, Finland, Iceland, Norway, and Sweden should become significantly more productive, and if air temperature also rises, most of them will grow even better.

In a study conducted at the Poplar Free Air $CO_2$ Enrichment (PopFACE) facility described by Miglietta *et al*. (2001), located near Viterbo in Central Italy, Bernacchi *et al*. (2003) worked with three hybrid poplars they describe as "so fast growing that they provide a rare opportunity to grow a plantation forest from planting to canopy closure of tall trees (greater than 9 m) in just 3 years." This was done in a field previously used for wheat cultivation planted with the hybrid *Populus* x *euramericana* Dode (Guinier)—(*P. deltoides* Bart. ex Marsh. x *P. nigra* L., I–214)—with the exception of six 30m x 30m square plots that each contained a 22m-diameter FACE ring. Three of the rings were maintained at 370 ppm $CO_2$, and the other three were maintained at 550 ppm $CO_2$. Within each of them were grown equal-area sections of *P. alba* L. (genotype 2AS1), *P. nigra* L. (genotype Jean Pourtet), and *P. x euramericana* (genotype I–214), which were maintained free of drought by a drip irrigation system. Periodic measurements of net photosynthesis and stomatal conductance were made over the three-year period of growth from the seedling to closed-canopy forest stage.

Bernacchi *et al*. found no response of leaf stomatal conductance to atmospheric $CO_2$ enrichment. In the case of net photosynthesis, however, the team of seven scientists observed a 38% increase in light-saturated net photosynthesis at 25°C, which they describe as being "close to the maximum theoretically possible," in response to the 49% increase in atmospheric $CO_2$ concentration employed in their study. Daily integrated rates of *in situ* photosynthesis were even higher, rising by 40% to almost 90% (approximately equivalent to 150% in response to a 300 ppm increase in the air's $CO_2$ concentration). The cause of this increase, Bernacchi *et al*. write, was "daytime leaf temperatures were typically over 30°C resulting in a larger stimulation of leaf photosynthesis by elevated $CO_2$ than would be evident at 25°C (Long, 1991)." This stimulation of daily net photosynthesis illustrates the enormous potential for Earth's trees, even in closed-canopy forests, to respond positively to the ongoing rise in the air's $CO_2$ content.

Su and Sang (2004) used an ecosystem process model, BIOME-BGC, to explore the sensitivity of the net primary productivity (NPP) of an oak (*Quercus liaotungensis* Koidz) forest ecosystem in the Beijing area of China to global climate changes projected to be caused by rising atmospheric $CO_2$ concentrations. Under a doubling of the air's $CO_2$ concentration from 355 to 710 ppm, the Beijing oak forest's NPP was calculated to rise by 14.0%, and with a concomitant temperature increase of 2°C, its NPP was calculated to rise by 15.7%. With an additional 20% increase in precipitation, it rose by 25.7%. Finally, with a 20% increase in precipitation and a 4°C increase in temperature, it rose by 25.7%.

In contrast to typical model-based claims of future climate, researchers find many projections of ecosystem responses to potential environmental change are not catastrophically negative, even when the increases in air temperature they employ are unrealistically large, such as the 4°C rise employed by Su and Sang. In fact, as in this particular case, many of the responses are actually positive, and strongly so.

One of the reasons for this discrepancy is the tendency of modelers to downplay or disregard altogether the many mitigating effects of atmospheric $CO_2$ enrichment, including increased plant growth, significantly reduced plant water loss by transpiration and thereby greatly enhanced plant water use efficiency, and physiological changes to plants to where they prefer warmer temperatures, a phenomenon expressed by an increase in the temperature at which plants photosynthesize most efficiently. Any projections of ecosystem responses to potential climate change, and especially those that assume the rising $CO_2$ content of the atmosphere is their cause, must include these very real phenomena. And when they are included, the results are often positive, as in the work of Su and Sang.

Hanson *et al*. (2005) used models that performed well in a multiyear simulation of the current carbon and water budgets of an upland-oak forest (Hanson *et al*., 2004) to evaluate the influence of single and multifactor environmental change scenarios projected for 2100, with and without modifications to account for physiological and growth responses learned from long-term field experimental studies (Winnett, 1998). The environmental changes they evaluated were a 385 ppm increase in $CO_2$, a 20 ppb increase in $O_3$, a 4°C increase in temperature, and a 20% increase in winter precipitation, and the responses to those changes "were derived primarily from field experimental studies on deciduous trees and forest systems."

Initial simplistic model projections of annual net ecosystem carbon exchange (NEEa) for the single-factor change scenarios yielded NEEa responses of +191% for $CO_2$, -206% for temperature, 0% for precipitation, and -35% for $O_3$; the combined influence of the four environmental changes yielded a 29% reduction in mean NEEa. However, as Hanson *et al*. report, "when experimentally observed physiological adjustments were included in the simulations (e.g. acclimation of leaf respiration to warming), the combined influence of the year 2100 scenario resulted in a 20% increase in NEEa, not a decrease." In addition, "consistent with the annual model's predictions, simulations with a forest succession model run for gradually changing conditions from 2000 to 2100 indicated an 11% increase in stand wood biomass in the future compared with current conditions." Thus, even with the unrealistically extreme temperature change investigated in their study, which came from IPCC's Third Assessment Report (Houghton *et al*., 2001) and the US National Assessment Synthesis Team's report on climate-change impacts (NAST, 2000), the knowledge gained from real-world experiments demonstrates desirable plant responses to atmospheric $CO_2$ enrichment are sufficient to override the negative influence of inflated warming and produce a significant enhancement in NEEa.

In a study published in the *Proceedings of the National Academy of Sciences*, a team of 19 researchers (Norby *et al*., 2005) note "experiments have unequivocally shown that plants can grow faster and larger in a $CO_2$-enriched atmosphere, and the mechanisms of response are well understood." Furthermore, they state computer simulations of climatic responses to atmospheric $CO_2$ "will be incorrect if the magnitude of the $CO_2$ fertilization effect is not represented accurately." To help overcome this deficiency (but one of many inherent in even the most advanced of today's climate models (Lupo and Kininmonth, 2013)), they provide an analysis of the net primary productivity (NPP) response of closed-canopy forests to increases in the air's $CO_2$ concentration in the only Free-Air $CO_2$ Enrichment (FACE) studies conducted on assemblages of trees large enough and spatially concentrated enough to meet this important criterion of realism.

The four multiyear experiments Norby *et al*. analyzed were: (1) the Duke-FACE study near Durham, North Carolina, USA, which was initiated in an established monoculture plantation of evergreen loblolly pine (*Pinus taeda*) trees, (2) the ORNL-FACE study near Oak Ridge, Tennessee, USA, which was initiated in an established monoculture of deciduous sweetgum (*Liquidambar styraciflua*) trees, (3) the Aspen-FACE study near Rhinelander, Wisconsin, USA, which was initiated on bare ground but ultimately comprised multi-tree assemblages dominated by *Populus* species, and (4) the POP-EUROFACE study near Tuscania (Viterbo), Italy, which also was initiated on bare ground and ultimately comprised of multi-tree assemblages dominated by *Populus* species.

To be compatible with the first two experiments in terms of the trees' state of development, no data were used from the latter two experiments until the trees had grown to the point where their canopies were completely closed. Under these conditions, and across all appropriate years of all experiments (six years in the Duke-FACE study, five years in the ORNL-FACE study, one and three years in different portions of the Aspen-FACE study, and two years in the POP-EUROFACE study), the average atmospheric $CO_2$ concentration in the ambient-air control plots was 376 ppm, and the average concentration in the $CO_2$-enriched plots was 550 ppm, yielding an average $CO_2$ concentration differential of 174 ppm between the two $CO_2$ treatments.

In what the four groups of researchers describe as a "surprising consistency of response across diverse sites," they found forest NPP was enhanced by 23 ± 2% at the median NPP of their combined data set in response to the 174 ppm increase in the air's $CO_2$ concentration. This NPP stimulation is substantial, considering most of the $CO_2$ stimulation figures seen in the scientific literature are for a 300 ppm increase in atmospheric $CO_2$ concentration. Linearly extrapolating Norby *et al*.'s median result to correspond to this greater $CO_2$ concentration differential yields a NPP stimulation of approximately 40% or just slightly less, because as the air's $CO_2$ content rises, the NPP stimulation provided by extra $CO_2$ rises slightly more slowly.

Norby *et al*. note the data in their analyses came from "fast-growing, early successional stands, and there had been no evidence to date for a negative feedback on NPP through nitrogen availability in these stands," as some had suggested would occur. Norby *et al*. confidently conclude, "the effect of $CO_2$ fertilization on forest NPP is now firmly established, at least for young stands in the temperate zone."

Nevertheless, nitrogen availability does play a role in this phenomenon. In the Duke-FACE study, for example, where Norby *et al*. say "a wide range of response to $CO_2$ enrichment across replicate plots correlated with differences in soil nitrogen availability," the scientists observed "under low nitrogen availability, $CO_2$ enrichment increased NPP by 19%, whereas under intermediate and high nitrogen availability the percent $CO_2$ stimulation was 27%," or 42% greater (27%/19% = 1.42). This observation is very important, for it is "almost certain," as Shaw *et al*. (2002) write, significant nitrogen deposition originating from anthropogenic activities will continue to accompany the ongoing rise in the atmosphere's $CO_2$ concentration throughout the foreseeable future; and this phenomenon should further boost forest NPP.

Lloyd (1999) calculated that from AD 1730 to the early 1980s the increase in temperate deciduous forest NPP due solely to the historical increase in the atmosphere's $CO_2$ concentration was approximately 7%, and the increase in NPP due to a modest proportional increase in nitrogen deposition over the same time period would have been about 25%. However, when $CO_2$ and nitrogen increased together in the model Lloyd employed, the NPP stimulation was 40%, even more than the sum of the individual contributions of the extra $CO_2$ and nitrogen. Although this exercise does not allow for a precise prediction of the percentage stimulation of forest NPP in response to future concomitant increases in atmospheric $CO_2$ content and nitrogen deposition, it does suggest the increase will likely be significantly larger than what is suggested by Norby *et al*., who deal solely with the effects of increasing $CO_2$.

In spite of the many positive responses discussed above, some researchers have suggested the biological response of forests to rising $CO_2$ may saturate sometime in the future, and the predicted climatic effects of anthropogenic $CO_2$ emissions might ultimately overpower this positive effect and cause a significant downturn in forest productivity. Davi *et al*. (2006) studied this possibility.

Noting "predictions for the second half of the 21st century diverge, with some models predicting that the terrestrial carbon sink will tend to level off, while others predict a decrease," Davi *et al*. say they were "hoping to shed more light on this important subject." To do so, they used a meteorological model and 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 the nine scientists used as input to a physiologically based multi-layer process-based ecosystem productivity model (which contained a carbon allocation sub-model coupled with a soil model) to evaluate the 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," Davi *et al*. write, 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) $m^{-2}$ $year^{-1}$)." They also report the $CO_2$ fertilization effect turns a warming-and-drying-induced "decrease of NEP into an increase." In addition, they write, "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." Therefore, even in the face of what was projected to be a truly "unprecedented" global warming and drying scenario, the real-world physiological effects of atmospheric $CO_2$ enrichment included in the ecosystem productivity model employed by Davi *et al*. more than compensated for the deleterious effects of the dramatic climate-change scenario on the productivity of major European forests.

Sefcik *et al*. (2007) studied the interactive effects of elevated atmospheric $CO_2$ concentration (658 ppm vs. the ambient concentration of 383 ppm), nitrogen (N) deposition (ambient and ambient + 30 kg N $ha^{-1}$ $year^{-1}$), and light availability (limited and saturated) for two full growing seasons on leaf photosynthesis, growth, and survival of understory seedlings of six different hardwood tree species—paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), eastern white pine (*Pinus strobus*), and black cherry (*Prunus serotina*)—which were enclosed by open-top chambers within a 90-year-old N-limited northern hardwood forest in northern Lower Michigan, USA.

Over the course of this two-year study, the 72% increase in the air's $CO_2$ concentration increased light-limited photosynthesis in the six tree species by an average of 47%, and it increased light-saturated photosynthesis by fully 60%. With respect to survival, at low N-availability seedling survival rates were similar in the ambient and elevated $CO_2$ treatments at 57% ± 5% and 55% ± 4%, respectively. In addition, as the researchers describe it, "for plants grown with high N availability, those grown in ambient $CO_2$ demonstrated 78 ± 4% survival, while those grown in elevated $CO_2$ exhibited the greatest survival rate of all of the treatment combinations with an 85 ± 2% survival rate." Sefcik *et al*. conclude, "N deposition may alleviate some photosynthetic acclimation [i.e., down-regulation] to long-term $CO_2$ enrichment in N-limited understory seedlings." They therefore further conclude, "increasing $CO_2$ and nitrogen deposition from fossil fuel combustion can directly impact seedling physiology and survivorship," quite obviously for the better.

Su *et al*. (2007) used a process-based model (BIOME-BGC) to investigate the likely response of *Picea schrenkiana* forest to future climate changes and atmospheric carbon dioxide concentration increases in the Tianshan Mountains of northwestern China, which they validated by comparing simulated net primary productivity (NPP) under current climatic conditions with independent, field-measured data. The specific climate change scenario employed in this endeavor was a double-$CO_2$-induced temperature increase of 2.6°C and a precipitation increase of 25%. When the precipitation increase predicted by the model was considered by itself, the NPP of the *P. schrenkiana* forest increased by 14.5%. The predicted temperature increase by itself increased forest NPP by 6.4%, and the $CO_2$ increase by itself boosted NPP by 2.7%. When the predicted increases in precipitation and temperature occurred together, forest NPP increased by a larger 18.6%, just slightly less than the sum of the two individual effects. When the $CO_2$ concentration increase was added to the mix and all three factors increased together, the Chinese researchers found forest NPP "increased dramatically, with an average increase of about 30.4%." Su *et al*. thus conclude, "the effects of precipitation and temperature change were simply additive," but the synergy between the effects of climate change and doubled $CO_2$ made the whole response much larger than the sum of its separate responses because "feedback loops associated with the water and nitrogen cycles [which may be influenced significantly by atmospheric $CO_2$ enrichment] ultimately influence the carbon assimilation response."

Koutavas (2008), in prefacing his work, notes "tree rings are the primary archive used in annually resolved climate reconstructions spanning recent centuries to millennia, and as such their response to non-climatic factors requires careful evaluation." Stating an important consideration in this regard "is whether radial growth in trees over the 20th century has been influenced by anthropogenic effects, particularly the rising concentration of $CO_2$ in the global atmosphere," he further notes "LaMarche *et al*. (1984) were the first to attribute late 20th century growth enhancement in high-elevation bristlecone and limber pines from the western US to $CO_2$ fertilization." He adds, "Graybill and Idso (1993) further argued that a $CO_2$ growth effect can be detected in tree-ring chronologies from the southwest US in species exhibiting a strip-bark morphology."

In further exploring this subject, Koutavas analyzed ring-width variations obtained from cores of eight Greek fir (*Abies cephalonica*) trees growing at elevations between 1,300 and 1,600 meters on the southern slopes of Mt. Ainos on the island of Cephalonia in the Ionian Sea west of mainland Greece, while employing climate data from the University of East Anglia to determine whether any growth changes noted over the period of the ring-width record (AD 1840–2005) could be ascribed to any regional climate changes to which the trees might have been exposed.

The results of Koutavas's work are depicted in Figure 1.2.1.2.1. As can be seen from these data, and as Koutavas states, there was a "strong acceleration of growth over the second half of the 20th century" and "the sustained increase in growth since 1990 in particular was unprecedented over the full length of the data set." He also states these positive growth trends "bear no relationship to regional temperature or precipitation variations and therefore are unlikely to be climatically induced." And he affirms "disturbance effects from human activities are also unlikely, as the study site lies in a remote forest area with difficult access." Thus, about the only rational explanation for the late twentieth-century growth acceleration seen in the ring-width data is Koutavas's suggestion: "the enhanced growth reflects a fertilization effect due to rising $CO_2$ in the global atmosphere."

Martinez-Vilalta *et al*. (2008) used tree-ring data from the Catalan Ecological and Forest Inventory "to study the temporal variability of Scots pine stem radial growth (period 1901–1997) across a relatively large region (Catalonia, NE Spain) situated close to

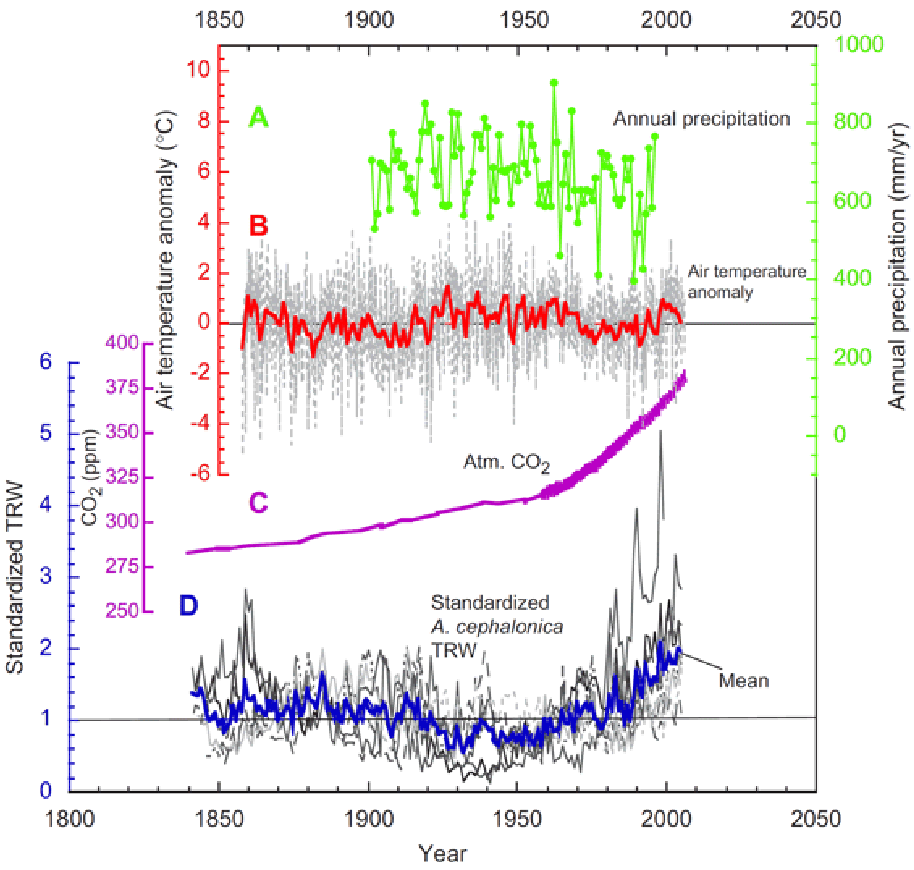

**Figure 1.2.1.2.1.** Annual precipitation totals, annual air temperature anomalies, atmospheric CO$_2$ concentrations (from Mauna Loa and Antarctica's Law Dome ice core), and the mean standardized tree-ring series (TRW) of the Greek fir trees. Adapted from Koutavas (2008).

the southern limit of the distribution of the species." The inventory included 10,664 plots randomly distributed throughout the forested area of Catalonia, where Scots pine was present in 30.2% of the plots and was the dominant tree species in 18.4% of them. The five researchers state their results "showed 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 note, "this trend was associated with increased atmospheric CO$_2$ concentra-tion," which they interpret to be "a fertilization effect." There was also, however, "a marked increase in temperature across the study region (0.19°C per decade on average)," but they report "this warming had a negative impact on radial growth, particularly at the drier sites," although "its magnitude was not enough to counteract the fertilization effect."

Peng *et al.* (2009) validated the process-based TRIPLEX model of forest growth and carbon and nitrogen cycling against observed data. They then used the calibrated model to investigate the potential impacts of projected increases in the atmosphere's CO$_2$ concentration on the climate of northeast China and its interactions with the aerial fertilization effect of the increase in atmospheric CO$_2$ in computing changes likely to occur in the net primary productivity (NPP) and carbon budget of the region's forests. The model validation results show "the simulated tree total volume, NPP, total biomass and soil carbon are consistent with observed data across the Northeast of China, demonstrating that the improved TRIPLEX model is able to simulate forest growth and carbon dynamics of the boreal and temperate forest ecosystems at regional scale." Second, the seven scientists note the application of the appropriately calibrated model indicates climate change would increase forest NPP and biomass carbon but decrease overall soil carbon under all three of the climate change scenarios they studied. However, they report, "the combined effects of climate change and CO$_2$ fertilization on the increase of NPP were estimated to be 10–12% for [the] 2030s and 28–37% in [the] 2090s," because "the simulated effects of CO$_2$ fertilization significantly offset the soil carbon loss due to climate change alone."

Peng *et al.* thus conclude "overall, future climate change and increasing atmospheric CO$_2$ will have a significant impact on the forest ecosystems of Northeastern China," also noting their findings clearly indicate the impact would be beneficial. In addition, they write, "the results of the effects of CO$_2$ fertilization on NPP simulated by TRIPLEX1.0 are consistent with the recent FACE experiments in temperate forests in North America and Europe (Norby *et al.*, 2005), global analyses of Melillo *et al.* (1993) and Mathews (2007), and site-specific investigations in Canadian boreal forest ecosystems (Peng and Apps, 1998, 1999).” This consistency leads them to the further conclusion, “the effect of $CO_2$ fertilization on forest NPP is now firmly established.”

Cole *et al.* (2010) note quaking aspen (*Populus tremuloides* Michx.) is “a dominant forest type in north-temperate, montane, and boreal regions of North America” and is, in fact, “the most widely distributed tree species on the continent.” They also note aspen and related poplars are “quintessential foundation species (Ellison *et al.*, 2005), shaping the structure and function of the communities and ecosystems in which they occur (Whitham *et al.*, 2006; Schweitzer *et al.*, 2008; Madritch *et al.*, 2009).” This being the case, they attempted to determine how this keystone species may have responded to the increase in atmospheric $CO_2$ concentration that occurred over the past several decades, especially within the context of the climatic changes that occurred concurrently.

To do so, the four researchers collected branches from 919 trees after their leaves had dropped in the fall, obtaining samples that represented 189 genets or clones (five trees per clone) at 11 sites distributed throughout three regions of Wisconsin (USA). The sampled trees ranged from five to 76 years of age and came from second-growth unmanaged forests south of the areas defoliated by forest tent caterpillars in 1980–1982, 1989–1990, and 2001–2002. In addition, they recorded trunk diameter at breast height for each sampled tree, which, in their words, “is very highly correlated with total biomass in aspen,” citing Bond-Lamberty *et al.* (2002).

Results of the analysis, they report, reveal “age-specific ring width increased over time” and “the greatest increase occurred for relatively young trees, so that young trees grew faster in recent years than did young trees several decades ago.” During the past half-century, for example, the growth of trees 11–20 years old rose by 60%. In addition, they observe “rising $CO_2$ causes ring width to increase at all moisture levels, apparently resulting from improved water use efficiency,” so “the overall increase results from historical increases in both $CO_2$ and water availability.” And when they separate out the impacts of the two factors, they find “the effect of rising $CO_2$ had been to increase ring width by about 53%,” as a result of “a 19.2% increase in ambient $CO_2$ levels during the growing season, from 315.8 ppm in 1958 (when $CO_2$ records began) to 376.4 ppm in 2003.”

This is a truly remarkable finding; and Cole *et al.* comment, “the magnitude of the growth increase uncovered by this analysis raises the question of how much other major forest species may have responded to the joint effects of long-term changes in $CO_2$ and precipitation.”It seems likely other tree species may have experienced similar growth stimulations, particularly in light of Tans (2009), who demonstrated Earth’s land surfaces were a net source of $CO_2$ to the atmosphere until about 1940—primarily due to the felling of forests and the plowing of grasslands to make way for expanded agricultural activities—but who reports, from 1940 onward, as shown in Figure 1.2.1.2.2, the terrestrial biosphere has become, in the mean, an increasingly greater sink for $CO_2$, and that it has done so even in the face of massive global deforestation, for which it has apparently more than compensated. The combined findings of the two studies of Tans and Cole *et al.* clearly attest to the ability of the ongoing rise in the air’s $CO_2$ content to transform the face of Earth.

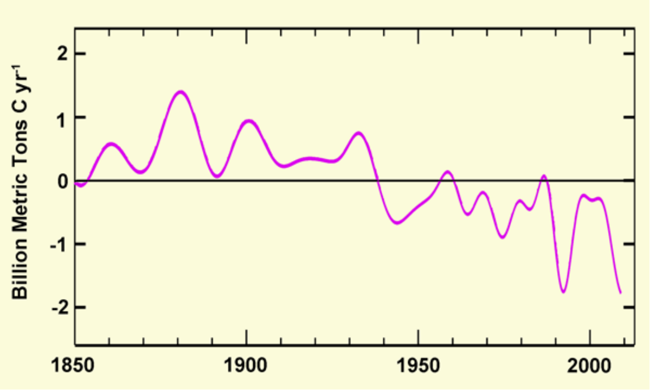

**Figure 1.2.1.2.2.** Five-year smoothed rates of carbon transfer from land to air (+) or from air to land (-) vs. time. Adapted from Tans (2009).

According to Knapp and Soule (2011), “atmospheric $CO_2$ concentrations have increased by over 27% since the early 20th century, resulting in enhanced radial tree growth in natural environments for numerous tree species in a variety of climatic regions (e.g., LaMarche *et al.*, 1984; Knapp *et al.*, 2001; Soule and Knapp, 2006; Voelker *et al.*, 2006; Wang *et al.*, 2006; Koutavas, 2008).” In addition, they note, “the principal benefit of elevated $CO_2$ for radial growth has been linked to increased intrinsic water use efficiency (iWUE), which is the ratio of net $CO_2$ assimilation through leaf stomata to leaf stomatal conductance.” And they report “increases in iWUE based on carbon isotope chronologies have been identified for trees growing in both controlled (e.g., Leavitt *et al.*, 2003) and natural environments (e.g., Bert *et al.*, 1997; Feng, 1999; Tang *et al.*, 1999;

Arneth *et al*., 2002; Saurer *et al*., 2004; Waterhouse *et al*., 2004; Liu *et al*., 2007).”

The two researchers “examined radial growth responses of ponderosa pine (*Pinus ponderosa* var. *ponderosa*) between 1905–1954 and 1955–2004 to determine if the effects of increased intrinsic water use efficiencies caused by elevated atmospheric $CO_2$ concentrations were age-specific,” working with 209 cores collected from mature trees (ranging in age from at least 100 to more than 450 years) from five sites in the USA’s northern Rocky Mountains. They also calculated iWUE using carbon isotope data from 1850 to 2004.

The authors found, “(1) responses to elevated atmospheric $CO_2$ in old-growth ponderosa forests are age-specific; (2) radial growth increases in older trees coincided with increased iWUE; (3) ponderosa had increased growth rates in their third, fourth, and fifth centuries of life; and (4) age-specific growth responses during 1955–2004 are unique since at least the mid-16th century.” They also report “increases in iWUE during 1955–2004 were 11% greater than during 1905–1954.”

Knapp and Soule say their findings “demonstrate that old-growth ponderosa pine forests of the northern Rockies have likely benefited from the effects of increased atmospheric $CO_2$ since the mid-20th century and that the benefits increase with tree age.” And since the $CO_2$-induced radial growth increases in the older trees “were significantly associated with rising iWUE,” they opine the “accelerated growth rates are likely caused by more efficient water use in the semiarid environment where the trees were sampled.”

In concluding, the two scientists state “old-growth trees can be highly responsive to environmental changes,” especially the ongoing rise in the air’s $CO_2$ content, as their work clearly demonstrates. They note even what many might call ancient trees are still “capable of increased growth rates several hundred years after establishment,” citing McDowell *et al*. (2003) and Martinez-Vilalta *et al*. (2007).

Using data from the website of the International Tree-Ring Data Bank as well as from cores collected previously and stored in their laboratory at The Pennsylvania State University (USA), Johnson and Abrams (2009) explored growth rate (basal area increment, BAI) relationships across age classes (from young to old) for eight tree species commonly found throughout the eastern United States: bigtooth aspen (*Populus grandidentata* Michx.), blackgum (*Nyssa sylvatica* Marsh.), black oak (*Quercus velutina* Lam.), chestnut oak (*Quercus Montana* L.), hemlock (*Tsuga canadensis* L. Carr.), pitch pine (*Pinus rigida* Mill.), red oak (*Quercus rubra*), and white oak (*Quercus alba* L.). The two researchers report “a remarkable finding of this study was that even the oldest trees of several species had slow but increasing BAI values, which continued throughout the life of most trees.” They characterize this finding as “remarkable,” they explain, because it “contradicts the sigmoidal growth model that predicts growth rate should plateau and then decline, as middle age trees approach old age,” citing Ryan and Yoder (1997) and Weiner and Thomas (2001). They also report, “over the last 50–100 years, younger trees within a species grew faster than did the older trees when they were of the same respective age,” which is what Knapp and Soule (2011) found for ponderosa pine trees in the USA’s northern Rocky Mountains.

Further discussing their findings, the two researchers from Pennsylvania State University’s School of Forest Resources write, “it seems reasonable to assume” the greater growth rates of older trees of the current era compared to older trees of older times “may be due to a stimulatory effect of anthropogenic global change defined in the broadest sense,” including “increased $CO_2$ levels, warming temperatures, increased precipitation, and changes in precipitation chemistry,” noting “yearly average temperatures, atmospheric $CO_2$ and nitrogen levels have increased in the eastern US (as well as much of the rest of the world) over the last 50–100 years.”

In another study from Soule and Knapp (2011), the two researchers “examined changes in and relationships between radial growth and intrinsic water use efficiency (iWUE) of ponderosa pine (*Pinus ponderosa*) trees, climate, and atmospheric $CO_2$ in the western United States since the mid-nineteenth century.” They developed “tree-ring chronologies for eight sites in three climate regions and using carbon isotope data to calculate pentadal values of iWUE,” and then “examined relationships among radial growth, climate, iWUE, and $CO_2$ via correlation and regression analyses.” They found “trends toward higher rates of iWUE for ponderosa pine are panregional, occurring at eight sites within three distinct climatic regimes and for two subspecies,” and these results “are similar to those reported by Feng (1999) for several coniferous tree species found throughout western North America.” They also note “increasing iWUE has been reported for conifers at other northern hemisphere locations (e.g., Bert *et al*., 1997; Saurer *et al*., 2004).” They conclude “future increases in iWUE are likely for ponderosa pine within our study regions as $CO_2$ levels increase," and they state they found "significant improvements in radial growth rates during drought years after 1950." These findings suggest "increased iWUE associated with rising $CO_2$ can positively impact tree growth rates in the western United States and is thus an evolving component of forest ecosystem processes." Soule and Knapp also state, "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."

Working within lichen woodlands of the forest zone of Eastern Canada between longitudes 70 and 72°W, Girard *et al*. (2011) acquired data enabling them to calculate radial, height, and volume growth rates at every 15 minutes of latitude from 47°30'N to 52°41'N for black spruce (*Picea mariana*) trees ranging in age from 34 to 188 years. Dividing the trees into a young group and an old group, with ages ranging between 34 and 93 years for the young group and between 109 and 188 years for the old group, the three Canadian researchers report same-age "radial, height and volume growth rates of trees in stands younger than 100 years were 46%, 51%, and 38%, respectively, greater than those of trees in stands older than 100 years." And for the two youngest stands, with mean ages of 34 and 43 years, they state "black spruce showed radial, height and volume growth rates of 66%, 74%, and 71%, respectively, greater than those in woodlands older than 100 years." Further discussing their findings, Girard *et al*. cite several other studies demonstrating "tree productivity in northern forests of eastern North America has increased significantly since the middle of the 19th century," namely Payette *et al*. (1985), D'Arrigo *et al*. (1987), D'Arrigo *et al*. (1992), and Lavoie and Payette (1994). They also note "similar trends have been observed in the American West," citing Graumlich *et al*. (1989) and Peterson *et al*. (1990).

Introducing his study, Parn (2012) writes "the potential productivity of a forest site has been regarded as natural and stable in a long-term perspective (Elfving *et al*., 1996)," but "environmental changes such as increase of $CO_2$ in the atmosphere, deposition of pollutants and climate changes since the 1950s have had various effects on forest ecosystems," and "the increasing human impact on the environment makes the stability of the site conditions questionable." Thus the author set out to learn whether these environmental changes may have affected the growth of Scots pine trees. Specifically, Parn studied the growth history of trees of identical cambial age but two different calendar ages at two different sites: Koiguste on Saaremaa island, the largest of the Estonian islands in the Baltic Sea, and Pirita in North Estonia near the Estonian capital. The age of the old stand at the Koiguste site was 160 years and that of the young stand 55 years, and the ages of the old and young stands at the Pirita site were 155 and 55 years, respectively. At both of these locations, Parn writes, "the differences in the radial growth of successive stand generations were assessed using the average tree-ring widths of the same cambial age of stands at age of 30, 40 and 50 years."

Parn found "the radial growth of young generations exceeded that of old stands at the same cambial age," and "approximately similar results were obtained when latewood widths were used instead of the tree-ring widths in the analysis." In addition, he reports "a fairly strong positive effect of the mean temperatures of the spring months on the latewood width can be observed." He notes a similar "strong link between the latewood width and spring temperatures was described by Miina (2000) for Scots pines in eastern Finland, by Savva *et al*. (2003) for pines from different provenances in Russia, and by Drobyshev *et al*. (2004) for pines in the Komi Republic." As for what was responsible for these findings, Parn suggests "it may be assumed that long-term climate change may have caused, at least partly, the increasing growth of young generations of pine" and "the increased nitrogen deposition and elevated $CO_2$ level during the second half of the 20th century may have had some positive influence."

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### *1.2.1.3 Growth Rates of Old vs. Young Trees*

- In contrast to frequently stated assumptions, old-growth forests can be significant carbon sinks, and their capacity to sequester carbon in the future will be enhanced as the air's $CO_2$ content rises.

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

Although simple in concept, this potential partial solution to the putative global warming problem has been under attack for several years by those who want to address the issue solely through forced reductions in anthropogenic $CO_2$ emissions (see Pearce, 1999). The tack they take in this campaign is to claim carbon sequestration by forests is viable only when forests are young and growing vigorously; as forests age, they assert, they gradually lose their carbon sequestering prowess, so forests more than one hundred years old become essentially useless for removing $CO_2$ from the air. They further claim such old stands yearly lose as much $CO_2$ via respiration as they acquire via photosynthesis. Here we examine the validity of such assertions based on actual measurements made on older trees.

In Panama (Condit *et al*., 1995), Brazil (Chambers *et al*., 1998; Laurance *et al*., 2004; Chambers *et al*., 2001), and many parts of the southwestern United States (Graybill and Idso, 1993), individual trees of a number of different species have been shown to live for nearly one-and-a-half millennia. At a hundred or so years of age, these super-consumers of $CO_2$ are mere youngsters. In their *really* old age, their appetite for the vital gas, though diminished, is not lost. Chambers *et al*. (1998) note the long-lived trees of Brazil continue to experience protracted slow growth even at 1,400 years of age. The protracted slow growth (evident in yearly increasing trunk diameters) of very old and large trees can absorb a tremendous amount of $CO_2$ out of the air each year, especially when—as noted by Chambers *et al*. (1998) with respect to the Brazilian forests in the central Amazon—about 50% of forests' aboveground biomass is contained in less than the largest 10% of their trees. Consequently, since the lifespan of these massive, long-lived trees is considerably greater than the projected lifespan of the entire "Age of Fossil Fuels," their cultivation and preservation represents an essentially *permanent* partial solution to the perceived problem of global warming that is ascribed to anthropogenic $CO_2$ emissions.

As important as are these facts about trees, however, an even more important fact comes into play in the case of forests and their ability to sequester carbon over long periods of time. This little-acknowledged piece of information is the fact that the forest itself—conceptualized as a huge super-organism—is the unit of primary importance in determining the ultimate amount of carbon that can be sequestered on a unit area of land.

That this difference in perspective can have enormous consequences is demonstrated by Cary *et al*. (2001), who note most models of forest carbon sequestration wrongly assume "age-related growth trends of individual trees and even-aged, monospecific stands can be extended to natural forests." When they compared the predictions of such models against real-world data gathered from northern Rocky Mountain subalpine forests that ranged in age from 67 to 458 years, they found aboveground net primary productivity in 200-year-old natural stands is almost twice as great as in modeled stands, and the difference between the two increases linearly throughout the entire sample age range.

What explains the huge discrepancy? Cary *et al*. suggest long-term recruitment and the periodic appearance of additional late-successional species (increasing biodiversity) may have significant effects on stand productivity, infusing the primary unit of concern (the ever-evolving forest super-organism) with greater vitality than would have been projected on the basis of characteristics possessed by the unit earlier in its life. They also note the failure to include effects of size- or age-dependent decreases in stem and branch respiration per unit of sapwood volume in models of forest growth can cause overestimates of respiration in older stands by a factor of two to five.

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

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

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

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

"Contrary to expectation," Binkley *et al.* write, "live tree mass in 2003 [186 Mg $ha^{-1}$] was significantly greater than in 1976 [149 Mg $ha^{-1}$] ($P = 0.02$), refuting the hypothesis that live tree mass declined." They report the annual net increment of live tree mass was about 1.37 Mg $ha^{-1}$ $yr^{-1}$ from age 96 to age 123 years, only 12% less than the mean annual increment of live tree mass experienced over the forest's initial 96 years of existence (149 Mg $ha^{-1}$ / 96 yr = 1.55 Mg $ha^{-1}$ $yr^{-1}$). Consequently, in response to the question they posed when embarking on their study—"Do old forests gain or lose carbon?"—Binkley *et al.* conclude, "old aspen forests continue to accrue live stem mass well into their second century, despite declining current annual increments."

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

What has put the planet's trees on this healthier trajectory of being able to sequester significant amounts of carbon in their old age, when past theory (based on past observations) decreed they should be in a state of no-net-growth or even negative growth? The answer is rather simple. For any tree of age 250 years or more, the greater portion of its life (at least two-thirds of it) was spent in an atmosphere of much-reduced $CO_2$ content. Up until 1920, for example, the air's $CO_2$ concentration had never been above 300 ppm throughout the entire lives of such trees, whereas it is currently 400 ppm, or 33% higher. And older trees spent even greater portions of their lives in air of even lower $CO_2$ concentration. Thus the phenomenon that has given new life to old trees and allows them to "live long and prosper" is most likely the aerial fertilization effect produced by the flooding of the air with the $CO_2$ that resulted from the Industrial Revolution and is currently being maintained by its aftermath (Idso, 1995).

Greenep *et al.* (2003) found "the capacity for enhanced photosynthesis in trees growing in elevated $CO_2$ is unlikely to be lost in subsequent generations." That finding and the others previously cited suggest Earth's forests will remain strong sinks for atmospheric carbon far beyond the date at which IPCC's models indicate they would have given back to the atmosphere most of the carbon they had removed from it over their existence to that point in time. Subsequent reports have validated this assessment.

Zhou *et al.* (2006), for example, also note "old-growth forests have traditionally been considered negligible as carbon sinks because carbon uptake has been thought to be balanced by respiration." Thus they report "the soil carbon balance of old-growth forests has received little attention." In an attempt to rectify this situation, they "conducted a study to measure the long-term (1979 to 2003) dynamics of soil organic carbon stock in old-growth forests (age > 400 years) at the Dinghushan Biosphere Reserve in Guangdong Province, China." The eight scientists report "soil organic carbon concentration in the top 20-cm soil layer increased between 1979 and 2003 from about 1.4% to 2.35% at an average rate of 0.035% each year," and "measurements on a total of 230 composite soil samples collected between 1979 and 2003 suggested that soil organic carbon stock in the top 20-cm soil layer increased significantly during that time ($P < 0.0001$), with an average rate of 0.61 Mg C ha$^{-1}$ year$^{-1}$." In discussing their findings, Zhou *et al.* state although "the driving forces for this observed high rate of soil organic carbon increase in the old-growth forests are not clear at present," their study "suggests that the carbon cycle processes in the belowground system of these forests are changing in response to the changing environment."

Luyssaert *et al.* (2008) conducted a literature survey to test the hypothesis that forests continue to acquire and sequester carbon from the atmosphere for hundreds of years. They compiled data from 519 plot studies conducted throughout the world's boreal and temperate forests (30% and 70% of the studies, respectively), skipping the tropics because of the low number of tropical sites that possessed the net ecosystem production (NEP) and forest age estimates needed for their analysis. They report, "in forests between 15 and 800 years old, the NEP is usually positive; that is, the forests are $CO_2$ sinks." In fact, they write, "young forests rather than old-growth forests are very often conspicuous sources of $CO_2$ because the creation of new forests (whether naturally or by humans) frequently follows disturbance to soil and the previous vegetation, resulting in a decomposition rate of coarse woody debris, litter and soil organic matter that exceeds the net primary production of the regrowth." Discussing the implications of their findings, the team of American, Belgian, British, French, German, and Swiss researchers writes, "because old-growth forests steadily accumulate carbon for centuries, they contain vast quantities of it," and "they will lose much of this carbon to the atmosphere if they are disturbed, so carbon-accounting rules for forests should give credit for leaving old-growth forests intact" to let them sequester even more carbon.

Phillips *et al.* (2008) note there was "a long held view," as they describe it, that "old trees exhibit little potential for growth." They therefore state "it may seem reasonable to conclude that old trees are not responsive to increased $CO_2$." They go on to demonstrate that view was far from correct.

The three researchers begin their analysis of the subject by stating, "hydraulic constraints in tall trees," such as those of great age, "constitute a fundamental form of water limitation; indeed, one that is indistinguishable from soil water limitations," citing Koch *et al.* (2004) and Woodruff *et al.* (2004). They also report "recent research indicates that tree size and its hydraulic correlates, rather than age *per se*, controls carbon gain in old trees," as indicated by Mencuccini *et al.* (2005). These findings imply, in their words, "factors that alleviate internal or external resource constraints on old trees could improve physiological function and ultimately growth," which is something elevated $CO_2$ does quite well by increasing plant water use efficiency. They list several phenomena that suggest "a fundamental potential for old growth trees to show greater photosynthesis and growth under industrial age increases in $CO_2$ than they would under constant, pre-industrial $CO_2$ levels."

Drawing from their own work, Phillips *et al.* report "500- and 20-year-old Douglas-fir trees both show high sensitivity of photosynthesis to atmospheric $CO_2$," presenting data that clearly demonstrate "under optimal conditions there exists the potential for an approximately 30% increase in photosynthetic rate with an increase in $CO_2$ from pre-industrial to current levels [i.e., from 280 to 385 ppm] in old trees." They note "the phenomenon of twentieth-century ring-width increase," which could thus be expected to accompany the twentieth century increase in the air's $CO_2$ concentration, has in fact been detected in several other studies, including LaMarche *et al.*, (1984), Jacoby (1986), Graybill (1987), Kienast and Luxmoore (1988), Graumlich (1991), Knapp *et al.* (2001), Bunn *et al.* (2005), and Soule and Knapp (2006), to which could be added Graybill and Idso (1993).

A year later, Phillips *et al.* (2009) noted, over the past quarter-century of intensive region-wide measurements, the productivity of the Amazon rainforest—even in its extreme old age—has been "increasing with time," citing the comprehensive observational studies of Phillips *et al.* (1998), Nemani *et al.* (2003), Baker *et al.* (2004), Lewis *et al.* (2004), and Ichii *et al.* (2005). Phillips *et al.* sought to determine what negative effect a severe drought might have on South America's surprisingly productive tropical mega-forest. What the international team of scientists wanted to know, essentially, was whether such a decline in the availability of water might wipe out the super ecosystem's biomass gains of prior decades, thereby fulfilling one of the models' worst-case catastrophic scenarios.

Focusing their attention on the Amazonian drought of 2005, which they describe as "one of the most intense droughts of the past 100 years" and "a possible analog of future events," the 66 researchers, who had monitored a host of forest plots across the Amazon basin over the prior quarter-century, utilized tree diameter, wood density, and allometric models to compute the basin's woody biomass at each time of measurement, both before and after the drought, deriving the results plotted in Figure 1.2.1.3.1.

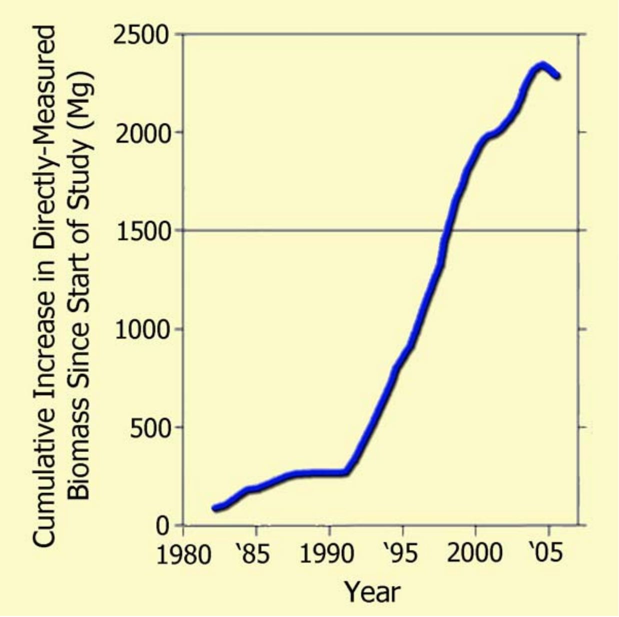

**Figure 1.2.1.3.1.** The post-1980 cumulative biomass increase of Amazon trees ≥ 10 cm in diameter as a function of the mid-date of each forest-plot census interval, portrayed as a 50-interval moving mean. Adapted from Phillips *et al.* (2009).

As may readily be seen from these real-world measurement-based results, the great Amazonian drought of 2005 resulted in only a slight hiatus in the strong upward trend of tree biomass accumulation exhibited over the prior two decades, which occurred, as Phillips *et al.* note, through a multidecadal period spanning both wet and dry conditions, the latter of which are not even detectable in their wood biomass data. Hence, although extremely severe drought conditions can indeed bring a temporary halt to biomass accumulation in old growth tropical forests—and sometimes even lead to minor reductions in biomass due to selective tree mortality—the vast majority of the trees are able to regain their photosynthetic capacity and add to their prior store of biomass once the moisture stress subsides, thanks in large measure to the enhanced growth (Lin *et al.*, 1998) and water use efficiency (Hietz *et al.*, 2005) experienced by nearly all woody plants as the air's $CO_2$ content rises.

Lloyd and Farquhar (2008) provide additional support for this attribution, concluding "the magnitude and pattern of increases in forest dynamics across Amazonia observed over the last few decades are consistent with a $CO_2$-induced stimulation of tree growth." Phillips *et al.* (2008) provided still more support for the premise, concluding the simplest explanation for the phenomenon is "improved resource availability has increased net primary productivity, in turn increasing growth rates." They also note "the only change for which there is unambiguous evidence that the driver has widely changed and that such a change should accelerate forest growth is the increase in atmospheric $CO_2$," because of "the undisputed long-term increase in [its] concentration, the key role of $CO_2$ in photosynthesis, and the demonstrated effects of $CO_2$ fertilization on plant growth rates."

Lewis *et al.* (2009) found further support for this view in records of old-growth forests of tropical Africa, where they had invested a great amount of time and effort in documenting changes in aboveground carbon storage in 79 permanent plots spanning 40 years (1968–2007), located in closed-canopy moist forest, spanning West, Central, and Eastern Africa, based on data from more than 70,000 individual trees across ten countries. They found "aboveground carbon storage in live trees increased by 0.63 Mg C $ha^{-1}$ $year^{-1}$ between 1968 and 2007" and "extrapolation to unmeasured forest components (live roots, small trees, necromass) and scaling to the continent implies a total increase in carbon storage in African tropical forest trees of 0.34 Pg C $year^{-1}$."

In discussing these results, the 33 researchers write the observed changes in carbon storage were "similar to those reported for Amazonian forests per unit area, providing evidence that increasing carbon storage in old-growth forests is a pan-tropical phenomenon." They also note "combining all standardized inventory data from this study and from tropical America and Asia together yields a comparable figure of 0.49 Mg C $ha^{-1}$ $year^{-1}$," which equates to "a carbon sink of 1.3 Pg C $year^{-1}$ across all tropical forests during recent decades," accounting for roughly half of the global missing carbon sink. Lewis *et al*. conclude, "taxon-specific analyses of African inventory and other data suggest that widespread changes in resource availability, such as increasing atmospheric carbon dioxide concentrations, may be the cause of the increase in carbon stocks, as some theory (Lloyd and Farquhar, 1996) and models (Friedlingstein *et al*., 2006; Stephens *et al*., 2007; Ciais *et al*., 2008) predict."

Tan *et al*. (2011) report stands of trees with ages greater than 200 years have been demonstrated by several research groups to act as carbon sinks in both coniferous and mixed forests, citing Hollinger *et al*. (1994), Law *et al*. (2001), Roser *et al*. (2002), Knohl *et al*. (2003), Paw U *et al*. (2004), Desai *et al*. (2005), and Guan *et al*. (2006). They buttress this claim with the results of their own study of the subject, in which they employed an eddy covariance technique to examine the carbon balance of a more-than-300-year-old subtropical evergreen broadleaved forest located in the center of the largest subtropical land area of the world in the Ailao Mountain Nature Reserve (24°32'N, 101°01'E) of Yunnan Province in Southwest China.

There, in addition to their micrometeorologically based eddy flux carbon budget estimation, the six scientists conducted a tree inventory of one hectare of forest located within the footprint of the eddy flux tower they employed in November 2003 and again in November 2007. They then compared measurements of tree diameter at breast height (DBH) between the two times and employed site-specific allometric equations to derive mean yearly biomass production. Finally, they assessed aboveground litter production via the amount captured each year in 25 litter traps randomly distributed within the one-hectare plot.

Tan *et al*. thus determined the mean annual net ecosystem production of the forest was approximately 9 tC/ha/year, which suggests, in their words, "this forest acts as a large carbon sink." In addition, their inventory data indicate about 6 tC/ha/year was contributed by biomass and necromass. And they report approximately 60% of the biomass increment was contributed by the growth of large trees with breast height diameters greater than 60 cm.

The research cited above clearly shows the notion of old trees contributing next to nothing to global carbon sequestration is manifestly invalid.

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### 1.2.1.4 Carbon Sequestration

As the $CO_2$ content of the air increases, nearly all plants, including those of various forest ecosystems, respond by increasing their photosynthetic rates and producing more biomass. These phenomena allow long-lived perennial species characteristic of forest ecosystems to sequester large amounts of carbon within their trunks and branches aboveground and their roots belowground for extended periods of time. These processes, in turn, significantly counterbalance $CO_2$ emissions produced by mankind's use of fossil fuels. The subsections below review information about forest-species sequestration of the carbon they remove from the atmosphere in response to rising atmospheric $CO_2$ and rising temperature.

#### 1.2.1.4.1 The Influence of $CO_2$

- Elevated $CO_2$ enhances photosynthetic rates and biomass production in forest trees, and both of these phenomena lead to greater amounts of carbon sequestration. Elevated $CO_2$ also enhances carbon sequestration by reducing carbon losses arising from plant respiration and in some cases from decomposition. Thus, as the air's $CO_2$ content rises, the ability of forests to sequester carbon rises along with it, appropriately tempering the rate of rise of the air's $CO_2$ content.

In reviewing studies of individual trees, it is clear elevated levels of atmospheric $CO_2$ increase photosynthesis and growth in both broad-leaved and coniferous species (see Section 1.1.3.1). When broad-leaved trembling aspen (*Populus tremuloides*) were exposed to twice-ambient levels of atmospheric $CO_2$ for 2.5 years, for example, Pregitzer *et al*. (2000) reported 17 and 65% increases in fine root biomass at low and high levels of soil nitrogen, respectively, and Zak *et al*. (2000) observed 16 and 38% $CO_2$-induced increases in total tree biomass when subjected to the same respective levels of soil nitrogen.

Also focusing on a broad-leaved species, Marek *et al*. (2001) constructed open-top chambers around 30-year-old mature oak (*Quercus ilex*) trees growing naturally in perennial evergreen stands in central Italy, where they were continually exposed to atmospheric $CO_2$ concentrations of either 350 or 700 ppm for five years, to determine the long-term effects of elevated $CO_2$ on photosynthesis in this important tree species. The researchers found the elevated $CO_2$ increased rates of net photosynthesis in Sun-exposed and shaded leaves by 68 and 59%, respectively, in comparison with control rates measured on similar leaves of trees exposed to ambient air. In addition, after measuring short-term photosynthetic rates at various atmospheric $CO_2$ concentrations, the four researchers found photosynthetic acclimation was not apparent in leaves of these mature trees exposed to long-term atmospheric $CO_2$ enrichment. They also report the $CO_2$ light compensation point—the light level at which photosynthetic carbon uptake is equivalent to respiratory carbon loss—was 24 and 30% lower in the Sun-exposed and shaded leaves, respectively, of the $CO_2$-enriched trees than what was measured in corresponding leaves of the ambient-air trees.

As the air's $CO_2$ content increases, therefore, it is likely the stimulatory effect of elevated $CO_2$ on photosynthesis in oak seedlings will persist in the long term within mature trees, without showing any signs of photosynthetic acclimation. And because elevated $CO_2$ significantly lowers the light compensation point in mature oak trees, which allows them to exhibit net carbon gains earlier in the mornings and maintain them later into the evenings, the stimulatory effect of elevated $CO_2$ on daily carbon uptake should be further enhanced. Together, these two observations suggest carbon sequestration by this and perhaps other tree species may be more substantial in future $CO_2$-enriched atmospheres than what had long been thought to be the case.

In a FACE study conducted at the Oak Ridge National Environmental Research Park in Roane County, Tennessee, USA, Norby *et al*. (2004) planted one-year-old bare-rooted sweetgum (*Liquidambar styraciflua* L.) seedlings in the ground in 1988 to create an experimental forest. Eight years later, five 25m-diameter FACE rings were constructed to enclose about 90 trees each. A year after that, when pretreatment measurements were made, the trees were about 2 m tall with an average diameter of 11 cm. At this point, the trees were in a linear growth phase and the canopy was no longer expanding. A year later, in April 1998, exposure to elevated $CO_2$ was begun in two of the plots and was continued each year thereafter throughout each subsequent growing season (April to November).

Over the last four years of the study (years 3–6), the atmospheric $CO_2$ concentrations of the ambient and $CO_2$-enriched plots averaged 391 ppm and 544 ppm (39% more than ambient), respectively. During this period, the net primary production of the $CO_2$-enriched plots averaged 22% more than the ambient plots, but there was no discernible "bulking up" of the trees. So where had the extra biomass attributable to the extra $CO_2$ been going?

In July 1997, the Oak Ridge scientists installed five mini-rhizotron tubes in each FACE plot. These transparent tubes extended to a depth of 60 cm below the soil surface and were inclined at a 60-degree angle from the vertical. Each was equipped with a video recorder collecting images biweekly throughout the growing season, and the data were digitized and used to calculate a number of different root parameters on the same biweekly basis. In analyzing the images, Norby *et al.* report "the $CO_2$ effect on annual [root] production was highly significant, with production 2.2-fold higher in $CO_2$-enriched plots from 2000–2003." They also state "$CO_2$ enrichment significantly increased peak-standing root crop by altering allocation such that the potential for root occupancy of the soil volume was increased," noting "this response was manifested especially in the deeper distribution of roots in the soil profile." In particular, they say the peak-standing root crop exhibited "3-fold more length at 30–45 cm and 4-fold more at 45–60 cm," impressive considering the enhancement of the air's $CO_2$ concentration employed in this study was only 39%.

The Oak Ridge investigators also determined the mass of fine roots produced in a given year accounted for 11–34% of forest net primary production. They remark this "preferential allocation to fine roots should significantly reduce the potential for additional carbon (C) sequestration in trees in elevated $CO_2$," which was proven true in their study. However, as they continue, "sequestration of some of that C in the forest remains a possibility" because "as fine roots die, their C enters the soil system where there is the potential for movement into long-lived organic matter pools." They note "soil analysis indicates that there is increased accumulation of new C in $CO_2$-enriched plots, particularly in micro-aggregate fractions that facilitate movement of C into pools with long residence times." And they state "it may become especially important that the greatest increases in root production in elevated $CO_2$ occur in deeper soil, where sequestration into longer-lived pools may be more likely."

Norby *et al.* further note "the $CO_2$-induced increase in fine-root standing crop in summer could also be an important mechanism for conferring increased resistance to late-season droughts," and "the stimulation of root growth in deeper soil could be particularly important in buffering trees against seasonal droughts." This being the case, the huge allocation of net primary production the $CO_2$-enriched trees send belowground and distribute to greater depths may enable them to sequester more biomass in their aboveground woody tissues, if it helps them remain able to produce biomass during droughty periods that might otherwise bring to a halt the net productivity of trees growing in ambient air.

Karberg *et al.* (2005) describe how "free air $CO_2$ and $O_3$ enrichment technology was used at the Aspen FACE project in Rhinelander, Wisconsin [USA] to understand how elevated atmospheric $CO_2$ and $O_3$ interact to alter $pCO_2$ and DIC [dissolved inorganic carbon] concentrations in the soil." The experimental setting consisted of three blocks of four treatments—control, elevated $CO_2$, elevated $O_3$, and elevated $CO_2$ + $O_3$—where ambient $CO_2$ was 360 ppm, elevated $CO_2$ was 542 ppm, ambient $O_3$ was 33 ppb, and elevated $O_3$ was 49 ppb. Half of each FACE ring was planted with trembling aspen, a quarter with a 1:1 mix of trembling aspen and paper birch, and a quarter with a mix of trembling aspen and sugar maple. In this setting, the researchers applied the $CO_2$ and $O_3$ treatments over the 2002 growing season, which ran from 28 May to 11 October, and retrieved biweekly samples of the soil air and solution from depths of 15, 30, and 125 cm for various chemical analyses in the laboratory.

The authors found "measured concentrations of soil $CO_2$ and calculated concentrations of DIC increased over the growing season by 14 and 22%, respectively, under elevated atmospheric $CO_2$ and were unaffected by elevated tropospheric $O_3$." In addition, Karberg *et al.* write, "the increased concentration of DIC altered inorganic carbonate chemistry by increasing system total alkalinity by 210%, likely due to enhanced chemical weathering [of primary minerals]," and they note a mixing model they employed "showed that new atmospheric $CO_2$ accounted for approximately 90% of the C leaving the system as DIC."

In discussing their findings, the Michigan scientists state the $CO_2$-induced increase in soil solution DIC, which ultimately makes its way to rivers that reach oceans, "represents a potential long-lived sequestration reservoir in deep ocean sediments," noting further it suggests "aggrading forest ecosystems may be used to capture and sequester atmospheric $CO_2$ through inorganic processes," which can transfer it to the bottoms of faraway seas, as also has been demonstrated and discussed by Raymond and Cole (2003) and Wang and Cai (2004). And, of course, increases in the air's $CO_2$ concentration can significantly increase this phenomenon.

Rasineni *et al.* (2011) write, "carbon sequestration as a climate change mitigation policy has received significant attention over the past several years," and planting young fast-growing trees to absorb excess atmospheric $CO_2$ "has recently gained potentiality, leading to identification of tree species with high $CO_2$ sequestration capacity." As their contribution, they grew well-watered and well-fertilized five-week-old fast-growing *Gmelina arborea* trees out-of-doors at the University of Hyderabad, India, in open-top chambers maintained at ambient and ambient plus 100 ppm atmospheric $CO_2$ concentrations throughout the 120 days of that region's spring and summer seasons, while they periodically made numerous measurements of the trees' physical properties and physiological performance.

At the conclusion of the spring and summer growing seasons, the three researchers found the trees in the modestly elevated $CO_2$ chambers exhibited net photosynthetic rates 38% greater than trees growing in ambient air. Aided by a significant $CO_2$-induced reduction in leaf transpiration rates, the mean instantaneous water use efficiency of the leaves of the $CO_2$-enriched trees was 87% greater than the ambient-treatment trees. These $CO_2$-induced plant physiological benefits raised the aboveground biomass of the $CO_2$-enriched trees at the end of the growing season to be 45% greater than trees growing in ambient air, and their total biomass (above and below ground) was 53% higher.

Discussing their findings, Rasineni *et al.* note elevated atmospheric $CO_2$ "persistently enhanced all the growth characteristics in *Gmelina*, including plant height, number of branches, internodes, internodal distance, aerial biomass and total plant biomass." They suggest "high sink demand and better growth dynamics" led to the huge sustained increase in carbon sequestration in the tropical deciduous tree. Thus, they conclude their findings point to the likelihood "there are management options for creating short-rotation deciduous tree plantations to achieve increased sequestration of carbon in a future elevated $CO_2$ environment."

Barton and Jarvis (1999) report fumigating branches of Sitka spruce (*Picea sitchensis*) with air of 700 ppm $CO_2$ for four years raised rates of net photosynthesis in current and second-year needles to be 100 and 43% higher, respectively, than photosynthetic rates of needles exposed to ambient air. In addition, ponderosa pine (*Pinus ponderosa*) grown at 700 ppm $CO_2$ for close to 2.5 years exhibited rates of net photosynthesis in current-year needles 49% greater than those of needles exposed to air containing 350 ppm $CO_2$ (Houpis *et al*., 1999). As to biomass production, Saxe *et al.* (1998) reviewed the then-existent literature on the topic, finding "close to a doubling" of the air's $CO_2$ concentration led to an approximate 50% increase in the biomass production of angiosperm trees and a 130% increase in the biomass production of coniferous species.

Pritchard *et al.* (2001) reconstructed ecosystems representative of regenerating longleaf pine communities of the southeastern USA in large soil bins placed in open-top chambers maintained at $CO_2$ concentrations of 365 and 720 ppm for 18 months, while they studied the effects of elevated $CO_2$ on root dynamics and growth in this important forest community. The five species included in the regenerating forest stands were longleaf pine (*Pinus palustris* Mill.), sand post oak (*Quercus margaretta*), a $C_4$ bunch grass called wiregrass (*Aristida stricta* Michx.), a $C_4$ perennial legume called rattlebox (*Crotalaria rotundifolia* Walt. Ex Genmel), and a herbaceous $C_3$ perennial called butterfly weed (*Asclepias tuberosa* L.).

They report the elevated $CO_2$ increased the total aboveground biomass of the longleaf pine and sand post oak by approximately 20 and 50%, respectively. It had no effect on the aboveground biomass produced by the three non-woody herbaceous species. Thus, at the ecosystem level, elevated $CO_2$ increased total aboveground biomass by an average of 35%, and belowground it increased the root biomass of longleaf pine by 62%. In contrast, sand post oak, which was very responsive to elevated $CO_2$ aboveground, exhibited no significant $CO_2$-induced changes belowground, and the three herbaceous species displayed an average $CO_2$-induced reduction in root biomass of 28%. At the whole-community level, therefore, the $CO_2$-enriched plots displayed 37% greater root length production per day and 47% greater root length mortality per day at soil depths between 10 and 30 cm than was observed in control plots exposed to ambient $CO_2$ concentrations.

Consequently, as the air's $CO_2$ content increases, the ability of longleaf pine trees to compete for soil moisture and nutrients in regenerating stands of longleaf pine savannahs will likely be enhanced by the large preferential $CO_2$-induced increases in the trees' root systems. This phenomenon likely will give longleaf pine a significant edge over its primary competitors—sand post oak and wiregrass. Pritchard *et al.* remark these competitive shifts suggest "longleaf pine savannahs may flourish in a future $CO_2$-enriched world." If that happens, the trees and the soil beneath them likely will become a major repository of sequestered carbon. Sand post oak also should do well as the air's $CO_2$ content increases, significantly enhancing the carbon-sequestering power of the total community, which should undergo a shift from savannah to forest, with a consequent greater storage of both above- and below-ground carbon.

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

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

The preceding findings fit well with the work of Fan *et al*. (1998), who used atmospheric measurements to calculate the broad-leaf forested region of North America between 15° and 51°N latitude possesses a current carbon sink that can annually remove all the $CO_2$ emitted into the air from fossil fuel combustion in both Canada and the United States. Looking to the future, White *et al*. (2000) calculated coniferous and mixed forests north of 50°N latitude likely will expand their northern and southern boundaries by about 50% as a result of the combined effects of increasing atmospheric $CO_2$, rising temperature, and nitrogen deposition.

Nitrogen deposition is an important variable. White *et al*. (2000) note it can play an interactive role with increasing atmospheric $CO_2$ to increase plant growth and carbon sequestration. Some researchers, however, have questioned the magnitude of that role. Nadelhoffer *et al*. (1999), for example, conclude nitrogen deposition from human activities is "unlikely to be a major contributor" to the large $CO_2$ sink that exists in northern temperate forests. Houghton *et al*. (1998), however, suggest nitrogen deposition holds equal weight with $CO_2$ fertilization in the production of terrestrial carbon sinks; and Lloyd (1999) demonstrates simultaneous $CO_2$ and nitrogen increases lead to greater modeled forest productivity than what is predicted by the sum of the individual contributions of these two variables.

Thomas *et al*. (2010) used "spatially extensive forest inventory data to discern [1] the effect of nitrogen deposition on the growth and survival of the 24 most common tree species of the northeastern and north-central United States, as well as [2] the effect of nitrogen deposition on carbon sequestration in trees across the breadth of the northeastern US." The four researchers found "nitrogen deposition (which ranged from 3 to 11 kg $ha^{-1}$ $yr^{-1}$) enhanced the growth of eleven species and decreased the growth of three species," and "enhanced [the] growth of all tree species with arbuscular mycorrhizal fungi associations." That led to "a 40% enhancement over pre-industrial conditions," which "includes the direct effects of nitrogen deposition on tree growth through soil fertilization, foliar nitrogen uptake and other potential interactions between nitrogen deposition and other environmental changes, including $CO_2$ fertilization." To give some feeling for the significance of the size of this response, they note it "exceeds the 23% enhancement of net primary production anticipated for the year 2050 from a doubling of atmospheric $CO_2$ over preindustrial levels, as estimated using free-air $CO_2$ enrichment studies," citing Norby *et al*. (2005).

Thomas *et al*. thus conclude "nitrogen deposition is an important mechanism contributing to carbon sequestration within these temperate forests," but they maintain this phenomenon is still "unlikely to explain all of the observed terrestrial carbon sink." Nevertheless, it goes a long way toward doing so, while demonstrating the major benefits of the concomitant increases in the air's $CO_2$ content and the temperature with which it has interacted over the course of the Industrial Revolution and after, the latter increases of which IPCC characterizes as negatively affecting the biosphere. Clearly, these $CO_2$ increases are not doing harm, and neither is the concomitant increase in anthropogenic nitrogen deposition. These phenomena have interacted with each other in such a way as to greatly increase the productivity of Earth's forests, both in temperate latitudes, as demonstrated by Thomas *et al*., and in tropical regions, as revealed by many of the other studies reviewed in this section and chapter.

On a related note, woody plant encroachment upon arid and semiarid grasslands and savannas has been a ubiquitous natural phenomenon experienced throughout the world over the past century or more (Idso, 1995), driven—at least partially, many believe—by the contemporaneous rise in the air's $CO_2$ concentration (Knapp and Soule, 1998; Soule and Knapp, 1999). This phenomenon may be responsible for sequestering much of the planet's so-called missing carbon, an unidentified but growing repository of organic matter needed to explain the less-than-predicted rate-of-rise of the air's $CO_2$ content calculated on the basis of known sources and sinks of this important greenhouse gas, as demonstrated by Hibbard *et al*. (2001).

Working in the La Copita Research Area southwest of Alice, Texas, Hibbard *et al*. analyzed several chemical and physical properties of the top ten centimeters of soils in remnant herbaceous areas and patches of woody vegetation in various stages of invasive development. Compared to soils beneath herbaceous vegetation, the soils beneath the tree/shrub areas were found to have much greater concentrations of both carbon (C) and nitrogen (N). A companion study of soil C and N across woody patches ranging in age from 10 to 110 years revealed these variables had experienced a linear increase through time.

The source of these C and N increases was woody plant roots. The authors write they "were surprised by the magnitude of root biomass in surficial soils of woody patches, which greatly exceeded that of herbaceous patches and which greatly exceeded that of foliar litter inputs." Citing a number of studies of rates of root turnover in herbaceous and woody-plant ecosystems, they conclude "the role of belowground inputs in fueling changes in surficial soil C and N stocks ... accompanying shifts from grass to woody plant domination may therefore be more substantial than previously appreciated."

As to how much more substantial such changes might be, the researchers note "the contrasts between woody and herbaceous patches reported here are conservative in that they do not include an assessment of whole plant C and N stocks," i.e., root biomass below ten centimeters depth and woody biomass aboveground. With respect to the first of these factors, they cite several studies that have detected greater soil C concentrations beneath woody vs. herbaceous vegetation to depths of 100 to 400 centimeters. With respect to the second factor, they likewise cite evidence suggesting "plant C mass has increased tenfold with the conversion of grassland to savanna woodland over the past 100 years."

As to what their findings imply about the world as a whole, Hibbard *et al*. note since "woody plant expansion into drylands has been geographically widespread over the past century," and "40% of the terrestrial biosphere consists of arid and semiarid savanna, shrubland, and grassland ecosystems, this type of vegetation change may be of significance to the global C and N cycle." However, they say, a full understanding of the significance of this phenomenon will require better information on "the historic or modern rate, areal extent, and pattern of woody plant expansion in the world's drylands."

McCarron *et al*. (2003) measured the effects of shrub encroachment in a mesic grassland on soil $CO_2$ flux, extractable inorganic N, and N mineralization beneath isolated $C_3$ shrub communities (islands) of *Cornus drummondii* and surrounding undisturbed native tallgrass prairie at the Konza Prairie Biological Station in northeast Kansas, USA, during the 1999 and 2000 growing seasons. They determined—as had Norris (2000) and Smith (2001) before them—the invasion of mesic grasslands by woody plants leaves soil carbon stores essentially unaltered while greatly boosting aboveground inventories of sequestered carbon. Those observations provide more evidence the invasion of mesic grasslands by shrubs and trees enhances the biological sequestration of carbon in these widespread and globally dispersed ecosystems that cover vast areas of the Earth's surface.

Hyvonen *et al*. (2007) led an international team of forest researchers—22 scientists from nine countries (Belgium, Denmark, France, Finland, Iceland, Italy, Sweden, the United Kingdom, and the United States)—investigating "whether the mature forests that are C sinks today will continue to be sinks as the climate changes." One way of addressing this question is to look at what has happened to forests that matured several decades ago and have experienced the concurrent increases in air temperature and atmospheric $CO_2$ concentration of the past half-century or more, a period over which IPCC claims both of these factors rose at unprecedented rates and to unprecedented levels.

Good candidates for this assessment are old-growth forests, such as those of Amazonia, which for most of the past century were believed to be close to dynamic equilibrium. In one of the first studies to dispel this long-held notion, Phillips and Gentry (1994) analyzed the turnover rates—which are close correlates of net productivity (Weaver and Murphy, 1990)—of 40 tropical forests around the world. They found the growth rates of these forests had been increasing steadily since at least 1960 and had undergone an apparent acceleration in growth rate some time after 1980. A few years later, Phillips *et al.* (1998) analyzed forest growth rate data for the period 1958 to 1996 for several hundred plots of mature tropical trees around the world. They found tropical forest biomass, as a whole, increased substantially over the period of record. The increase in the Neotropics was equivalent to approximately 40% of the missing terrestrial carbon sink of the entire globe. Laurance *et al.* (2004a) reported accelerated growth in the 1990s relative to the 1980s for the large majority (87%) of tree genera in 18 one-hectare plots spanning an area of about 300 $km^2$ in central Amazonia, and Laurance *et al.* (2004b) observed similarly accelerated tree community dynamics in the 1990s relative to the 1980s.

This wealth of pertinent positive findings provides strong reason to reject the model-based view of forest carbon sinks turning into forest carbon sources in the decades ahead. If anything, real-world observations suggest today's forest carbon sinks may become even stronger carbon sinks as air temperatures and atmospheric $CO_2$ concentrations continue to rise.

Agren *et al.* (2007) used official forestry statistics on standing tree volumes and harvests to estimate the standing stock of tree components for each year between 1926 and 2000 throughout all of Sweden for the country's two most dominant tree species—Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*)—which together constituted 80.6% of the country's standing tree stock. For each of these tree components they estimated annual litter production, the decomposition of different litter fractions in the soil, and ultimate turnover rates, with soil carbon stocks for all sites evaluated to a depth of one meter or to bedrock, if bedrock was encountered at less than a meter depth.

Agren *et al.* report "there was a steady increase in carbon stocks in Swedish forests in the period 1926–2000," such that forest ecosystems in 2000 contained 35% more carbon than they did in 1926, with tree biomass being responsible for nearly three-quarters of the total increase in carbon stocks. For comparative purposes, they note the total amount of carbon sequestered amounted to just under half that emitted to the air by the burning of fossil fuels in Sweden.

With respect to the soil component of the carbon sequestered, the Swedish scientists arrived at a value of 1.7 Tg/year, or just under a quarter of the total sequestered carbon (7.1 Tg/year). In addition, they write, "the current soil carbon stock is not in equilibrium with the current rate of litter production," as "the increase in soil carbon stocks since 1926 is only 33% of what would be required to be in equilibrium with current tree biomass." This state of affairs, however, was only to be expected, as Agren and Bosatta (1998) calculate, for forest litter typical of coniferous needles and Swedish climatic conditions, "50% of the steady state value is reached after ca. 200 years but 15,000 years are required to reach 80%."

Clearly, carbon stocks in Swedish forests have been growing significantly faster than expected, especially considering that from 1951 to 2000, the forested area of the country actually declined by 1%. Modern global warming, atmospheric $CO_2$ enrichment, nitrogen deposition, and management factors all probably contributed to the increase, which as noted above has compensated for just under half the country's carbon emissions from the burning of fossil fuels. In addition, forest extraction of carbon from the air likely will continue well into the future in Sweden, as Agren *et al.* opine "the time since the last glaciation has probably not been long enough to reach a steady state," and since the factors that determine steady state appear to be changing in ways that continue to increase the magnitude of the equilibrium condition.

Smittenberg *et al.* (2006) begin their paper by noting "refractory organic matter makes up approximately half of the SOC [soil organic carbon] pool because of its resistance to degradation, and it is this pool that is ultimately responsible for long-term terrestrial carbon storage." However, they suggest current ideas about the long-term buildup of SOC are questionable because our understanding of the phenomenon is largely derived from studies of present-day soils, due to a paucity of long-term records of SOC dynamics.

To provide more information about this

phenomenon, the scientists worked with high-temporal-resolution sediments of Saanich Inlet, Canada, obtained from seven well-dated cores that contained layers ranging in age from recent to 5,500 years before present, as well as layers just below the well-dated section and a late Pleistocene layer. Smittenberg *et al*. analyzed the distribution, stable carbon isotopic composition, and radiocarbon composition of long-chain *n*-alkanes derived predominantly from $C_3$ vascular plant material produced upon boreal-forest-covered watersheds that drain into rivers that empty into the inlet. These *n*-alkanes may thus serve as proxies for recalcitrant terrigenous organic matter produced upon the watersheds.

The scientists found the average *n*-alkane ages have been increasing in a near-linear fashion toward the present, strongly suggesting any loss due to mineralization or erosion is still largely outpaced by the accumulation. They interpret this finding to imply "the accumulation of refractory organic carbon in soils that developed after the deglaciation of the American Pacific Northwest is ongoing and may still be far from equilibrium with mineralization and erosion rates." This further suggests, in their words, "the turnover time of this carbon pool is 10,000 to 100,000 years or more and not 1,000 to 10,000 years as is often used in soil carbon models."

Smittenberg *et al*. therefore conclude their findings "challenge the notion that the current production of refractory organic matter is balanced by decomposition and erosion after a few thousand years, as inferred via chrono-sequences or soil respiration measurements." They also state their findings place the terrestrial biosphere "in a more prominent position as a slow but progressively important atmospheric carbon sink on geologic time scales," and it "may even influence current predictions about carbon cycling and soil carbon storage in response to elevated atmospheric $CO_2$ levels," hinting the potential for refractory organic carbon sequestration in a world with a $CO_2$-accreting atmosphere may be greater than what previously has been believed, but with the effect having its main impact on time scales of more than a thousand years.

Ciais *et al*. (2008a) analyzed national forest inventory data and timber harvest statistics of the EU-15 countries excluding Luxembourg, plus Norway and Switzerland, for the period AD 1950–2000. They found over this half-century interval, the net primary productivity (NPP) of Europe's forests rose by about 67%, while their biomass carbon stocks rose by approximately 75%. This build-up of forest carbon stocks, in the words of the 13 researchers, "appears to result from woody NPP exceeding losses by timber harvest and natural disturbances such as fire and wind throw," and they note their analyses suggests 70–80% of the observed increase in NPP has likely been due to "changes in climate and to the fertilizing effect of $CO_2$."

Buttressing their conclusions in this regard, Ciais *et al*. note "another independent model-based analysis that accounted for changing age-classes, management and land use (Zaehle *et al*., 2006) further indicates that forest NPP increases were mainly driven by climate change and $CO_2$." In addition, they note "real increases of biomass increment have occurred and are still occurring," as "corroborated by tree-ring studies and by measurements of long-term permanent sample plots (Becker *et al*., 1995; Nicolussi *et al*., 1995; Spiecker, 1996; Rolland *et al*., 1998; Motta and Nola, 2001)."

The international group of scientists (from Belgium, China, Finland, France, Germany, Italy, the Netherlands, Romania, and the United States) write, "European forests still have the potential to realize a build-up of their carbon stocks by a factor of two, within the next century." However, they state this "potential $CO_2$ sink is threatened by the proposal of the European Commission to increase the share of renewable energy to 20% of the total energy consumption by 2020," and "this will almost double the wood demand for biomass energy (Ragwitz *et al*., 2005) in the EU-15 from 55% of harvested wood in 2001 to 100% in 2020 at current harvest levels." Summing up this latter situation, Ciais *et al*. conclude "a return to using wood as biofuel ... could cancel out the benefits of carbon storage over the past five decades."

Lewis *et al*. (2009) invested a great amount of time and effort in documenting changes in aboveground carbon storage in "79 permanent sample plots spanning 40 years (1968–2007), located in closed-canopy moist forest, spanning West, Central and Eastern Africa," based on data from more than 70,000 individual trees across ten countries. They found "aboveground carbon storage in live trees increased by 0.63 Mg C $ha^{-1}$ $year^{-1}$ between 1968 and 2007," and "extrapolation to unmeasured forest components (live roots, small trees, necromass) and scaling to the continent implies a total increase in carbon storage in African tropical forest trees of 0.34 Pg C $year^{-1}$."

The 33 researchers say the observed changes in carbon storage "are similar to those reported for Amazonian forests per unit area, providing evidence that increasing carbon storage in old-growth forests is a pan-tropical phenomenon," and "combining all standardized inventory data from this study and from tropical America and Asia together yields a comparable figure of 0.49 Mg C $ha^{-1}$ $year^{-1}$." This equates to "a carbon sink of 1.3 Pg C $year^{-1}$ across all tropical forests during recent decades," which can account for roughly half of the so-called missing carbon sink.

In identifying the driving force that breathed new life into old trees, Lewis *et al*. write in the concluding sentence of the abstract of their paper, "taxon-specific analyses of African inventory and other data suggest that widespread changes in resource availability, such as increasing atmospheric carbon dioxide concentrations, may be the cause of the increase in carbon stocks, as some theory (Lloyd and Farquhar, 1996) and models (Friedlingstein *et al*., 2006; Stephens *et al*., 2007; Ciais *et al*., 2008b) predict."

All these findings indicate elevated $CO_2$ enhances photosynthetic rates and biomass production in forest trees, both of which lead to greater amounts of carbon sequestration. Elevated $CO_2$ also enhances carbon sequestration by reducing carbon losses arising from plant respiration. Karnosky *et al*. (1999), for example, report aspen seedlings grown for one year at 560 ppm $CO_2$ displayed dark respiration rates 24% lower than rates exhibited by trembling aspen grown at 360 ppm $CO_2$. Also, elevated $CO_2$ has been shown to decrease maintenance respiration, which it did by 60% in western hemlock seedlings exposed to an atmospheric $CO_2$ concentration of nearly 1,600 ppm (McDowell *et al*., 1999).

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

Still, some researchers have expressed concern about the fate of the extra carbon stored in plant tissues as a consequence of atmospheric $CO_2$ enrichment, fearing it may rapidly return to the atmosphere following tissue senescence and decomposition, as opposed to being locked away for long periods of time.

In addressing such concerns, it is important to note atmospheric $CO_2$ enrichment typically reduces, or has no effect upon, decomposition rates of senesced plant material. De Angelis *et al*. (2000), for example, note when leaf litter from Mediterranean forest species exposed to 710 ppm $CO_2$ for 3.5 years was collected and allowed to decompose at 710 ppm $CO_2$ for approximately one year, it decomposed at a rate 4% less than leaf litter produced and incubated at ambient $CO_2$ for one year. Similarly, leaf litter collected from yellow-poplar (*Liriodendron tulipifera*) seedlings exposed to 700 ppm $CO_2$ for four years contained 12% more biomass than leaf litter collected from seedlings grown at ambient $CO_2$, following two years of decomposition at their respective $CO_2$ growth concentrations (Scherzel *et al*., 1998). Hirschel *et al*. (1997) found no significant $CO_2$-induced effects on decomposition rates in tropical rainforest species, as Scherzel *et al*. (1998) also found for eastern white pine (*Pinus strobes*). Others have reported similar findings.

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

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

Conway *et al*. (2000) grew two-year-old ash tree seedlings in solar domes maintained at atmospheric

$CO_2$ concentrations of 350 and 600 ppm, after which naturally senesced leaves were collected, inoculated with various fungal species, and incubated for 42 days. They found the elevated $CO_2$ significantly reduced the amount of nitrogen in the senesced leaves, thus giving the $CO_2$-enriched leaf litter a higher carbon-to-nitrogen ratio than the litter collected from the seedlings growing in ambient air. This change likely contributed to the observed reductions in the amount of fungal colonization present on the senesced leaves from the $CO_2$-enriched treatment, which would be expected to result in reduced rates of leaf decomposition.

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

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

Thus it would appear the ongoing rise in the air's $CO_2$ content will not materially alter the rate of decomposition of the world's soil organic matter. This means the rate at which carbon is sequestered in forest soils should continue to increase as the productivity of Earth's plants is increased by the aerial fertilization effect of the rising atmospheric $CO_2$ concentration.

Another concern, which for a time was thought to limit the sequestering power of forests under rising atmospheric $CO_2$ but which has been thoroughly debunked, is what has come to be known as the progressive nitrogen limitation hypothesis. Some researchers suggested the striking $CO_2$-induced growth enhancements initially experienced by woody plants in scientific studies would disappear gradually over time, as the plants slowly deplete the soils in which they are growing of their initial store of nitrogen.

Long-term atmospheric $CO_2$-enrichment experiments show this progressive nitrogen limitation hypothesis is not supported by real-world data, as even soils low in nitrogen at the start of many long-term atmospheric $CO_2$ enrichment experiments have continued to supply sufficient nitrogen to maintain the initial high level of the $CO_2$-induced stimulation of plant growth.

In the introduction to a paper on the subject that summarizes nine years of work at the Duke Forest FACE experiment in North Carolina (USA), where portions of an aggrading loblolly pine (*Pinus taeda*) plantation had been continuously exposed to an extra 200 ppm of $CO_2$ since 1996, Lichter *et al.* (2008) note progressive nitrogen limitation (PNL) may "accompany C sequestration in plants and soils stimulated by $CO_2$ fertilization, gradually attenuating the $CO_2$ response." They then describe what they learned about this PNL hypothesis over the nine years of the Duke Forest experiment.

First, the nine researchers report 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 "a substantial increase in forest-floor C storage under elevated $CO_2$ (i.e. 29%)," and which they attribute to "increased litterfall and root turnover during the first 9 years of the study." Second, below the forest floor, they say, of the mineral soil C formed during the past nine years, "approximately 20% has been allocated to stable pools that will likely remain protected from microbial activity and associated release as $CO_2$."

The research team also found "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 $CO_2$." Pritchard *et al.* (2008) report this $CO_2$-induced increase in productivity amounts to approximately 30% annually, and they add there is "little evidence to indicate a diminished response through time," citing Finzi *et al.* (2007), who found the same to be true at the long-term forest FACE studies being conducted at Rhinelander, Wisconsin (USA), Oak Ridge National Laboratory (USA), and Tuscania (Italy).

Thus, contrary to the PNL hypothesis, in the case of North Carolina's Duke Forest, "even after nine years of experimental $CO_2$ fertilization," as Lichter *et al.* describe it, "attenuation of the $CO_2$-induced productivity enhancement has not been observed."

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 soils in which they grow that they induce what Finzi and Schlesinger (2003) describe as "a state of acute nutrient deficiency that can only be reversed with fertilization." No fertilization was done during the Duke Forest FACE study.

Langley *et al*. (2009) note "it has been suggested that stimulation of productivity with elevated $CO_2$ ties up nitrogen in plant litter, which, if not offset by increases in N-use efficiency or N supply, will limit the ecosystem $CO_2$ response," citing Reich *et al.* (2006). The six scientists "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 a multiple open-top-chamber facility on a barrier island located at NASA's Kennedy Space Center on the east coast of central Florida, USA. Langley *et al*. report 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 to only "roughly one-third of the increase in plant biomass that occurred in the same experiment." In addition, the strongest increases in net N mineralization were observed 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%," according to Hungate *et al.* (2006).

Much more information rebutting the PNL hypothesis is presented in Chapter 3, Section 3.11, where is it demonstrated 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, which increases total ecosystem carbon content, resulting in a negative feedback to anthropogenic $CO_2$ emissions. As the air's $CO_2$ content rises, the ability of forests to sequester carbon rises along with it, while tempering the rate of rise of the air's $CO_2$ content.

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### *1.2.1.4.2 The Influence of Temperature*

- If air temperatures rise in the future they likely will have a positive effect on carbon storage in forests and their associated soils.

The planting of forests with the objective of removing $CO_2$ from the atmosphere and sequestering its carbon in soil organic matter—which tends to slow the rate of rise of the air's $CO_2$ content—has come under fire as being only a stopgap measure in the quest to moderate global warming. Pearce (1999) even referred to the concept as a dangerous delusion, saying "planned new forests, called 'carbon sinks,' will swiftly become saturated with carbon and begin returning most of their carbon to the atmosphere."

The rationale for this contention was that rising temperatures will increase rates of soil respiration, thereby causing forest ecosystems to return $CO_2$ to the air at a faster rate than they remove it from the atmosphere via photosynthesis. Proponents of the theory argue future rates of photosynthesis will "flatten out," according to Pearce, and respiration rates will "soar." Much like the theory of $CO_2$-induced global warming, however, a number of studies have shown quite conclusively this theory is not supported by real-world observations, which in fact directly contradict the theory.

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

Liski *et al.* (1999) studied soil carbon storage across a temperature gradient in a modern-day Finnish boreal forest, reporting carbon sequestration in the soil of this forest increased with temperature. Contemporaneously, King *et al.* (1999) showed aspen seedlings increased their photosynthetic rates and biomass production as temperatures rose from 10 to 29°C, putting to rest the idea that high-temperature-induced increases in respiration rates would cause net losses in carbon fixation.

Giardina and Ryan (2000) analyzed organic carbon decomposition data derived from forest soils of 82 sites on five continents. Based on this worldwide assemblage of real-world data, they state carbon decomposition rates "are not controlled by temperature limitations to microbial activity, and that increased temperature alone will not stimulate the decomposition of forest-derived carbon in mineral soil." They report, "despite a 20°C gradient in mean annual temperature," soil carbon mass loss was "insensitive to temperature."

A group of 30 scientists (Valentini *et al*., 2000) collected data on net ecosystem carbon exchange in 15 European forests, and they report their results "confirm that many European forest ecosystems act as carbon sinks." Their data also demonstrate the warmer forests of southern Europe annually sequester far more carbon than the cooler forests of northern Europe, again in direct contradiction of claims warmer temperatures must inevitably lead to forest carbon loss.

Grace and Rayment (2000) present still more evidence refuting the claim forests "will swiftly become saturated with carbon and begin returning most of their carbon to the atmosphere." Specifically, they cite a number of additional studies that "show quite clearly," as they put it, "that old undisturbed forests, as well as middle-aged forests, are net absorbers of $CO_2$." They also note these real-world observations mean "forests are serving as a carbon sink, providing a global environmental service by removing $CO_2$ from the atmosphere and thus reducing the rate of $CO_2$-induced warming." Further commenting on the work of Giardina and Ryan (2000) and Valentini *et al.* (2000), Grace and Rayment unequivocally state, "the results from these two papers should send a powerful message to those working with models of global vegetation change," namely, "that the doomsday view of runaway global warming now seems unlikely."

One of the simpler ways Earth's deciduous forests increase their storage of carbon is to leaf out progressively earlier each spring and remain photosynthetically active increasingly later every fall. This gradual lengthening of the growing season allows trees to remove more carbon dioxide from the atmosphere each succeeding year. This phenomenon, in turn, reduces the annual rate of rise of the air's $CO_2$ content, completing a negative feedback loop that slows the $CO_2$-induced portion of the warming that originally set the whole process in motion.

White *et al.* (1999) investigated in detail several aspects of this multistage phenomenon in a study of 88 years of data spanning the period 1900 to 1987, obtained from 12 locations in the eastern U.S. deciduous forest from Charleston, SC (32.8°N latitude) to Burlington, VT (44.5°N latitude). They determined a 1°C increase in mean annual air temperature increased the length of the forest's growing season by approximately five days. In addition, they demonstrated this relationship was linear over the entire mean annual air temperature range investigated, which stretched from 7 to 19°C and included growing seasons ranging in length from

150 to 210 days.

The second step of White *et al.*'s analysis was a bit more complicated, as they had to determine how much extra $CO_2$ was removed from the air for each day's temperature-induced extension of the growing season. They began by using an ecosystem process model that had previously been validated in other studies to predict carbon fluxes for the 12 forest sites. Using daily meteorological data, the model first calculated annual dates of the appearance and disappearance of "greenness"—the length of the photosynthetically active growing season—for each of the 88 years of records at each site. Then it calculated the net ecosystem production (NEP = gross primary production minus the sum of autotrophic and heterotrophic respiration) for each day of the 88 growing seasons at each site and summed each year's results to obtain 88 annual NEP totals for each site.

Plotting these yearly totals of net $CO_2$ removal from the atmosphere as functions of yearly growing season length for each site, White *et al.* report a one-day extension in growing season increased the mean forest NEP of the 12 sites by 1.6%, with greater increases in the colder northern sites (1.9% for Burlington, VT) and smaller increases in the warmer southern sites (1.4% for Charleston, SC).

As for how significant these numbers are, if Earth were to undergo a mean global warming of 1°C, according to the first of the two relationships derived by White *et al.*, this temperature increase would result in the eastern U.S. deciduous forest increasing the length of its growing season by approximately five days. Their second relationship suggests this growing season expansion would lead to an 8% increase in total carbon sequestration (5 days x 1.6% per day = 8%).

Moreover, this temperature-driven phenomenon may be much stronger than is implied by this simple exercise. In a study of 30 years of phenological data derived from observations of identical clones of trees and shrubs maintained by the European network of the International Phenological Gardens—located in the area bounded by latitudes 42 and 69° N and by longitudes 10° W and 27° E—Menzel and Fabian (1999) report the mean date of spring bud-break had increased by fully six days "since the early 1960s," and leaf senescence in the fall was delayed by an average of 4.8 days over the same period. Using the northernmost NEP enhancement factor derived by White *et al.*—which in all likelihood is a conservative choice, as White *et al.*'s northernmost forest site is at about the same latitude as the southernmost part of the latitudinal gradient spanned by Menzel and Fabian's study area—the 10.8 extra warming-induced growing-season days produce a 20.5% increase in annual carbon sequestration (10.8 days x 1.9% per day = 20.5%).

Melillo *et al.* (2002) studied an even-aged mixed hardwood stand of the Harvard Forest in central Massachusetts, USA, where they installed buried heating cables at 10cm depths, spaced 20cm apart, in 6m by 6m plots, half of which were not operated to produce any heat (serving as "disturbance control" plots) and half of which maintained the average soil temperature approximately 5°C above ambient. At monthly intervals from April through November of each year of their 10-year study, the researchers measured $CO_2$ evolution rates from the soils of both sets of plots.

Over the first six years of the study, Melillo *et al.* observed an approximate 28% increase in $CO_2$ emissions from the heated plots relative to the non-heated plots. However, "over the last four years of the study, the 'stimulatory' effect of warming on soil respiration markedly decreased"; so much so, in fact, that from 1998 through 2000 there was "only about a 5% increase in soil respiration in the warmed versus disturbance control plots," and by the tenth year of the study "soil respiration showed no significant response to warming."

This exemplary study showed just how important it is to do experiments … and to do *long-term* experiments. Most prior theoretical studies, for example, had tended to predict what the scientists observed over the first six years of their measurement program—a large warming-induced increase in respiratory carbon loss from the forest soil—which likely would have been accepted as the long-term truth if they had terminated their work at any time during that period. Continuing their measurements for four more years, however, the scientists discovered what is likely the true long-term response—no significant change in soil respiratory carbon loss. That was but the beginning of what they learned.

Concurrent with their soil $CO_2$ evolution measurements, Melillo *et al.* measured rates of net nitrogen mineralization, finding "over the entire 10-year study period, warming resulted in a cumulative increase in net nitrogen mineralization." Also, partially overlapping Melillo *et al.*'s long-term warming experiment was a long-term nitrogen fertilization study of a similar hardwood stand in the Harvard Forest described by Magill *et al.* (2000), where after nine years, they report, "12.7% of the total amount of nitrogen fertilizer added ended up in the woody tissue of the stand's trees."

Assuming an identical portion of the increased nitrogen made available by the warming of their experiment ended up in the woody tissues of the trees they studied, Melillo *et al.* calculate this phenomenon "would result in an additional 1560 g $m^{-2}$ of carbon storage in the vegetation over the decade of warming." Hence, having previously determined the soil carbon loss stimulated by their applied warming for the entire 10-year period was 944 g $m^{-2}$, the net result of the two competing phenomena for the complete forest ecosystem was a net carbon gain on the order of 600 g $m^{-2}$.

In discussing the significance of this unexpected but positive finding, Melillo *et al.* note there is other independent "direct field evidence that soil warming enhances carbon storage in trees." Citing Bergh *et al.* (1999) and Jarvis and Linder (2000), they say in a similar long-term study these investigators also found "there was a significant (more than 50%) increase in stem-wood growth of the trees on the heated plots relative to the controls."

These independent experimental observations suggest claims to the contrary have no backing in empirical science. Both the aerial fertilization effect of atmospheric $CO_2$ enrichment and the soil fertilization effect of the increase in nitrogen mineralization induced by global warming increase carbon sequestration in forest ecosystems, providing a strong, double-barreled, negative-feedback brake on the impetus for warming created by the enhanced greenhouse effect of the ongoing rise in the air's $CO_2$ content.

Perfors *et al.* (2003) utilized overhead infrared radiative heaters to continuously warm five plots of ungrazed montane meadow at the Rocky Mountain Biological Laboratory in Gunnison County, Colorado, USA. Five similar but unheated plots served as controls. In the heated plots, the extra downward flux of infrared radiation warmed the top 15 cm of soil by about 1.5°C and dried it by about 15% on a gravimetric basis during the growing season, prolonging the snow-free season at each end by a total of approximately 20 days. The scientists also developed and applied a method for extracting the age-detrended growth rate of common sagebrush—*Artemisia tridentata* (Nutt.), ssp. *vaseyana*, a perennial shrub that is abundant throughout much of the semiarid western United States—to determine the effect of a modest warming on the distribution of this common woody plant.

The scientists found annual sagebrush growth rates in the heated plots were approximately 50% greater than those in the control plots, due primarily to the warming-induced increase in the length of the snow-free season. The three researchers report their observations and analysis "suggest that global climate change, which is expected to result in a contracted period of snow accumulation in the montane west, will result in increased growth and range expansion of sagebrush near high-elevation range boundaries in the western US." And although Saleska *et al.* (2002) had demonstrated the experimental warming treatment decreased soil organic carbon content, Perfors *et al.* suggest, over the long term, "because sagebrush litter is more recalcitrant to decomposition than is the litter from the forb species that are in decline in the heated plots of our climate manipulation experiment, enhanced sagebrush growth could also contribute to a negative feedback [to $CO_2$-induced warming] by increasing the turnover time of soil carbon."

Monson *et al.* (2006) studied the effect of changes in snow cover on soil carbon cycling during natural climatic variations over a six-year period at the Niwot Ridge AmeriFlux site in the U.S. Rocky Mountains (40°1'58"N, 105°32'47"W). They used eddy covariance measurements to assess the net $CO_2$ exchange of a subalpine montane forest ecosystem, special chambers for measuring soil respiration beneath snow, various instruments to characterize a number of snow properties, and standard techniques for identifying soil microbial populations and assessing their growth kinetics and substrate-use. They report "microbes collected from under the snowpack could grow exponentially at 0°C," and "their growth rates increased rapidly with increasing temperature," so anything that decreased the temperature of their environment decreased forest soil respiration in winter, as they typically observed to be the case. They also note "a shallower snowpack has less insulation potential, causing colder soil temperatures," and "long-term monitoring of mountain snow packs in the western USA and Europe have shown trends towards decreasing depth, with several mountain ranges experiencing 50–75% decreases, and these have been attributed to positive temperature anomalies (Laternser and Schneebeli, 2003; Scherrer *et al*., 2004; Mote *et al*., 2005)."

Because rising air temperatures cause decreases in snow depth, decreases in snow depth in turn lead to colder soil temperatures, and colder soil temperatures lead to reduced microbial respiration, global warming may actually lead to greater quantities of carbon being trapped in the soils of montane forest ecosystems. As Monson *et al.* describe it, "decreases in the winter snow pack will generally cause decreases in the loss of respired $CO_2$ from the soils of forest ecosystems, thus enhancing the potential for soil carbon sequestration." Thus their work reveals yet another negative feedback mechanism whereby Earth's biosphere acts to resist changes in temperature caused by thermal pressures exerted by independent climate forcing factors.

Chen *et al.* (2006) note "$CO_2$ fluxes measured on micrometeorological towers in many flux networks worldwide (Baldocchi *et al.*, 2001) ... can only sample a very small fraction of the land surface as each can only represent a footprint area of about 1 $km^2$." Hence they sought "ways to retrieve carbon cycle information from atmospheric $CO_2$ concentration measurements, which have much larger footprints ($10^3$–$10^4$ $km^2$) (Lin *et al.*, 2003) than flux towers." They analyzed a 13-year (1990–1996, 1999–2004) hourly averaged atmospheric $CO_2$ concentration database obtained from a 40 m tower at Fraserdale, Ontario, Canada (together with temperature, humidity, and wind speed measured at 20 and 40 meters and precipitation at ground level). They compared their results with a marine boundary layer $CO_2$ dataset representing the free troposphere above the tower.

The eight researchers report in warmer years the planetary boundary layer over their measurement site was more depleted of $CO_2$, which suggests the $10^3$–$10^4$ $km^2$ land area of the boreal ecosystem upwind of the tower sequestered more carbon in such years. They say this finding "suggests that gross primary productivity increased considerably faster with temperature than did ecosystem respiration," a relationship they found to be true for both annual temperatures (from year to year) and 10-day mean temperatures (throughout the growing season). These findings led them to conclude "the fact that the temperature sensitivity of gross primary productivity is larger than that of ecosystem respiration suggests that global warming could lead to increased carbon sequestration in boreal ecosystems."

Burton *et al.* (2008) note "increases in terrestrial ecosystem respiration as temperatures warm could create a positive feedback that causes atmospheric $CO_2$ concentration, and subsequently global temperature, to increase more rapidly," but they also note "if plant tissue respiration acclimates to temperature over time, this feedback loop will be weakened, reducing the potential temperature increase." In an attempt to determine which of these scenarios is more likely to occur, the three researchers employed published values of annual root respiration rates to assess "the cross-ecosystem rate of increase with temperature." They then examined "the potential for trade-offs between root metabolic capacity and biomass in regulating ecosystem root respiration, using published values for mid-growing season root specific respiration rates and root biomass." Finally, they determined whether "relationships that occur across ecosystems adapted to different climates might also exist within an ecosystem that is subjected to warming," by analyzing data obtained "from soil warming studies, including recent measurements of fine root respiration made at three warming experiments at Harvard Forest."

Burton *et al.* report their analyses of the pertinent scientific literature show "a clear trend for decreasing root metabolic capacity (respiration rate at a standard temperature) with increasing mean annual temperature"; "no instances of high growing season respiration rates and high root biomass occurring together"; and in the soil warming experiments at Harvard Forest, "decreases in metabolic capacity for roots from the heated plots." Thus Burton *et al.* conclude "these findings clearly suggest that modeling efforts that allow root respiration to increase exponentially with temperature, with $Q_{10}$ values of 2 or more, may over-predict root contributions to ecosystem $CO_2$ efflux for future climates and underestimate the amount of carbon available for other uses, including net primary productivity," rebuffing long-espoused claims to the contrary.

The studies cited above indicate rising air temperatures likely would have a positive effect on carbon storage in forests and their associated soils, instead of exerting a negative influence on forest carbon sequestration.

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### 1.2.2 Grasslands

Most of Earth's terrestrial plant life evolved around 500 to 400 million years ago, when the atmospheric $CO_2$ concentration was possibly 10 to 20 times higher than it is today. As a consequence, the biochemical pathways and enzymes involved in carbon fixation should be better adapted to significantly higher-than-present atmospheric $CO_2$ levels, which has in fact been demonstrated to be the case. As the atmosphere's $CO_2$ content has dropped from that early point in time, it has caused most of Earth's vegetation to become less efficient at extracting carbon dioxide from the air. However, the recent ongoing rise in atmospheric $CO_2$ concentration is gradually increasing photosynthetic rates and stimulating vegetative productivity and the terrestrial sequestration of carbon around the globe. The subsections below review some of the recent evidence for these phenomena in various grassland species.

### *1.2.2.1 General Responses to Elevated $CO_2$*

- As the air's $CO_2$ concentration increases, the productivity of Earth's grassland species also should increase, even under unfavorable growing conditions characterized by less-than-adequate soil moisture, inadequate soil nutrition, elevated air temperature, and physical stress imposed by herbivory.

Wand *et al.* (1999) provided an overview of the effects of elevated atmospheric $CO_2$ concentrations on photosynthesis in grasses by analyzing the pertinent peer-reviewed literature published between 1980 and 1997. These authors report a doubling of the air's $CO_2$ content increases photosynthetic rates of $C_3$ and $C_4$ grasses by 33 and 25%, respectively. Importantly, their results also demonstrate, contrary to some circulating opinions, $C_4$ plants can—and do—respond positively to increases in the air's $CO_2$ content.

Another good summary of grassland community responses to atmospheric $CO_2$ enrichment followed a year later in the comprehensive review of Campbell *et al.* (2000), who compiled and analyzed more than 165 peer-reviewed scientific journal articles dealing with pastures and rangelands. Although their review includes many responses of individual species, it provides a conservative estimate of community responses as well: an average 17% increase for a doubling of the air's $CO_2$ content. Therefore, as the atmospheric $CO_2$ concentration increases, it is likely grassland communities will exhibit increases in photosynthesis and biomass production, which will invariably lead to enhanced carbon sequestration in the soils beneath them. This conclusion is borne out in many additional studies.

Szente *et al.* (1998) grew two grass and two broad-leaved species common to loess grasslands of Budapest in open-top chambers for 231 days at atmospheric $CO_2$ concentrations of 350 and 700 ppm. The elevated $CO_2$ caused photosynthetic enhancements of 136 and 486% in the grass and broad-leaved species, respectively. After growing microcosms of the $C_3$ grass *Danthonia richardsonii* for four years in glasshouses receiving atmospheric $CO_2$ concentrations of 360 and 720 ppm, Lutze and Gifford (1998) report the elevated $CO_2$ increased total microcosm biomass by an average of 24%. Similarly, in the four-year study of Leadley *et al.* (1999), species-rich Swiss grasslands exposed to atmospheric $CO_2$ concentrations of 600 ppm in open-top and open-bottom chambers produced 29% more community biomass than control grasslands exposed to air of 350 ppm $CO_2$. And tallgrass prairie ecosystems in Kansas, USA, exposed to twice-ambient levels of atmospheric $CO_2$ displayed significant $CO_2$-induced enhancements of biomass, but only during relatively dry years (Owensby *et al.*, 1999).

Cotrufo and Gorissen (1997) grew three grasses (*Lolium perenne*, *Agrostis capillaries*, and *Festuca ovina*) at atmospheric $CO_2$ concentrations of 350 and 700 ppm for approximately two months before harvesting. On average, atmospheric $CO_2$ enrichment increased plant biomass by approximately 20%, with greater carbon partitioning to roots, as opposed to shoots. Also, in a much shorter two-week study performed on tall fescue (*Festuca ovina*), Newman *et al.* (1999) report twice-ambient levels of atmospheric $CO_2$ increased plant biomass by 37% relative to plants grown in ambient air.

In two additional studies, researchers grew perennial ryegrass (*Lolium perenne*) in controlled environmental chambers receiving atmospheric $CO_2$ concentrations of 350 and 700 ppm for approximately 14 weeks. After assessing plant growth, the authors reported $CO_2$-induced increases in shoot (van Ginkel and Gorissen, 1998) and root (van Ginkel *et al.*, 2000) biomass of 28 and 41%, respectively. Hodge *et al.* (1998) also report, for the same species, plants grown at an atmospheric $CO_2$ concentration of 720 ppm for a mere 21 days exhibited total biomass values 175% greater than those observed for control plants exposed to air of 450 ppm $CO_2$.

Lüscher *et al.* (1998) collected nine to 14 genotypes for each of 12 native grassland species from two permanent meadows near Zurich, Switzerland, and transplanted them into artificial gaps created in well-fertilized swards of *Lolium perenne* growing in FACE arrays maintained at 350 and 700 ppm $CO_2$, to determine inter- and intraspecific species growth responses to elevated $CO_2$ by harvesting aboveground biomass several times over a three-year period. $CO_2$-induced biomass increases varied with plant type, being greatest for legumes followed by non-legume dicotyledonous species and, last, monocotyledonous grasses. There were no significant differences in $CO_2$ responsiveness within genotypes for any of the 12 species.

Suter *et al*. (2002) grew perennial ryegrass (*Lolium perenne* L.) in field plots, as part of a FACE experiment, and in controlled-environment chambers, to compare growth and carbon allocation responses of this important forage crop to elevated atmospheric $CO_2$ concentrations under different experimental protocols. In both regimes, the control and elevated $CO_2$ concentrations were maintained for approximately two months at 350 and 600 ppm, respectively. The overall growth response of perennial ryegrass to elevated $CO_2$ was consistently greater for plants grown in the FACE experiment than for plants grown in the controlled-environment chambers. Elevated $CO_2$, for example, increased total dry matter production by 65 and 54% in the FACE and controlled-environment chambers, respectively. In addition, it enhanced root dry weights by 109 and 47% for plants gown in the FACE and controlled-environment chambers, respectively.

Bhatt *et al*. (2007) transplanted 30-day-old seedlings of *Cenchrus ciliaris* to open-top chambers—maintained at either the ambient atmospheric $CO_2$ concentration (360 ppm) or at an elevated $CO_2$ concentration (600 ppm)—in which the plants were grown for an additional 120 days, "using recommended agronomical practices" and with irrigation "given as and when required." During this time of outdoor field growth, the researchers measured numerous plant properties and physiological processes. At the end of the experiment, the plants were harvested and other pertinent measurements made. Among other things, Bhatt *et al*. report the extra 240 ppm of $CO_2$ employed in their experiment increased several plant parameters by the following percentages: plant height (44%), number of tillers (33%), leaf length (23%), leaf width (51%), leaf area index (234%), net photosynthetic rate per unit leaf area (25%), net photosynthetic rate per unit ground area (316%), total fresh weight (134%), total dry weight (193%), and whole-crop photosynthetic water use efficiency (34%). The three Indian researchers conclude "*C. ciliaris* grown in elevated $CO_2$ throughout the crop season may produce more fodder in terms of green biomass."

Several researchers have examined the effects of $CO_2$ enrichment on grasslands under varying soil nitrogen and fertility regimes. In a model-based study, Cannell and Thornley (1998) used the Hurley Pasture Model to simulate growth responses of perennial ryegrass (*Lolium perenne* L.) to a step increase in atmospheric $CO_2$ concentration (350 to 700 ppm) under conditions of low and high soil nitrogen. At high soil nitrogen conditions, elevated $CO_2$ stimulated net primary productivity and plant biomass by approximately 30% within a few years. Under low soil nitrogen conditions, elevated $CO_2$ caused a much greater stimulation of approximately 114%, although it took longer (five to ten years) to attain this greater degree of growth enhancement.

Navas *et al*. (1999) grew mixed communities of two grasses and two legumes across a range of soil nitrogen contents at ambient (357ppm) and enriched (712 ppm) atmospheric $CO_2$ concentrations for two months. Although soil nitrogen content had a much greater influence on community productivity than did atmospheric $CO_2$ concentration, communities fumigated with $CO_2$-enriched air tended to produce greater amounts of biomass than those exposed to ambient air. Likewise, Jongen and Jones (1998) report an eight-month exposure to twice-ambient levels of atmospheric $CO_2$ increased the community biomass of semi-natural grasslands characteristic of the Irish lowlands by 26%.

Reich *et al*. (2001) grew 16 perennial grassland species as monocultures in FACE plots maintained at atmospheric $CO_2$ concentrations of 360 and 560 ppm and low and high levels of soil nitrogen for two years. Interestingly, they found no interactions between atmospheric $CO_2$ concentration and soil nitrogen for any measured plant parameter. Nonetheless, elevated $CO_2$ increased total plant biomass for forbs, legumes, and $C_3$ grasses by 31, 18, and 9%, respectively, and it decreased the growth of $C_4$ grasses by 4%.

In a two-year study, Stocklin *et al*. (1999) grew simulated low-fertility Swiss grasslands in glasshouses receiving atmospheric $CO_2$ concentrations of 360 and 600 ppm. The authors report elevated $CO_2$ concentrations stimulated total biomass production by an average of 23% in these nutrient-poor grassland communities. And in another two-year experiment, Niklaus *et al*. (1998) note swards of calcareous grasslands exposed to atmospheric $CO_2$ concentrations of 600 ppm displayed total biomass values 25% greater than those exhibited by control swards grown in ambient air of 350 ppm $CO_2$.

Zaller and Arnone (1999) established open-top chambers in a species-rich grassland located near Basel, Switzerland and fumigated them continuously with atmospheric $CO_2$ concentrations of 350 and 600 ppm, except during winter months, for nearly one-and-a-half years, to see whether graminoids, non-legume forbs, and legumes growing near earthworm surface casts were more responsive to atmospheric $CO_2$ enrichment than those growing further away from these nutrient-rich microsites. Generally, plants growing in close proximity to earthworm casts produced more biomass than similar plants growing further away, regardless of $CO_2$ concentration. When assessing the influence of earthworm casts on plant responsiveness to atmospheric $CO_2$ enrichment, no statistically significant results were detected. Nonetheless, the average growth response of graminoids to elevated $CO_2$ was greater for those plants growing closer to earthworm casts than for those growing further away from them. This finding suggests plant growth responses to atmospheric $CO_2$ enrichment may be increased if local plant niches are closely associated with earthworm casts, which provide limiting nutrients to facilitate greater plant growth.

Also working in Switzerland, Niklaus *et al.* (2003) enriched the air above plots of a nutrient-poor, species-rich calcareous grassland in the northwestern portion of the country with an extra 240 ppm of $CO_2$ via a set of novel windscreens that "operated around the clock" except during midwinter (December-February). Among several other findings, the authors report during the six years of their experiment, aboveground plant biomass accumulation increased in response to $CO_2$ by an average of 21%. Simultaneously, there was an increase in soil moisture due to $CO_2$-induced reductions in plant transpiration. They also report microbial nitrogen (N) pools did not change, "indicating that elevated $CO_2$ did not stimulate net microbial immobilization of N which could have imposed a negative feedback on plant growth [but didn't]."

Contemporaneously, in a paper produced from the same experimental site, Ebersberger *et al.* (2003) assessed the impact of the extra $CO_2$ after six growing seasons on N-mineralization in the grassland soil and the activities of the soil microbial enzymes invertase, xylanase, urease, protease, arylsulfatase, and alkaline phosphatase in both the spring and summer. Results indicate the extra $CO_2$ increased N-mineralization significantly ($P = 0.02$, *a priori* linear contrast) by 30% in the spring and insignificantly ($P = 0.6$) by 3% in the summer. In addition, at both sampling times all measured enzyme activities were higher in the $CO_2$-enriched treatment, with the single exception of xylanase in summer. The strongest responder in the spring was alkaline phosphatase (up 32%, $P = 0.02$), followed by urease (up 21%, $P = 0.13$). In the summer, the best responder was urease (up 21%, $P = 0.2$), followed by protease (up 17%, $P = 0.09$) and invertase (up 14%, $P = 0.07$). The authors attribute the increased N-mineralization and enzyme activity of the soil biota to the higher moisture content of the soil in the $CO_2$-enriched plots (due to a $CO_2$-induced decrease in stand transpiration) and/or the $CO_2$-induced increase in root biomass (up 24%, $P = 0.02$, in June 1999).

The observations of Ebersberger *et al.* are significant because soil microorganisms hold a key position in terrestrial ecosystems, as they mineralize organic matter and make its nitrogen available for use by plants. Hence, it is encouraging to note, in the words of the authors, "that elevated $CO_2$ will enhance below-ground C- and N-cycling in grasslands," even nutrient-poor grasslands such as the one they studied.

Morgan *et al.* (2001) grew the $C_3$ grass *Pascopyrum smithii*, the $C_4$ grass *Bouteloua gracilis*, and the $C_3$ legume *Medicago sativa* for 20 days post-defoliation in growth chambers receiving atmospheric $CO_2$ concentrations of 355 and 700 ppm and low or high levels of soil nitrogen, to determine how these factors affect the regrowth of these forage species. After 20 days post-defoliation, *Medicago sativa* plants grown in elevated $CO_2$ had attained total dry weights about 62% greater than those reached by ambiently grown plants, regardless of soil nitrogen, the scientists report. *Pascopyrum smithii* plants were more sensitive to soil nitrogen; whole plant regrowth was stimulated by 150 and 68% under conditions of high and low soil nitrogen, respectively. Elevated $CO_2$ had no positive effect on the regrowth of the $C_4$ grass, which fared better under high vs. low soil nitrogen conditions.

As the $CO_2$ concentration of the air increases, $C_3$ forage species subjected to natural or mechanical defoliation likely will respond by increasing their regrowth biomass in a plant-dependent and soil-nitrogen-dependent manner. Leguminous nitrogen-fixing $C_3$ species, for example, likely will exhibit enhanced regrowth irrespective of soil nitrogen content, and non-nitrogen-fixing $C_3$ species likely will exhibit greater regrowth on soils containing more, rather than less, nitrogen. Moreover, the regrowth of $C_4$ species may be less responsive to atmospheric $CO_2$ enrichment than $C_3$ species. Thus, future increases in the air's $CO_2$ content should promote, or at the very least not impair, prairie regrowth following defoliation by either animals or machinery.

Edwards *et al.* (2005) grew well-watered mixtures of two plants—the legume white clover

(*Trifolium repens* L.) and $C_4$ buffalo grass (*Stenotaphrum secundatum* (Walt.) Kuntze)—which were initially equal in plantlet size, number, and spatial distribution—for 15 months in sand placed in large plastic containers located in greenhouses maintained at different atmospheric $CO_2$ concentrations (360 and 700 ppm) under three sand nutrient conditions (zero-N/low-P, zero-N/high-P, plus-N/high-P). Ten harvests were made of all plant biomass over a height of 5 cm above the sand surface, after which the scientists determined the total carbon contents of the whole plants and their respective soils. The slightly less than a doubling of the air's $CO_2$ concentration employed in this study led to increases of 27%, 55%, and 23% in final-harvest whole plant biomass in the zero-N/low-P, zero-N/high-P, and plus-N/high-P soil treatments, respectively.

Hartwig *et al*. (2002) grew perennial ryegrass (*Lolium perenne* L.) in environmental chambers receiving atmospheric $CO_2$ concentrations of 350 and 600 ppm for 60 days. In addition, they subjected plants to low and high levels of soil nitrogen and inoculated some with arbuscular mycorrhizal fungi. Thus the authors studied the interactive effects of elevated $CO_2$, soil nitrogen, and arbuscular mycorrhizal fungi on growth in this important grassland species. They found elevated $CO_2$ increased plant biomass by 10 and 17% at low and high levels of soil nitrogen, respectively. When plants were inoculated with the arbuscular mycorrhizal fungi, elevated $CO_2$ enhanced plant biomass only by 3% at low soil nitrogen, but it increased it by 41% at high soil nitrogen. Thus, at high soil nitrogen, the presence of this symbiotic fungi more than doubled the plant growth response to atmospheric $CO_2$ enrichment. In addition, the amount of root colonization by the arbuscular mycorrhizal fungi increased by 56% in the high $CO_2$ treatment.

Arbuscular mycorrhizal fungi are important because nearly all grassland species form symbiotic relationships with mycorrhizal fungi. Arbuscular mycorrhizal fungi commonly colonize roots of grasses and form symbiotic structures known as arbuscules, short-lived organs that facilitate carbon and nutrient exchange between the fungi and their host plants. The presence of these symbiotic relationships often increases grassland vitality and productivity, and several other researchers have set out to understand how rising atmospheric $CO_2$ concentrations may affect these relationships.

In an earlier study, Wilson and Hartnett (1998) grew 36 grass species common to tallgrass prairie ecosystems with and without the presence (induced by inoculation) of arbuscular mycorrhizae. They report fungal inoculation increased the average dry mass of perennial $C_4$ species by 85%. Fungal inoculation had no significant effects on dry mass production in perennial $C_3$ species or in any annual grasses, regardless of their photosynthetic physiology. Thus, a large number of plant-fungal interactions exist at ambient $CO_2$ concentrations that may be modified by exposure to elevated $CO_2$.

In a similar study, Rillig *et al*. (1998a) grew monocultures of three grasses and two herbs that co-occur in Mediterranean annual grasslands, in pots placed in open-top chambers receiving ambient and twice-ambient concentrations of atmospheric $CO_2$ for four months. They report elevated $CO_2$ significantly increased the percent root colonization by arbuscular mycorrhizal fungal hyphae in all five species, which ultimately could lead to greater biomass production in these annual grassland plants.

In another four-month study using the same experimental enclosures, Rillig *et al*. (1998b) grew the annual grass *Bromus hordeaceus* at ambient and elevated atmospheric $CO_2$ concentrations. In this study, elevated $CO_2$ did not increase the percent root colonized by fungal hyphae, but it did significantly increase the percent root colonized by arbuscules, indicating elevated $CO_2$ can enhance fungal-plant interactions by modifying fungal structures other than hyphae.

In two related long-term studies, Rillig *et al*. (1999a,b) constructed open-top chambers on two adjacent serpentine and sandstone grassland communities in California, USA, fumigating them with air containing 350 and 700 ppm of $CO_2$ for six years. In corroboration of their earlier short-term results, they report elevated $CO_2$ did not increase the percent root colonized by fungal hyphae (Rillig *et al*., 1999a) but it enhanced the percent root colonized by arbuscules in serpentine and sandstone grasslands by three- and ten-fold, respectively (Rillig *et al*.,1999b). Such observations suggest increases in the air's $CO_2$ concentration will positively impact plant-fungal interactions on grasslands by increasing percent root colonization by either mycorrhizal fungal hyphae or arbuscules, both of which aid in carbon and nutrient exchanges between the two interacting symbionts. Earth's grasslands thus should exhibit increased productivity—even above and beyond that normally caused by atmospheric $CO_2$ enrichment—due to these enhanced relationships that can make soil nutrients more available for plant uptake and use.

Johnson *et al*. (2003) grew communities of 14 common prairie plants in 12 greenhouse chambers at

Flagstaff, Arizona, USA. Six of the chambers were maintained at an atmospheric $CO_2$ concentration of 450 ppm, and six were maintained at 688 ppm (equivalent to 368 and 560 ppm at sea level, respectively) during daylight hours. Each of the $CO_2$ treatments also was subdivided into treatments possessing living or dead arbuscular mycorrhizal (AM) fungal inoculum and low or enriched soil nitrogen (N) content. After one growing season under these conditions, Johnson *et al*. write, "plant species richness was highest in mesocosms with elevated $CO_2$, +AM fungi, and low soil N." They conclude, "in some plant species elevated $CO_2$ can increase the net benefits of mycorrhizae by reducing their relative carbon cost." Thus, not only did the extra $CO_2$ directly help the various plant species involved in the study, it also helped them indirectly—by promoting the growth of AM fungi that provided additional benefits to the plants. This study also suggests increases in the air's $CO_2$ content should have a tendency to maintain, and possibly even increase, the species richness of prairie ecosystems, especially those where soil nitrogen content is less than optimal.

Also focusing on species richness, or biodiversity, Edwards *et al*. (2001) conducted a FACE experiment utilizing atmospheric $CO_2$ concentrations of 360 and 475 ppm on a sheep-grazed dry-land pasture located in Manawatu, New Zealand. In each of the two years of their study, elevated $CO_2$ increased seed production and dispersal in seven of the eight most abundant pasture species: the grasses *Anthoxanthum odoratum*, *Lolium perenne*, and *Poa pratensis*; the legumes *Trifolium repens* and *Trifolium subterranean*; and the herbs *Hypochaeris radicata* and *Leontodon saxatilis*. In some of these species, the elevated $CO_2$ increased the number of seeds produced per reproductive structure, and in all of the species it increased the number of reproductive structures per unit ground area.

These $CO_2$-induced increases in seed production contributed to the increase in the numbers of species observed in the $CO_2$-enriched experimental plots. In addition, atmospheric $CO_2$ enrichment helped maintain biodiversity by increasing the number of *H. radicata*, *L. saxatilis*, *T. repens*, and *T. subterranean* seedlings that survived for at least seven months in both study years, and it additionally lengthened the survival time of *A. odoratum* and *L. perenne* in the initial year of experimentation. As the atmospheric $CO_2$ concentration increases further, therefore, it should help to maintain, and maybe even increase, the biodiversity of these dry-land pasture communities by increasing the numbers of both common and uncommon species they contain.

Teyssonneyre *et al*. (2002) grew three $C_3$ grasses (*Lolium perenne*, *Festuca arundinacea,* and *Holcus lanatus*) as monocultures and two-species mixtures for five months in plastic tunnels maintained at atmospheric $CO_2$ concentrations of 350 and 700 ppm, cutting the grasses either frequently or infrequently to stimulate competition for light. In monoculture, the high-$CO_2$ treatment increased total aboveground biomass by 22%, 22%, and 4% in *Festuca*, *Holcus,* and *Lolium*, respectively. In two-species mixtures, elevated $CO_2$ caused a 22% reduction in the amount of *Lolium* in the *Lolium x Festuca* mixture under the infrequent cutting regime, and it caused 30% and 67% reductions in the amount of *Lolium* in the *Lolium x Holcus* mixture under the frequent and infrequent cutting regimes, respectively.

De Deyn *et al*. (2003) begin their study by noting aboveground vertebrate herbivores "can indirectly benefit subdominant plant species through selective feeding on dominants (Crawley, 1997; Olff and Ritchie, 1998)." They then note root symbionts below the soil surface "can enhance plant species diversity by improving the nutrient uptake and growth of subdominants (van der Heijden *et al*., 1998)," further noting root pathogens "can do so by suppressing dominant host plant species (Bever, 1994)." They then expanded the scope of these types of interactions by exploring the impact of invertebrate soil fauna on plant biodiversity.

De Deyn *et al*. established 32 microcosms of plant species mixtures characteristic of recently abandoned grassland (early succession), grassland under restoration for 20 years (mid-succession), and species-rich natural grassland (the ultimate target state). These microcosms were inoculated with soil fauna from one of the three grassland successional stages. The density and composition of the soil fauna added to the microcosms were the same as those of the three grassland successional stages and included microfauna (nematodes), mesofauna (micro-arthropods), and macrofauna (beetle larvae). After four and six months of these treatments, the researchers clipped the microcosm plants at 4 cm above the soil surface and determined the harvested dry weights of all individual plant species. After 12 months they clipped the plants at the soil surface and determined their root dry weights again.

De Deyn *et al*. report "the soil fauna decreased the shoot biomass of the early succession plant species after 6 months, as well as plant species from the mid-succession stage, whereas the shoot biomass of the target plant species was increased." Hence, they note, "addition of the soil fauna also enhanced plant species diversity." Results obtained at the end of the experiment further suggest "the invertebrate root herbivores were selectively feeding on roots of dominant plants," which "provided an indirect advantage for the subdominant plant species, which were only marginally suppressed in the presence of soil fauna." The researchers also report the positive contributions of soil fauna and mycorrhizal fungi seemed to be additive. Such findings suggest the ongoing rise in the air's $CO_2$ content may enhance ecosystem species richness, as a consequence of the tendency for atmospheric $CO_2$ enrichment to increase both mycorrhizal fungi and soil fauna populations.

Working in central Texas (USA) with elongated field chambers designed to expose tallgrass prairie vegetation comprised of a mix of seven different species—four $C_4$ grasses (*Bouteloua curtipendula*, *Schizachyrium scoparium*, *Sorghastrum nutans,* and *Tridens albescens*) and three forbs (*Salvia azurea*, *Solidago canadensis*, and *Desmanthus illinoensis*)—to a continuous atmospheric $CO_2$ gradient spanning the preindustrial to elevated $CO_2$ concentration range of 250 to 500 ppm, Polley *et al.* (2011) measured the concentrations of ten elements found in the aboveground tissues of three of the $C_4$ grasses (*B. curtipendula*, *S. scoparium,* and *S. nutans*) that are common competitive dominants in assemblages of tallgrass prairie vegetation, which they grew on three soil types over three growing seasons. Polley *et al.* report "the $CO_2$ effect on relative abundances of *Bouteloua* and *Sorghastrum* had far greater impact on element concentrations in grass stands than did change in element levels of individual species," and "elements that were most limiting relative to the nutritional requirements of cattle generally occurred at lowest concentrations in *Bouteloua*, the species most strongly disadvantaged at elevated $CO_2$." Also, "$CO_2$ enrichment favored a grass, *Sorghastrum*, with relatively high concentrations of these elements, thereby increasing mean concentrations of several elements in grass assemblages."

The four researchers say their results "highlight the importance of accounting for change in species abundances and composition when predicting $CO_2$ effects on ecosystem functioning and services," as is also indicated by Polley *et al.* (2010), who conclude, "by favoring one grass species over another, $CO_2$ enrichment from pre-industrial to elevated levels increased concentrations of several nutritionally important elements in prairie grasses," further noting this "improvement in the nutritional quality of plants for herbivores" represents an "underappreciated impact that $CO_2$ enrichment may have on ecosystem functioning by changing plant composition."

Isbell *et al.* (2013) write, "anthropogenic drivers of environmental change often have multiple effects, including changes in biodiversity, species composition, and ecosystem functioning," but "it remains unknown whether such shifts in biodiversity and species composition may, themselves, be major contributors to the total, long-term impacts of anthropogenic drivers on ecosystem functioning." To discover how this phenomenon may operate, Isbell *et al.* set out to analyze temporal trends in the effects of nitrogen enrichment on the productivity, plant diversity, and species compositions of naturally assembled grasslands in a long-term nitrogen-addition experiment conducted at the Cedar Creek Ecosystem Science Reserve in central Minnesota (USA), where they measured aboveground peak biomass and the number and abundances of plant species in each plot from 1982 to 2008. They then similarly analyzed data from the BioCON (Biodiversity, $CO_2$ and N) experiment located at the same reserve, "to quantify the extent to which N enrichment and elevated $CO_2$ influence productivity by non-randomly changing grassland plant diversity," which they did in the latter instance from 1998 to 2011.

The six scientists report "although chronic nitrogen enrichment initially increased productivity, it also led to loss of plant species, including initially dominant species, which then caused substantial diminishing returns from nitrogen fertilization." In contrast, they report, "elevated $CO_2$ did not decrease grassland plant diversity" but "consistently promoted productivity over time," both by its direct aerial fertilization effect and by its non-significant yet real tendency to enhance species diversity.

Greer *et al.* (2000) studied the effects of elevated air temperature and $CO_2$ concentration on photosynthesis in five pasture species grown for approximately one month in controlled environment chambers. They found the $CO_2$-induced photosynthetic enhancement rose with increasing air temperature. At twice-ambient levels of atmospheric $CO_2$, average photosynthetic rates were 36 and 70% greater than for control plants grown under ambient $CO_2$ concentrations at air temperatures of 18 and 28°C, respectively.

Kudernatsch *et al.* (2008) conducted a warming-only (no change in $CO_2$) experiment on species-rich *Carex sempervirens* (CS) and species-poor *Carex firma* (CF) calcareous grasslands in the Berchtesgaden National Park of Southeast Germany. They installed several open-top chambers on the plants in each of three successive years just after snowmelt was complete in the spring and removed them just before snowfall commenced in the autumn. This led to snow-free-season increases in mean daily air temperature of 0.7°C in the CS grasslands and 1.4°C in the CF grasslands, along with corresponding mean daily soil temperature increases of 0.2 and 0.8°C. The authors report "growth and/or reproduction of 12 of the 14 studied species were significantly stimulated by warming," "only two species showed no response," and "none of the species experienced decreases in growth or reproduction." They also found "a significant effect of warming on nutrient availability could not be detected," leading them to conclude "the observed response of vegetation is therefore mainly caused by direct and not by indirect temperature effects."

In 1982–1984, Madsen *et al*. (2011) "studied the ecology of non-breeding moulting geese in Jameson Land, low Arctic East Greenland," finding the geese "consumed most of the graminoid production in available moss fens," leading them to conclude "the geese had filled up the available habitat." Nevertheless, they came back in 2008 to see what had happened over the intervening period of significant global—and local—warming.

Madsen *et al*. replicated what they had done in their earlier study in terms of both methodology and analysis. In addition, they determined the aboveground biomass of the graminoid marsh vegetation, to compare it with what it had been determined to be in 1983 and 1984 by Madsen and Mortensen (1987). The researchers report the data they obtained in late July 2008 yielded a standing crop biomass of 98.2 $g/m^2$, which was 2.34 times greater than what had been measured in the same location in late July 1984. After listing three lines of evidence for concluding from their original field studies in 1982–1984 the "habitat capacity of Jameson Land for moulting geese was close to being reached," they now report, between that earlier time and 2008, "the number of moulting geese in Jameson Land tripled."

In further support of their observations, they note, "on Bylot Island, northeast Canada, graminoid aboveground production in wetlands has increased by 84% between 1990 and 2007, most likely as a consequence of climate warming," citing Cadieux *et al*. (2008). Also, they write, "on Svalbard, it is known that early snow melt has a dramatic positive effect on the density of nesting geese and their fecundity," citing Madsen *et al*. (2007) and noting "the climate in East Greenland has been warming during the last 30 years."

Other researchers have investigated the impact of elevated $CO_2$ and water stress on grasslands.

Szente *et al*. (1998) studied two grasses and two broad-leaved species common to loess grasslands in the vicinity of Budapest in open-top chambers maintained at atmospheric $CO_2$ concentrations of 350 and 700 ppm. After 231 days, the grasses and broad-leaved species exhibited $CO_2$-induced increases in seasonal plant water use efficiencies of 72 and 366%, respectively, the scientists report. Clark *et al*. (1999) likewise note mixed grassland species from a New Zealand pasture exposed to an atmospheric $CO_2$ concentration of 700 ppm consistently displayed greater water use efficiencies than species growing in ambient air, due mostly to $CO_2$-induced increases in photosynthesis. In a two-year $CO_2$-enrichment study of a tallgrass prairie ecosystem located in Kansas, USA, Adams *et al*. (2000) found plants in open-top chambers fumigated with twice-ambient levels of atmospheric $CO_2$ exhibited significantly reduced rates of stomatal conductance and transpirational water loss, which also enhanced plant daily average water use efficiency throughout the entire study, but via reduced water loss as opposed to the enhanced photosynthesis observed by Clark *et al*.

In an eight-year $CO_2$-enrichment study of a tallgrass prairie ecosystem located in Kansas, USA, Owensby *et al*. (1999) report prairie communities in open-top chambers fumigated with twice-ambient levels of atmospheric $CO_2$ maintained greater amounts of soil moisture than communities exposed to ambient air in every year of the study. Likewise, in an experiment lasting four years, Lutze *et al*. (1998) grew swards of *Danthonia richardsonii* at various soil nitrogen contents in glasshouses receiving atmospheric $CO_2$ concentrations of 360 and 720 ppm. Averaged across all nitrogen regimes, $CO_2$-enriched swards used about 25% less water than swards grown at 360 ppm $CO_2$, which consequently allowed the $CO_2$-enriched microcosms to maintain greater soil water contents throughout the study.

In a two-year experiment, Arnone and Bohlen (1998) grew intact monoliths of calcareous grasslands in controlled environments fumigated with air containing 350 and 600 ppm $CO_2$. They found $CO_2$-induced reductions in transpirational water loss were likely responsible for the higher soil moisture contents observed in the $CO_2$-enriched monoliths, which were 10 to 20% greater than those observed in monoliths exposed to ambient air. And Zaller *et al*. (1997) established open-top and open-bottom chambers in a species-rich grassland located near Basel, Switzerland, subjecting them to atmospheric

$CO_2$ concentrations of 350 and 600 ppm. They report mean annual soil moisture contents in the $CO_2$-enriched chambers were 10% greater than those observed in control chambers treated with air containing 350 ppm $CO_2$.

Grunzweig and Körner (2001) constructed model grasslands representative of the Negev of Israel and placed them in growth chambers with atmospheric $CO_2$ concentrations of 280, 440, and 600 ppm for five months, to determine the effects of elevated $CO_2$ on these semi-arid plant communities. They found elevated $CO_2$ reduced rates of evapotranspiration and increased soil moisture contents in model grassland communities exposed to atmospheric $CO_2$ concentrations of 440 and 600 ppm. Between two periods of imposed drought, soil moisture was 22 and 27% higher in communities exposed to 440 and 600 ppm $CO_2$, respectively, than in control communities exposed to pre-industrial levels of atmospheric $CO_2$. Such increases in soil moisture content may have contributed to peak ecosystem $CO_2$ uptake rates 21 and 31% greater at 400 and 600 ppm $CO_2$ than at 280 ppm $CO_2$. In addition, atmospheric $CO_2$ enrichment had no effect on nighttime respiratory carbon losses from the ecosystems. Thus, these semi-arid grasslands were acting as carbon sinks under $CO_2$-enriched conditions. Elevated $CO_2$ (440 and 600 ppm) increased total community biomass by 14% over that produced by communities exposed to the subambient $CO_2$ concentration. Also, when the total biomass produced was related to the total amount of water loss via evapotranspiration, communities grown at atmospheric $CO_2$ concentrations of 440 and 600 ppm exhibited $CO_2$-induced increases in water use efficiency 17 and 28% higher than those displayed by control communities exposed to air of 280 ppm $CO_2$.

As atmospheric $CO_2$ concentrations increase, semi-arid grasslands common to the Negev of Israel likely will exhibit increases in photosynthesis and biomass production, as the study shows. Moreover, such increases in biomass likely will occur while using less water. Model ecosystems exposed to elevated atmospheric $CO_2$ concentrations lost less water through evapotranspiration and consequently had greater soil moisture contents than ecosystems that were not $CO_2$-enriched. Thus it would appear the water-use efficiencies of these grasslands likely will increase in future years as the air's $CO_2$ content increases further. Most importantly, the gas exchange measurements—including the null effect of elevated $CO_2$ on dark respiration—and the biomass data obtained for the ecosystems demonstrate these grasslands likely will become increasingly effective carbon sinks, removing ever-greater amounts of carbon from the air.

Derner *et al.* (2001) grew two $C_4$ grasses (*Schizachyrium scoparium* Nash and *Andropogon gerardii* Vitman.) common to tallgrass prairies in pots placed in a 38-meter-long controlled environment chamber located in a ventilated glasshouse. This chamber was composed of five 7.6m lengths of a 0.76m-deep and 0.45m-wide soil container topped with a transparent and tunnel-shaped polyethylene cover attached to its upper edges. Various other plants placed in this tunnel served as photosynthetic "sinks" for $CO_2$ as a commercial blower moved air through the chamber sections. Thus a $CO_2$ gradient was created through the "long and winding tunnel," from near 350 ppm at its entrance to approximately 200 ppm at its end. In addition, these two $C_4$ grasses were subjected to relative soil water contents 90 or 50% of their total soil water holding capacities. Thus the authors were able to study how the historical rise in the air's $CO_2$ content has influenced growth in these grasses under different soil moisture conditions.

Data from the two $C_4$ grasses were pooled, as there were no significant differences between species. With respect to aboveground growth, shoot biomass was 57% greater at the ambient (350 ppm), rather than the subambient (200 ppm), atmospheric $CO_2$ concentration, and the increase in relative water content enhanced shoot biomass by 82%. Root growth (root length, mass, surface area, and volume) was 15–27% greater at the ambient, as opposed to the subambient, atmospheric $CO_2$ concentration, and 40–51% greater at high, versus low, soil water content.

Since the 150 ppm increase in atmospheric $CO_2$ concentration employed in this study is actually less than the rise in this parameter that has occurred since the end of the last great ice age, Derner *et al.* state "$C_4$ grasses may have already experienced an augmentation in root growth which is comparable to that experienced with a doubling of current $CO_2$ concentrations." There is every reason to conclude such grasses will continue to respond positively to future increases in the air's $CO_2$ content. In addition, as the atmospheric $CO_2$ concentration rises, it likely will decrease water use in these prairie grasses, due to $CO_2$-induced reductions in stomatal conductance, causing the indirect effects of greater soil moisture to enhance their growth further.

Working with open-top chambers maintained at ambient and twice-ambient atmospheric $CO_2$ concentrations, Ferretti *et al.* (2003) investigated "the dynamics of soil water isotopes and water cycling in a mixed $C_3/C_4$ grassland in the western Great Plains region of the USA," which is predominantly carpeted by the $C_4$ grass *Bouteloua gracilis* (H.B.K.) Lag. (blue grama) and the $C_3$ grasses *Stipa comata* Trin and Rupr. (needle-and-thread grass) and *Pascopyrum smithii* (Rydb.) A. Love (western wheatgrass). In addition to documenting a mean plant biomass increase of 50% in the elevated $CO_2$ treatment over the two years of their study, the authors observed significantly wetter soils in the elevated $CO_2$ treatment, which they say were "most likely a result of improved soil-water conservation as a result of reduced stomatal conductance under elevated $CO_2$."

Noting "elevated $CO_2$ had the effect of increasing soil-water conservation as has been previously found (e.g., Morgan *et al*., 2001; Volk *et al*., 2000)," and "reduced evaporation was mainly responsible for greater soil water content under elevated $CO_2$," Ferretti *et al*. remark "the most significant effect of elevated $CO_2$ on the hydrologic budget in water limited ecosystems is likely to be an increase in soil water storage (Jackson *et al*., 1998)," as was found in their study. It is likely this phenomenon contributed significantly to the growth enhancement observed in the $CO_2$-enriched treatment, which was more than what might have been expected from the aerial fertilization effect of elevated $CO_2$ operating alone.

Also focusing on water stress, Niklaus and Körner (2004) used screen-aided $CO_2$ control (SACC) technology to enrich the air above a water-limited and phosphorus-poor temperate calcareous grassland in Switzerland with an extra 235 ppm of $CO_2$ for a total of six years, over which period they measured several individual and community plant parameters. They report peak percentage increases in biomass production in years 1 through 6 of the experiment were, respectively, 5%, 20%, 22%, 27%, 31%, and 18%, for an average of 23.6% over the last five years of the study. Year-to-year variability in this factor was best predicted by precipitation and resulting soil moisture differences, with the "obvious mechanism," the authors write, being "soil moisture savings due to reduced stomatal conductance under elevated $CO_2$," which would tend to "alleviate effects of water limitation more in dry years." In addition, although Niklaus and Körner note "low available phosphorous ultimately limited community productivity and responses to $CO_2$," this deficiency—coupled with a deficiency of water—was not sufficient to counter the growth-promoting effect of atmospheric $CO_2$ enrichment, which in this case was equivalent to a 30% increase in growth in response to a standard 300 ppm increase in the air's $CO_2$ concentration.

Because many grasslands are subject to grazing pressure from herbivores, it is also important to see how this stress phenomenon affects photosynthetic responses to atmospheric $CO_2$ enrichment. Rogers *et al*. (1998) grew swards of perennial ryegrass in a FACE experiment utilizing atmospheric $CO_2$ concentrations of 360 and 600 ppm. In addition, they supplied swards with low and high levels of soil nitrogen and subjected them to cutting treatments to simulate herbivory. Under these conditions, elevated $CO_2$ stimulated photosynthetic rates by approximately 35%, regardless of soil nitrogen supply or cutting treatment. In a similar FACE experiment, two forbs and one grass species common to chalk grassland swards of Europe were grown for 14 months at 355 and 600 ppm $CO_2$ to study the influence of simulated grazing on their photosynthetic responses to atmospheric $CO_2$ enrichment (Bryant *et al*., 1998). Prior to simulated grazing, the $CO_2$-induced photosynthetic response of the grass and one forb species were both around 28%, and the other forb was non-responsive to elevated $CO_2$. After grazing, however, both forbs exhibited a much larger 40% increase in photosynthesis, and the grass slightly increased its positive response to 30%. The data from these two studies suggest grazing pressure from herbivores will not reduce $CO_2$-induced increases in photosynthesis, and may in fact cause them to rise.

The studies reviewed above suggest increases in the air's $CO_2$ concentration lead to rising productivity of Earth's grassland species, even under unfavorable growing conditions characterized by less-than-adequate soil moisture, inadequate soil nutrition, elevated air temperature, and physical stress imposed by herbivory.

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### *1.2.2.2 Carbon Sequestration*

- Research indicates soils beneath grasslands will significantly increase their carbon-storing capability as atmospheric $CO_2$ concentrations rise.

Carbon sequestration by grasslands is a less-investigated topic than carbon sequestration by forests. Nevertheless, several researchers have examined how grassland ecosystems might respond in this regard as the air's $CO_2$ concentration rises.

Fitter *et al.* (1997) transferred monoliths of two contrasting grasslands, a species-rich turf growing over limestone and a species-poor turf growing over a peaty soil, from Moor House National Nature Reserve in the United Kingdom to four "solardomes" at Lancaster University, where they maintained them for two years under natural daylight and air temperatures close to ambient. One set of two solardomes was exposed to ambient air and another set to air enriched with an extra 250 ppm $CO_2$. At various times throughout the experiment, the researchers made a number of measurements of above- and below-ground growth.

Shoot biomass was unaltered by the elevated level of atmospheric $CO_2$, but root biomass was enhanced by 40 to 50%. Furthermore, especially in the peat soil, root turnover was highly accelerated in the $CO_2$-enriched treatment—so much so, in fact, the authors conclude the increase in root biomass observed at the end of the experiment "was almost certainly a large underestimate of the amount of carbon transferred to the soil." The authors further note the increased productivity the two grassland ecosystems exhibited under elevated atmospheric $CO_2$ concentrations, along with the consequent increases in soil organic matter, are "likely to persist."

Cotrufo and Gorissen (1997) grew three grass species (*Lolium perenne* L. cv. Barlet, *Agrostis capillaris* L. cv. Bardot, and *Festuca ovina* L. cv. Barok) in 0.65-liter pots under two different levels of soil nitrogen in growth chambers maintained at 350 and 700 ppm $CO_2$ in continuously $^{14}C$-labeled atmospheres. They harvested half the plants after 32 days and the other half after 55 days. They analyzed the shoots, roots, and soils for total carbon (C) and $^{14}C$ content.

They found elevated $CO_2$ increased the whole-plant dry weights of all three species by an average of 20% and, in general, increased root growth more than shoot growth. It also increased soil microbial biomass by slightly more than 15%. Of the $^{14}C$ that was fixed, 90% remained in the plant and 10% was transferred to the soil. There, 7% was found in the bulk soil and 3% was found in the rhizosphere soil close to the plant roots, split about equally between soil microbial biomass and soil residue.

The authors state what they observed "is consistent with the general finding that the soil microbial biomass is C-limited, and supports the hypothesis that a greater C input below-ground, as a result of increased size of the root system, at high $CO_2$ elicits an increase in soil microbial biomass." They also state "elevated $CO_2$ will induce an increase in relative C allocation to below-ground sinks independent of nitrogen level." Finally, they conclude their findings for all three grasses confirm "elevated $CO_2$ could result in greater soil C stores due to increased C-input into soils," as well as "a higher residence time for C in soils, thus counteracting increased decomposition under higher temperatures." Thus, they write, "we may well expect that this increased C input below-ground will be sustained in the longer term." This phenomenon clearly would be expected to reduce the level to which atmospheric $CO_2$ concentrations would rise in its absence.

Casella and Soussana (1997) grew perennial ryegrass (*Lolium perenne* L. cv. Preference) swards in large containers at two different levels of soil nitrogen supply for two years at ambient and elevated (700 ppm) $CO_2$ concentrations, as well as at ambient and elevated (+3°C) temperature. The soils were maintained at field capacity via irrigation, but the water supply was reduced in summer to simulate characteristic summer water deficits. Throughout the experiment, they made a number of measurements on the plants and soils, including canopy gas exchanges, plant water soluble carbohydrates, and biomass production. The authors report "a relatively large part of the additional photosynthetic carbon is stored below-ground during the two first growing seasons after exposure to elevated $CO_2$, thereby increasing significantly the below-ground carbon pool." At low and high soil nitrogen supply, for example, the elevated $CO_2$ increased soil carbon storage by 32 and 96%, respectively, "with no significant increased temperature effect." The elevated temperature actually helped to increase soil carbon storage, because the enhanced soil desiccation at +3°C helped restrict below-ground respiration. Casella and Soussana conclude "this stimulation of the below-ground carbon sequestration in temperate grassland soils could exert a negative feed-back on the current rise of the atmospheric $CO_2$ concentration."

Lutze and Gifford (1998) grew microcosms of the $C_3$ grass *Danthonia richardsonii* for four years in glasshouses with atmospheric $CO_2$ concentrations of 360 or 720 ppm and three levels of soil nitrogen to determine the effects of elevated $CO_2$ and soil nutrition on microcosm carbon gain and water use. They conducted destructive harvests of plant material at six-month intervals throughout the project. Results indicated carbon accumulation in the microcosms was strongly correlated with soil nitrogen: Nitrogen was limiting productivity, even in the highest fertilization treatment. Nevertheless, when averaged across all harvests and nitrogen regimes, elevated $CO_2$ significantly increased total microcosm carbon gains by 15–34%, in spite of a 9% reduction in leaf area index. In addition, elevated $CO_2$ increased senesced leaf material per unit ground area at all harvests and nitrogen treatments by an average of 31%. Consequently, these phenomena led to final soil carbon contents in $CO_2$-enriched microcosms 4, 9, and 17% greater than in ambient microcosms at low, medium, and high soil nitrogen treatments, respectively. Elevated $CO_2$ also reduced microcosm water use by 25% across all nitrogen treatments, thereby allowing greater soil volumetric water contents to exist in $CO_2$-enriched microcosms.

Nitschelm *et al.* (1997) report white clover exposed to an atmospheric $CO_2$ concentration of 600 ppm for one growing season channeled 50% more newly fixed carbon compounds into the soil than similar plants exposed to ambient air. In addition, the clover's roots decomposed at a rate 24% slower than roots of control plants, as also has been reported for white clover by David *et al.* (2001). These observations suggest rising $CO_2$ content will greatly enhance soil carbon sequestration under white clover ecosystems.

Van Ginkel *et al.* (1996) exposed mini-ecosystems comprised entirely of perennial ryegrass species to an atmospheric $CO_2$ concentration of 700 ppm for two months, finding a 92% increase in root growth and 19% and 14% decreases in root decomposition rates one and two years, respectively, after incubating ground roots in soils. Van Ginkel and Gorissen (1998) followed up this work, showing a 13% reduction in the decomposition rates of $CO_2$-enriched perennial ryegrass roots in both disturbed and undisturbed root profiles. This and other work led the authors to calculate $CO_2$-induced reductions in the decomposition of perennial ryegrass litter, which enhances soil carbon sequestration, could be large enough to remove over half of the anthropogenic $CO_2$ emissions that may be released in the next century (Van Ginkel *et al*., 1999).

Van Ginkel *et al.* (2000) found elevated $CO_2$

decreased root decomposition rates of perennial ryegrass grown at 700 ppm $CO_2$ by 14% after 230 days of incubation in elevated $CO_2$. In addition, the scientists determined raising the incubation temperature by 2 °C had little effect on the $CO_2$-induced reductions in decomposition rate, for they were still 12% lower than those measured at 350 ppm $CO_2$. In a shorter-term experiment the researchers found even a 6 °C increase in air temperature could not counterbalance the $CO_2$-induced reductions in decomposition rate.

These results suggest future increases in the air's $CO_2$ content likely will cause slight reductions in rates of plant litter decomposition, thus allowing more carbon to remain sequestered from the atmosphere for longer periods of time, and this will be the case even if Earth's air temperature rises.

In some cases, however, atmospheric $CO_2$ enrichment has been reported to have little or no significant effect on litter quality and subsequent rates of litter decomposition. Hirschel *et al*. (1997) took fallen leaves from species common to alpine and calcareous grasslands and incubated them in mesh nylon bags placed on the soil surfaces of their respective mesocosms, subjecting them to ambient and twice-ambient concentrations of atmospheric $CO_2$. After one year of incubation, the decomposition rates of the litter produced under the ambient and elevated $CO_2$ conditions did not differ significantly from each other, except in the case of one alpine sedge, which exhibited reduced rates of decomposition under atmospheric $CO_2$ enrichment. Dukes and Field (2000) reported similar results after incubating litter derived from various combinations of grassland species common to California, USA, for an eight-month period at atmospheric $CO_2$ concentrations of 350 and 700 ppm and finding minimal effects of elevated $CO_2$ on decomposition rates.

In a five-year study of a grassland growing on a moderately fertile soil at Stanford University's Jasper Ridge Biological Preserve in central California—which utilized 20 open-top chambers (ten each at 360 and 720 ppm $CO_2$)—Hu *et al*. (2001) found a doubling of the air's $CO_2$ content increased both soil microbial biomass and plant nitrogen uptake. With less nitrogen left in the soil to be used by a larger number of microbes, microbial respiration per unit of soil microbe biomass significantly declined in the elevated $CO_2$ environments; with this decrease in microbial decomposition, there was an increase in carbon accumulation in the soil.

Hu *et al*. conclude this $CO_2$-induced chain of events could readily cause terrestrial grassland ecosystems to become significantly stronger net carbon (C) sinks than they are currently, especially if their plants become more efficient at acquiring nitrogen (N) from soils of low C:N organic matter ratio. They also suggest such $CO_2$-enhanced grassland N acquisition might be prompted by increased root colonization by symbiotic mycorrhizal fungi, which has been found to be a rather common consequence of atmospheric $CO_2$ enrichment (Rillig *et al*., 1998, 2000). Hence, the scientists conclude, as have many others, the carbon sequestered by these means "could partially offset the effects of anthropogenic $CO_2$ emissions on atmospheric $CO_2$ [concentration]."

How much extra carbon can be sequestered in the planet's grassland soils as a result of a doubling of the air's $CO_2$ content? A good first approximation at an answer is provided by Williams *et al*. (2000), who studied this phenomenon for eight years in a Kansas (USA) tallgrass prairie, utilizing open-top chambers enclosing mixtures of $C_3$ and $C_4$ grasses continually fumigated with air of either ambient or twice-ambient atmospheric $CO_2$ concentration. Williams *et al*. found the average soil water content in the first 15 cm of the soil profile was approximately 15% greater beneath the chambers receiving the extra supply of $CO_2$, due, presumably, to $CO_2$-induced reductions in plant stomatal conductance that blunted transpirational water loss. The saved moisture, in turn, enabled plants to be more productive during the growing season, and with a significant portion of that extra productivity directed belowground into roots, there was a nearly equivalent increase in soil microbial activity across the final five years of the study. The authors report there was an 8% increase in total soil carbon content over the course of the study.

Extrapolating this value to all of Earth's temperate grasslands, which make up about 10% of the land area of the globe, Williams *et al*. calculate the $CO_2$-induced increase in soil carbon sequestration could amount to an additional 1.3 Pg of carbon being sequestered in just the top 15 cm of the world's grassland soils over the next century.

Riedo *et al*. (2000) used a mechanistic pasture simulation model (PaSim) to predict changes in net primary productivity and carbon stocks in differently managed grasslands in response to increased atmospheric $CO_2$ concentration and climate change. Results indicated elevated $CO_2$ alone, or in combination with increased air temperature, enhanced net primary productivity at all simulated sites by 30 to 40%. In addition, the effects of elevated $CO_2$ and elevated air temperature were generally positive with respect to grassland carbon stocks. Such simulations suggest the increasing $CO_2$ content of the air likely will stimulate primary productivity in managed grasslands, thus leading to greater biomass production and enhanced carbon storage in their associated soils. Grasslands cover nearly 20% of the land surface of the globe and store at least 10% of the soil organic matter of the planet.

Cardon *et al*. (2001) erected open-top chambers on two Mediterranean grassland communities in California, USA. They fumigated them for two years with air containing either ambient or twice-ambient atmospheric $CO_2$ concentrations. In addition, plants were grown with either low or high soil nutrient availability. The main thrust of this research was to use isotopic labeling to study the effects of elevated atmospheric $CO_2$ and soil nutrient availability on the decomposition of old and new organic carbon in the two grassland soils. Results indicated when soil nutrient availability was high, elevated $CO_2$ reduced the decomposition of older soil organic carbon by approximately 30% throughout the study. Thus, the turnover time and stabilization of this soil carbon pool was increased by elevated $CO_2$ exposure. However, the movement of newly fixed carbon into the older stabilized pools was decreased with atmospheric $CO_2$ enrichment, due to its preferential utilization by soil microbes. Thus, soil microbes switched from using older to newer soil organic carbon under $CO_2$-enriched conditions.

Thus, as the atmosphere's $CO_2$ content rises, carbon sequestration in the soils of Mediterranean grasslands likely will increase for two reasons. First, it should rise as a consequence of the greater retention times conferred upon the carbon in older soil organic carbon pools, which represent the largest reservoir of terrestrial carbon on Earth. Second, even though soil microbes exhibit a preference for newer carbon under $CO_2$-enriched conditions, it should rise because of the great increase in the amount of carbon going into newer soil carbon pools due to $CO_2$-enhanced root exudation, root turnover, and other types of litter production.

Higgins *et al*. (2002) constructed open-top chambers in portions of an annual grassland located in a Mediterranean-type climate in California, USA. They fumigated them with air of either 360 or 720 ppm $CO_2$ to study the effects of elevated $CO_2$ on root production and turnover. By the end of the growing season, the plants in the elevated-$CO_2$ chambers had increased their production of new root length by nearly 60%, but their root turnover rates were no different from those of the plants in the ambient-treatment chambers. There was also an 18% increase in soil moisture content in the $CO_2$-enriched chambers. Thus, as the $CO_2$ content of the air increases, belowground biomass production should increase in this particular type of annual grassland, either directly from $CO_2$-induced increases in photosynthesis or indirectly from $CO_2$-induced reductions in water use, which tend to increase soil moisture content.

Hartwig *et al*. (2002) grew swards of perennial ryegrass (*Lolium perenne* L.) and the $N_2$-fixing white clover (*Trifolium repens* L.) in boxes placed in FACE plots receiving atmospheric $CO_2$ concentrations of 350 and 600 ppm in combination with low and high soil nitrogen fertilization for four years, to study the interactive effects of these variables on biomass production and nitrogen retention in these two contrasting ecosystems. They found elevated $CO_2$ increased average aboveground biomass in the white clover ecosystem by 80% but had no effect on aboveground biomass production in the perennial ryegrass ecosystem. Below the surface of the soil, however, just the opposite occurred: the extra $CO_2$ increased root biomass in the perennial ryegrass ecosystem by 94% while having no effect on the root biomass of white clover.

The total amount of nitrogen taken into the white clover ecosystem was significantly greater than that taken into the perennial ryegrass ecosystem. Elevated $CO_2$ exposure could explain much of this increase, as it roughly doubled the amount of nitrogen input through symbiotic $N_2$-fixation in the white clover. Nonetheless, all combinations of variables led to ecosystem nitrogen gains after four years of growth, with greater gains under higher, rather than lower, nitrogen fertilization. In addition, elevated $CO_2$ increased ecosystem nitrogen gains in all cases except in perennial ryegrass under low nitrogen fertilization.

These findings suggest as the air's $CO_2$ concentration increases, swards of perennial ryegrass and white clover likely will display increased rates of photosynthesis and greater biomass production. $CO_2$-induced increases in biomass most likely will be manifested aboveground in white clover and belowground in perennial ryegrass. In addition, both ecosystems should exhibit increased gains in nitrogen (except, perhaps, in the case of perennial ryegrass growing on low-nitrogen soils), with greater nitrogen gains occurring in white clover, as a result of $CO_2$-induced increases in symbiotic $N_2$-fixation.

Pendall *et al*. (2004) explain rhizodeposition is "the addition of C [carbon] from roots to soil C pools," and they note "because up to 80% of the biomass and at least 50% of net primary production can occur below-ground in grasslands, changes in rhizodeposition will have a large impact on C cycling in these ecosystems (Milchunas and Lauenroth, 2001)," which may significantly impact the amount of carbon sequestered in grassland soils. Against this backdrop, Pendall *et al.* used open-top chambers to study various responses of a native $C_3$-$C_4$ grassland ecosystem in the shortgrass steppe region of northeastern Colorado, USA, to a doubling of the air's $CO_2$ concentration (from 360 to 720 ppm) in an experiment that lasted five years. Total aboveground biomass was increased by an average of 33% over the course of the study in the $CO_2$-enriched chambers, and belowground biomass increased by an average of 23%. In addition, over the last four years of the experiment, rhizodeposition increased by 137% in the chambers exposed to elevated $CO_2$. However, Pendall *et al.* report "decomposition increased nearly as much as rhizodeposition," leading to little net increase in soil C storage in the $CO_2$-enriched chambers relative to that found in the ambient-air chambers.

Although there was little increase in soil carbon sequestration in the $CO_2$-enriched chambers of this particular study, more biomass was produced in them each year, both above- and below-ground, than in the ambient-air chambers; and much more biomass made its way into the soil of the $CO_2$-enriched chambers. Hence it is likely that over the course of several decades the small yearly differences in soil C storage would eventually end up producing a substantially larger stash of carbon in the soil of the $CO_2$-enriched chambers.

Over the course of an eight-year open-top-chamber $CO_2$-enrichment (to twice ambient concentrations) study of a pristine (annually burned) tallgrass prairie north of Manhattan, Kansas, USA, composed of a mixture of $C_3$ and $C_4$ species, Williams *et al.* (2004) measured changes in the active, slow, and passive pools of carbon (C) and nitrogen (N), to determine how they were affected by the doubled atmospheric $CO_2$ concentration of their reasonably long-term experiment. They report, "on average, elevated $CO_2$ induced a 60% increase in root growth," citing Owensby *et al.* (1999). They also found potentially mineralizable C was enhanced by 19% and 24%, respectively, in the 0–5 cm and 5–15 cm soil horizons, which they suggest implies "increases in plant inputs have outpaced increases in decomposition rates" in those layers. Likewise, they report potentially mineralizable N was enhanced by 14% in the 0–5 cm layer, and $CO_2$ enrichment resulted in greater recalcitrant N in the 5–15 cm soil layer. Regarding these latter findings, they hypothesize "greater N translocated to aboveground biomass from deeper soil depths could ultimately be stored in roots and rhizomes near the soil surface, and would eventually turnover and become a part of the surface soil N pool."

Williams *et al.* conclude "the 60% increase in root growth during the 8-year study was the likely catalyst for the greater potentially mineralizable soil C pools in the enriched $CO_2$ treatment," and this finding "confirms that C can accrue in soils under elevated $CO_2$." Specifically, they determined the total amount of extra new carbon sequestered in the soil due to their doubling of the air's $CO_2$ concentration was 4 Mg C $ha^{-1}$ over the eight-year period, for an annual rate of extra ($CO_2$-induced) carbon sequestration of 0.5 Mg $ha^{-1}$ $year^{-1}$.

Working with a temperate grassland on the North Island of New Zealand under permanent grazing by sheep, cattle, and goats since at least 1940, Allard *et al.* (2005) measured above- and below-ground plant growth and litter production, along with root turnover and soil particulate organic matter quantity and quality, after almost four years of exposure to an extra ~105 ppm of atmospheric $CO_2$ (a target concentration of 475 ppm) in a moderate-term FACE experiment. The researchers report the elevated $CO_2$ did not alter aboveground herbage biomass and leaf litter production, but root growth rate and turnover "were strongly stimulated by $CO_2$ particularly at low soil moisture contents during summer." As a result of the root responses, they also found "significantly more plant material was returned to the soil under elevated $CO_2$ leading to an accumulation of coarse (>1 mm) particulate organic matter (POM)," with a similar but not-yet-significant trend in fine POM. In addition, they state there was a $CO_2$-induced lowering of POM carbon/nitrogen ratio, which they "attributed to the higher proportion of legumes in the pasture under elevated $CO_2$."

The six New Zealand and French researchers say their results "show that in grazed pastures with high plant species diversity we might expect extra carbon sequestration in soil organic matter mainly through an increase in carbon input rather than a decreasing quality of accumulating organic matter." That they could detect the changes they did over so short a time interval, and with so small an increase in the atmosphere's $CO_2$ concentration, is impressive, but it is just one among many similar findings of Jastrow *et al.* (2005) and the many studies the latter scientists reviewed in their meta-analysis of the subject. In addition, Allard *et al.* found indications of increased soil nitrogen in their $CO_2$-enriched treatment, just as Jastrow *et al.* did, reinforcing the latter group's conclusions about this subject as well.

Edwards *et al.* (2005) grew well-watered mixtures of two plants—the legume white clover (*Trifolium repens* L.) and $C_4$ buffalo grass (*Stenotaphrum secundatum* (Walt.) Kuntze)—which were initially equal in plantlet size, number, and spatial distribution, for 15 months in sand placed in large plastic containers in greenhouses maintained at different atmospheric $CO_2$ concentrations (360 and 700 ppm) under three sand nutrient conditions (zero-N/low-P, zero-N/high-P, plus-N/high-P). They made ten harvests of all plant biomass over a height of 5 cm above the sand surface, after which the total carbon contents of the whole plants and their respective soils were determined. The slightly less than a doubling of the air's $CO_2$ concentration employed in this study led to increases of 22%, 41%, and 374% in the amounts of new carbon found in the soils in the zero-N/low-P, zero-N/high-P, and plus-N/high-P soil treatments, respectively. In addition, corresponding increases of 22%, 53%, and 53% in total new mesocosm carbon contents (comprised of soil plus plant carbon) were reported in each respective treatment. Thus, soil P deficiency in this study severely limited the ability of elevated $CO_2$ to stimulate total mesocosm carbon capture, and lack of N was most harmful to soil carbon capture. Consequently, in grasslands managed for animal production, Edwards *et al.* say "it may be possible to increase their potential to sequester C as atmospheric $CO_2$ increases by altering land management," especially in ways that relieve these nutrient deficiencies, as also has been suggested by Jones and Donnelly (2004).

Pendall and King (2007) conducted a series of long-term (170–330 days) laboratory incubation experiments to examine changes in soil organic matter pool sizes and turnover rates in soil collected from an open-top chamber (OTC) atmospheric $CO_2$ enrichment study in the shortgrass steppe of northeastern Colorado, USA, where the air in the ambient $CO_2$ chambers (ACs) and elevated $CO_2$ chambers (ECs) had atmospheric $CO_2$ concentrations of 360 and 720 ppm, respectively. This degree of $CO_2$ enrichment enhanced both above- and below-ground plant growth by 15–35%. The authors found the "active pool carbon increased in EC relative to AC treatments systematically over the first 3 years of exposure to elevated $CO_2$ in topsoils and to a lesser degree in subsoils," noting "these results are consistent with independent results from the same OTC study showing that rhizodeposition rates doubled (Pendall *et al.*, 2004) and root production increased under elevated $CO_2$ (Milchunas *et al.*, 2005)." In addition, they report "new carbon turnover was not enhanced by elevated $CO_2$," indicating "new carbon inputs under elevated $CO_2$ are not simply lost to mineralization" and "pool sizes may continue to increase under elevated $CO_2$." Such findings, in the words of the two researchers, "suggest that soil carbon storage may increase in semi-arid grasslands under elevated $CO_2$."

Adair *et al.* (2009) employed mass balance calculations to quantify the effects of biodiversity, atmospheric $CO_2$ concentration, and soil nitrogen (N) content on the total amount of C allocated belowground by plants (total belowground C allocation or TBCA), as well as ecosystem C storage, in an eight-year experiment that was part of the BioCON study of a periodically burned Minnesota grassland. The authors report annual TBCA increased in response to all three treatment variables—"elevated $CO_2$, enriched N, and increasing diversity"—and it was also "positively related to standing root biomass." Upon removing the influence of root biomass, however, they state the effects of N and diversity became neutral or even negative (depending on the year), but "the effect of elevated $CO_2$ remained positive." In years with fire, "greater litter production in high diversity, elevated $CO_2$, and enhanced N treatments increased annual ecosystem C loss." Thus, under normal non-fire conditions, elevated $CO_2$, N, and biodiversity generally tend to increase ecosystem carbon gain, but if grasslands are frequently burned, they could remain neutral in this regard.

Belay-Tedla *et al.* (2009) note "the stability of carbon (C) and nitrogen (N) in soil organic matter (SOM) to perturbations such as global warming is critically important," because "on a global scale, the soil contains 1500 Pg (1 Pg = $10^{15}$ g) of organic carbon and 300 Pg of total nitrogen" in its uppermost meter, so "relatively small changes in the amounts of soil C and N may therefore bring about substantial effects on atmospheric concentrations," which in the case of the carbon contained in $CO_2$ may feed back either positively or negatively to enhance or reduce the original global warming.

In a study designed to explore these interactions in a specific biome, Belay-Tedla *et al.* "used sulfuric acid hydrolysis to quantify changes in labile and recalcitrant C and N fractions of soil in a tallgrass prairie ecosystem that had been continuously warmed with or without clipping for about 2.5 years," conducting their work in "an old-field tallgrass prairie abandoned from agriculture 30 years ago and without grazing during the past 20 years" in the Great Plains Apiaries of McClain County, Oklahoma, USA. Infrared heaters suspended 1.5 m above the ground warmed half the plots 24 hours a day, 365 days a year, for the 2.5-year period, increasing the daily mean air temperature at 25 cm above the ground by 1.1°C and soil temperature at 2.5 cm depth by 2.0°C.

The five researchers found "significant increases in both labile C and N (including microbial biomass) pools in response to experimental warming," which "largely resulted from increased above- and below-ground biomass." They also observed "a possible shift to a fungi-dominated microbial community," noting "such a shift could favor soil C storage" as well. In addition, they report evidence suggesting "warming increased the percentage of total N for microbial biomass N," and this enhanced N use efficiency "may be conducive for a continued supply of organic inputs." Belay-Tedla *et al.* conclude their combined findings favor "long-term N retention and C accumulation in soils, leading to negative feedbacks of terrestrial ecosystems to climate warming."

Ayres *et al.* (2008) investigated various responses of 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. The authors state "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)." As to the plants, the authors state "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, the researchers write, "$CO_2$ 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." Commenting on these findings, the seven researchers state "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."

The research findings discussed above suggest grasslands will become increasingly productive and provide an ever-increasing brake on the upward trend in the air's $CO_2$ concentration.

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## 1.2.3 Peatlands

- In contrast to IPCC projections, the thawing of permafrost caused by increases in air temperature and $CO_2$ will not likely transform peatlands from carbon-sink to carbon-source ecosystems. Instead, as permafrost thaws, plants and trees can begin to grow again on these lands and in so doing, they sequester carbon.

Peatlands contain a vast amount of sequestered carbon—about as much, in fact, as is contained in the entire atmosphere. As a result, they are vital elements of the planet's carbon cycle and can significantly impact its climate. This section reviews the findings of several papers that bear upon this topic.

IPCC predicts global warming will release long-sequestered carbon in Earth's peatlands to the atmosphere, possibly freeing enough of it at a sufficiently rapid rate to rival $CO_2$ emissions from anthropogenic sources. The end result of this scenario would be a strong positive feedback to the ongoing rise in the air's $CO_2$ content, which IPCC contends will lead to further warming of the planet. However, multiple studies have shown this scenario to be highly unlikely or altogether false.

One of the first cracks in this positive-feedback hypothesis was revealed by Oechel *et al.* (2000). They showed long-term measurements of net ecosystem $CO_2$ exchange rates in wet-sedge and moist-tussock tundra communities of the Alaskan Arctic indicated these ecosystems were changing gradually from carbon sources to carbon sinks. The transition occurred between 1992 and 1996, at the apex of a regional warming trend that culminated with the highest summer temperature and surface water deficit of the previous four decades.

The scientists who documented this dramatic and unexpected biological transformation describe it as "a previously undemonstrated capacity for ecosystems to metabolically adjust to long-term changes in climate." This ecological acclimation process is only one of several recognized phenomena that have caused scientists to radically revise their thinking about global change in Arctic regions.

Camill *et al.* (2001) investigated changes in peat accumulation across a regional gradient of mean annual temperature in Manitoba, Canada; net aboveground primary production and decomposition for major functional plant groups of the region; and soil cores from several frozen and thawed bog sites used to determine long-term changes in organic matter accumulation following the thawing of boreal peatlands. In direct contradiction of earlier thinking on the subject, but in confirmation of the more recent findings of Camill (1999a,b), the researchers report aboveground biomass and decomposition "were more strongly controlled by local succession than regional climate." In other words, over a period of several years, natural changes in plant community composition generally "have stronger effects on carbon sequestration than do simple increases in temperature and aridity." Their core-derived assessments of peat accumulation over the past two centuries demonstrated rates of biological carbon sequestration can almost double following the thawing of permafrost, in harmony with the findings of Robinson and Moore (2000) and Turetsky *et al.* (2000), who found rates of organic matter accumulation in other recently thawed peatlands to have risen by 60–72 percent.

Griffis and Rouse (2001) drew on the findings of experiments conducted over the past quarter-century at a subarctic sedge fen near Churchill, Manitoba, Canada, to develop an empirical model of net ecosystem $CO_2$ exchange there. The fundamental finding of this endeavor was "carbon acquisition is greatest during wet and warm conditions," as is generally predicted for the world as a whole by today's most advanced climate models. However, regional climate change predictions are not very dependable, so the two scientists investigated the consequences of a 4°C increase in temperature accompanied by both a 30 percent increase and decrease in precipitation. "In all cases," they observe, "the equilibrium response showed substantial increases in carbon acquisition." One of the reasons for this finding, Griffis and Rouse explain, is "arctic ecosystems photosynthesize below their temperature optimum over the majority of the growing season," so increasing temperatures enhance plant growth rates considerably more than they increase plant decay rates.

In summing up their findings, Griffis and Rouse state "warm surface temperatures combined with wet soil conditions in the early growing season increase above-ground biomass and carbon acquisition throughout the summer season." They note, "wet spring conditions can lead to greater CO$_2$ acquisition through much of the growing period even when drier conditions persist." They thus conclude if climate change plays out as described by current climate models—if the world becomes warmer and wetter—"northern wetlands should therefore become larger sinks for atmospheric CO$_2$."

Mauquoy *et al*. (2002) analyzed three cores obtained from a raised peat bog in the UK (Walton Moss) and a single core obtained from a similar bog in Denmark (Lille Vildmose) for macro- and micro-fossils (pollen), bulk density, loss on ignition, carbon/nitrogen ratios, and humification, which they $^{14}$C dated by accelerator mass spectrometry. Among a variety of findings, they determined "the lowest carbon accumulation values for the Walton Moss monoliths between ca. cal AD 1300 and 1800 and between ca. cal AD 1490 and 1580 for Lille Vildmose occurred during the course of Little Ice Age deteriorations." They describe this finding as being much the same as the observation "made by Oldfield *et al*. (1997) for a Swedish 'aapa' mire between ca. cal AD 1400 and 1800." They also report carbon accumulation before this, in the Medieval Warm Period, was higher, as was also the case after the Little Ice Age, as Earth transitioned to the Modern Warm Period. Consequently, whereas IPCC predicts warming will hasten the release of carbon from ancient peat bogs, real-world data demonstrate just the opposite is more likely.

In a similar study, but one that concentrated more on the role of nitrogen than of temperature, Turunen *et al*. (2004) derived recent (0–150 years) and long-term (2,000–10,000 years) apparent carbon accumulation rates for several ombrotrophic peatlands in eastern Canada with the help of $^{210}$Pb- and $^{14}$C-dating of soil-core materials. This work revealed the average long-term apparent rate of C accumulation at 15 sites was $19 \pm 8$ g C m$^{-2}$ yr$^{-1}$, comparable to long-term rates observed in Finnish bogs by Tolonen and Turunen (1996) and Turunen *et al*. (2002). Recent C accumulation rates at 23 sites, however, were much higher, averaging $73 \pm 17$ g C m$^{-2}$ yr$^{-1}$ These results, the scientists write, are "similar to results from Finland (Tolonen and Turunen, 1996; Pitkanen *et al*., 1999) and for boreal *Sphagnum* dominated peat deposits in North America (Tolonen *et al*., 1988; Wieder *et al*., 1994; Turetsky *et al*., 2000)." Noting recent rates of C accumulation are "strikingly higher" than long-term rates, Turunen *et al*. suggest increased N deposition "leads to larger rates of C and N accumulation in the bogs, as has been found in European forests (Kauppi *et al*., 1992; Berg and Matzner, 1997), and could account for some of the missing C sink in the global C budget."

Payette *et al*. (2004) quantified the main patterns of change in a subarctic peatland on the eastern coast of Canada's Hudson Bay, which were caused by permafrost decay between 1957 and 2003, based on detailed surveys conducted in 1973, 1983, 1993, and 2003. They found there was continuous permafrost thawing throughout the period of observation, so "about 18 percent of the initial frozen peatland surface was melted in 1957," and thereafter "accelerated thawing occurred with only 38 percent, 28 percent and 13 percent of the original frozen surface still remaining in 1983, 1993 and 2003, respectively." This process, in their words, was one of "terrestrialization" via the establishment of fen/bog vegetation, which nearly always results in either no net loss of carbon or actual carbon sequestration. Thus Payette *et al*. conclude, "contrary to current expectations, the melting of permafrost caused by recent climate change does not transform the peatland to a carbon-source ecosystem." Instead, they write, "rapid terrestrialization exacerbates carbon-sink conditions and tends to balance the local carbon budget."

In a study of experimental warming of Icelandic plant communities designed to see whether the warming of high-latitude tundra ecosystems would result in significant losses of species and reduced biodiversity, Jonsdottir *et al*. (2005) conducted a field experiment to learn how vegetation might respond to moderate warming at the low end of what is predicted by most climate models for a doubling of the air's CO$_2$ content. They studied the effects of three to five years of modest surface warming (1°–2°C) on two widespread but contrasting tundra plant communities; one was a nutrient-deficient and species-poor moss heath, the other a species-rich dwarf shrub heath. At the end of the study, no changes in community structure were detected in the moss heath. In the dwarf shrub heath, the number of deciduous and evergreen dwarf shrubs increased more than 50%, bryophytes decreased by 18%, and canopy height increased by 100%, but the researchers report they "detected no changes in species richness or other diversity measures in either community and the abundance of lichens did not change." Although Jonsdottir *et al.*'s study was a relatively short-term experiment as far as ecosystem studies go, its results indicate a rise in temperature need not diminish the species diversity of high-latitude tundra ecosystems and may have a positive influence on plant growth.

In a study with an entirely new element of complexity, Cole *et al.* (2002) constructed 48 small microcosms from soil and litter they collected near the summit of Great Dun Fell, Cumbria, England. Subsequent to "defaunating" this material by reducing its temperature to –80°C for 24 hours, they thawed and inoculated it with native soil microbes. Half of the microcosms were incubated in the dark at 12°C and half at 18°C for two weeks, to establish near-identical communities of the soils' natural complement of microflora in each microcosm. The first temperature was chosen to represent mean August soil temperature at a depth of 10 cm at the site of soil collection, and the latter was picked to be "close to model predictions for soil warming that might result from a doubling of $CO_2$ in blanket peat environments."

Next, ten seedlings of *Festuca ovina*, an indigenous grass of blanket peat, were planted in each of the microcosms, and 100 enchytraeid worms were added to each of half of the mini-ecosystems, producing four experimental treatments: ambient temperature, ambient temperature plus enchytraeid worms, elevated temperature, and elevated temperature plus enchytraeid worms. Then, the 48 microcosms—sufficient to destructively harvest three replicates of each treatment four times throughout the course of the 64-day experiment—were arranged in a fully randomized design and maintained at either 12° or 18°C with alternating 12-hour light and dark periods, given distilled water every two days to maintain their original weights.

The researchers report finding elevated temperature reduced the ability of the enchytraeid worms to enhance the loss of carbon from the microcosms. At the normal ambient temperature, the presence of the worms enhanced dissolved organic carbon (DOC) loss by 16 percent, while at the elevated temperature expected for a doubling of the air's $CO_2$ content they had no effect on DOC. In addition, Cole *et al.* note, "warming may cause drying at the soil surface, forcing enchytraeids to burrow to deeper subsurface horizons," and since the worms are known to have little influence on soil carbon dynamics below a depth of about 4 cm (Cole *et al.*, 2000), the researchers conclude this additional consequence of warming will further reduce the ability of enchytraeids to enhance carbon loss from blanket peatlands. In summing up their findings, Cole *et al.* conclude "the soil biotic response to warming in this study was negative," because it resulted in a reduced loss of carbon to the atmosphere.

As to the effects of elevated $CO_2$ itself on the loss of DOC from soils, Freeman *et al.* (2004) note riverine transport of DOC has increased markedly in many places throughout the world over the past few decades (Schindler *et al.*, 1997; Freeman *et al.*, 2001; Worrall *et al.*, 2003), and they suggest this phenomenon may be related to the historical increase in the air's $CO_2$ content.

The researchers' first piece of evidence for this conclusion came from a three-year study of monoliths (11cm diameter x 20cm deep cores) taken from three Welsh peatlands—a bog that received nutrients solely from rainfall, a fen that gained more nutrients from surrounding soils and groundwater, and a riparian peatland that gained even more nutrients from nutrient-laden water transported from other terrestrial ecosystems via drainage streams—which they exposed to either ambient air or air enriched with an extra 235 ppm of $CO_2$ in a solardome facility. This study revealed the DOC released by monoliths from the three peatlands was significantly enhanced—by 14% in the bog, 49% in the fen, and 61% in the riparian peatland—by the additional $CO_2$ to which they were exposed. That is the order of response expected from what is known about the stimulation of net primary productivity due to atmospheric $CO_2$ enrichment—it is low in the face of low soil nutrients, intermediate when soil nutrient concentrations are intermediate, and high when soil nutrients are present in abundance. Consequently, Freeman *et al.* conclude the DOC increases they observed "were induced by increased primary production and DOC exudation from plants."

To further test their hypothesis, they followed the translocation of labeled $^{13}C$ through the plant-soil systems of the different peat monoliths for about two weeks after exposing them to ~99 percent-pure $^{13}CO_2$ for five hours. This exercise revealed the plants in the ambient-air and $CO_2$-enriched treatments assimilated 22.9 and 35.8 mg of $^{13}C$ from the air, respectively; the amount of DOC recovered from the leachate of the $CO_2$-enriched monoliths was 0.6% of that assimilated, or 0.215 mg (35.8 mg x 0.006 = 0.215 mg); and the proportion of DOC in the soil solution of the $CO_2$-

enriched monoliths derived from recently assimilated $CO_2$ (the $^{13}C$ labeled $CO_2$) was 10 times higher than the control.

This latter observation suggests the amount of DOC recovered from the leachate of the ambient-air monoliths was only about a tenth as much as that recovered from the leachate of the $CO_2$-enriched monoliths, which puts the former amount at about 0.022 mg. Hence, what really counts—the net sequestration of $^{13}C$ experienced by the peat monoliths over the two-week period (which equals the amount that went into them minus the amount that went out), comes to 22.9 mg minus 0.022 mg = 22.878 mg for the ambient-air monoliths and 35.8 mg minus 0.215 mg = 35.585 mg for the $CO_2$-enriched monoliths. In the end, therefore, even though the $CO_2$-enriched monoliths lost 10 times more $^{13}C$ via root exudation than did the ambient-air monoliths, they still sequestered about 55% more $^{13}C$ overall, primarily in living-plant tissues.

Cai and Yu (2011) employed multiproxy data derived from a sediment core they extracted from Tannersville Bog near the edge of the Pocono Mountains in Monroe County, Pennsylvania (USA) to document the bog's historical peat accumulation pattern and rate, as well as climate variations experienced by this "temperate tree-covered poor fen" located at "the extreme warm end of climate space for northern peatlands."

The two authors report, "carbon accumulation rates increased from 13.4 to 101.2 g C/m$^2$/year during the last 8,000 years," with a long-term average value of 27.3 g C/m$^2$/year. This mean rate significantly exceeds the 18.6 g C/m$^2$/year obtained for boreal, subarctic, and arctic peatlands based on measurements made at 33 sites in the Northern Hemisphere (Yu *et al*., 2009). This fact led the authors to conclude their relatively high accumulation rate "was likely caused by high primary production associated with a warmer and wetter temperate climate." Cai and Yu say their study implies "northern peatlands can continue to serve as carbon sinks under a warmer and wetter climate, providing a negative feedback to climate warming."

Beilman *et al*. (2009) undertook further illumination of the relationship between climate and carbon accumulation in peatlands. They used "a network of cores from 77 peatland sites to determine controls on peat carbon content and peat carbon accumulation over the last 2000 years across Russia's West Siberian Lowland," the world's largest wetland region. They found carbon accumulation over the past two millennia varied significantly with mean annual air temperature, growing ever-greater as air temperature rose from -9 to 0°C, with maximum carbon accumulation occurring between -1 and 0°C, which is "where air-soil temperature differences optimize net primary production relative to soil respiration, e.g., near 0°C (Swanson *et al*., 2000)." On average, the researchers report "cores from non-permafrost sites have accumulated four times more peat by depth and twice as much carbon than cores from permafrost sites."

In light of these findings, Beilman *et al*. write, the "relationship between temperature and peat carbon sequestration, and the current spatial distribution of peatland ecosystems, should be an important consideration in future attempts to anticipate the impact of climate warming on the carbon sink potential of the West Siberian Lowland region." With respect to that impact, they opine, "permafrost thaw may promote a boost in peat carbon sequestration in affected sites," and, therefore, "future warming could result in a shift northward in long-term West Siberian Lowland carbon sequestration."

Bao *et al*. (2010) also counter the claim peatland ecosystems will release great quantities of previously sequestered carbon to the atmosphere in the form of $CO_2$ and methane as temperatures warm. Working in the Changbai mountain region that runs along the boundary between China and North Korea, this group of researchers extracted eight peat cores, which they analyzed for numerous parameters, including those required to calculate the recent rate of carbon accumulation (RERCA) in the peatlands of that region over the past two centuries.

The four researchers report "obvious increasing trends in RERCA were observed in all peat cores," as "organic carbon content declined from the top to the substrate." In addition, they state the temporal increase in RERCA in the upper regions of the cores—which likely corresponded to the warmest segment of their two-century study period—"changed to a much greater extent in recent decades than in the earlier period of peat formation."

Flanagan and Syed (2011) write, "northern peatland ecosystems are consistent net carbon (C) sinks that account for between one-quarter to one-third of the global soil carbon pool (Gorham, 1991; Turunen *et al*., 2002)," noting their sequestration of carbon "results from moderate rates of ecosystem photosynthesis that exceed decomposition and autotrophic plant respiration (Gorham, 1991)." The scientists set out to conduct a long-term experiment to explore IPCC's contention that "exposure to warmer temperatures and drier conditions associated with climate change will shift the balance between ecosystem photosynthesis and respiration providing a positive feedback to atmospheric $CO_2$ concentration." They used the eddy covariance technique "to determine the sensitivity of ecosystem photosynthesis, respiration and net $CO_2$ exchange to variations in temperature and water table depth associated with inter-annual shifts in weather over a six-year period."

Their work was conducted in "a moderately rich treed fen"—which they described as "the most abundant peatland type in western Canada"—at a peatland flux station northeast of Athabasca, Alberta, which was established in 2003 as part of the Fluxnet-Canada Research Network (Margolis *et al*., 2006), and which during 2007–2009 was part of the follow-on Canadian Carbon Program. The researchers report, "contrary to previous predictions, both ecosystem photosynthesis and respiration showed similar increases in response to warmer and drier conditions," such that "the ecosystem remained a strong net sink for $CO_2$ with an average net ecosystem production of 189 ± 47 $gC/m^2/year$." These "current net $CO_2$ uptake rates were much higher than carbon accumulation in peat determined from analyses of the relationship between peat age and cumulative carbon stock." Flanagan and Syed conclude, "in the absence of fire or other major disturbance, significant net carbon sequestration could continue for decades at this site and help to reduce the positive feedback of climate change on increasing atmospheric $CO_2$ concentration."

Also working in Canada, Turetsky *et al*. (2007) explored "the influence of differing permafrost regimes (bogs with no surface permafrost, localized permafrost features with surface permafrost, and internal lawns representing areas of permafrost degradation) on rates of peat accumulation at the southernmost limit of permafrost in continental Canada." The five American researchers say the work revealed "surface permafrost inhibits peat accumulation and that degradation of surface permafrost stimulates net carbon storage in peatlands." In fact, they report, "unfrozen bogs and internal lawns had net organic matter accumulation rates two-times faster than rates of accumulation in localized permafrost features over the most recent 25-year horizon."

Turetsky *et al*. say their data suggest "permafrost degradation within peatland environments, likely triggered by climate change, could serve as a negative feedback to net radiative forcing via enhanced carbon accumulation as peat." They note, however, "increased methane emissions to the atmosphere will partially or even completely offset this enhanced peatland carbon sink for at least 70 years following permafrost degradation." Nevertheless, they write, because "internal lawns succeed relatively quickly (within 70 years) to more bog-like conditions and [since] bogs in continental Canada are associated with low methane emissions, the degradation of localized permafrost in peatlands is likely over the long-term to serve as a negative feedback to radiative forcing."

Daimaru *et al*. (2002) dug 27 soil pits at various locations in and around the central location of a snowpatch grassland on the southeastern slope of Japan's Mt. Zarumori (~39.8°N, 140.8°E), examining the peat content of the soil and determining its age based on $^{14}C$ dating and tephrochronology. They report "peaty topsoils were recognized at seven soil pits in the dense grassland" where the snow melts earlier in the season and the period for plant growth is the longest. In contrast, soils located in areas where the snowmelt occurs later in the season "lacked peaty topsoil." Beneath these carbon-poor topsoils, Daimaru *et al.* found a carbon-rich layer they were able to date back to the Medieval Warm Period, suggesting the buried peat layers in the poor vegetation area accumulated in consequence of the warmer temperatures of that period. Consequently, as has been found in each of the other peatland studies referenced above, real-world observations show IPCC-based predictions—in terms of the influence of Earth's peatlands on the planet's temperature—do not match observational data. In stark contrast, these land types provide a negative feedback to global warming: When peatlands warm, they extract more, not less, $CO_2$ from the atmosphere, effectively applying a brake on rising temperatures, as opposed to pushing the planet past a tipping point toward a state of catastrophic runaway global warming.

At least one model-based study has reached the same conclusion. Noting "throughout the Holocene, northern peatlands have both accumulated carbon and emitted methane," so "their impact on climate radiative forcing has been the net of cooling (persistent $CO_2$ uptake) and warming (persistent $CH_4$ emission)," Frolking and Roulet (2007) developed Holocene peatland carbon flux trajectories based on estimates of contemporary $CH_4$ flux, total accumulated peat C, and peatland initiation dates, which they used as inputs to a simple atmospheric perturbation model to calculate the net radiative impetus for surface air temperature change. The two researchers determined the impact on the current atmosphere of northern peatland development and carbon cycling through the Holocene is a net deficit of 40–80 Pg $CO_2$-C (~20–40 ppm of atmospheric $CO_2$) and a net excess of ~200–400 Tg $CH_4$ (~75–150 ppb of atmospheric $CH_4$).

Frolking and Roulet note early in the Holocene the capture of $CO_2$ and emission of $CH_4$ by Earth's northern peatlands is likely to have produced a net warming impetus of up to +0.1 W $m^{-2}$. Over the following 8,000 to 11,000 years, however, they say Earth's peatlands have been doing just the opposite, and the current radiative forcing due to these atmospheric $CO_2$ and $CH_4$ perturbations represents a net cooling force on the order of -0.22 to -0.56 W $m^{-2}$, further establishing that the impetus for global cooling due to carbon sequestration by Earth's peatlands historically has been—and currently is—significantly greater than the global warming potential produced by their emissions of methane.

Finally, in an experimental as opposed to historical study, Fenner *et al.* (2007) collected intact peat monoliths—comprised predominantly of *Sphagnum* (*S. subnitens* Russ. and Warnst.) and *Festuca ovina* L., with small amounts of *Juncus effusus* L. and *Polytrichum commune* Hedw.—in perfusion systems that allowed for fine control of the water table and lateral water movements, which they maintained for approximately three years in solardomes with atmospheric $CO_2$ concentrations of ambient or ambient plus 235 ppm, while daily supplying the mini-ecosystems with synthetic rainwater comparable in volume and nutrient content to that received at the site from which the monoliths were extracted.

At the end of their three-year experiment, the seven UK researchers write, "species composition showed a shift from a *Sphagnum*-dominated community to one in which vascular monocotyledonous species dominated," as *S. subnitens* cover declined by 39% under elevated $CO_2$, whereas *J. effusus* cover increased from less than 1% in the control perfusion systems to 40% in the systems exposed to elevated $CO_2$. Also, "aboveground plant biomass showed a substantial increase under elevated $CO_2$ (115%, $P < 0.01$) as did belowground biomass (96%, $P < 0.01$)." In addition, they report "*J. effusus* roots were observed to be particularly thick, deep, and extensive under elevated $CO_2$."

The research summarized above suggests as the air's $CO_2$ content rises, the carbon content of the planet's peatlands most likely also will continue to rise, and dramatically so, notwithstanding model-based projections to the contrary.

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### 1.2.4 Wetlands

- Rising atmospheric $CO_2$ likely will enhance the productivity and carbon sequestering ability of wetlands. In addition, elevated $CO_2$ may assist some coastal wetlands in counterbalancing the negative impacts of rising seas.

The early works of Jacob *et al*. (1995) and Drake *et* *al*. (1996a) were among the first to demonstrate atmospheric $CO_2$ enrichment enhances vegetative productivity in wetland ecosystems. Drake *et al*. (1996b) also showed elevated levels of atmospheric $CO_2$ reduce insect and fungal damage to wetland plants (Drake *et al*., 1996b). Since that time, many other studies have reinforced these initial findings and revealed still other positive wetland impacts of the ongoing rise in the air's $CO_2$ content.

Rasse *et al*. (2003) developed a model for calculating net ecosystem exchange (NEE) of $CO_2$ between $C_3$ wetland sedge (*Scirpus olneyi* Gray) communities and the atmosphere, based on published ecophysiological data and measurements of various photosynthetic parameters made at the Chesapeake Bay $CO_2$-enrichment study described by Curtis *et al*. (1989a,b). This model indicated the *S. olneyi* community responded favorably to a near-doubled atmospheric $CO_2$ concentration by increasing its NEE by 35–40%, which Rasse *et al*. compare to the mean net photosynthetic increase of 60% reported by Norby *et al*. (1999) in an extensive review that included several tree species and ecosystems. Rasse *et al*. write, "because *Scirpus*-dominated ecosystems are extremely productive (Drake and Leadley, 1991), a 35–40% productivity increase might represent a larger additional amount of carbon fixed as compared to a 60% increase in less productive forest ecosystems." In addition, because there are about six million square kilometers of wetlands worldwide, with approximately 15% of that area located in temperate regions (Mitsch *et al*., 1994), Rasse *et al*. conclude "temperate $C_3$ wetlands have a huge potential for increased plant productivity [and, therefore, carbon sequestration] during the 21st century."

Dakora and Drake (2000) exposed plant communities of *Scirpus olneyi* and the $C_4$ grass *Spartina patens* to atmospheric $CO_2$ concentrations of 360 and 660 ppm in open-top chambers to study the effects of elevated $CO_2$ on nitrogenase activity and nitrogen fixation in these plants and in the non-symbiotic nitrogen-fixing microbes that inhabit the sediments in which the plants grow. They report the extra $CO_2$ increased nitrogenase activity by 35 and 13% in *S. olneyi* and *S. patens*, respectively, and these stimulations led to increases in nitrogen incorporation of 73 and 23%, respectively, in the same plants. These responses, they add, are "in rough proportion to the relative effect of elevated $CO_2$ on canopy photosynthesis measured throughout the day." They also report the elevated $CO_2$ significantly stimulated nitrogenase activity in the non-symbiotic nitrogen-fixing microbes living in the soil sediments, suggesting increases in the air's $CO_2$ content produce "an increase in the $N_2$-fixing activity of free-living [microbes] in the marsh ecosystem."

Hussein *et al*. (2004) measured carbon sequestration along two transects across submerging coastal landscapes (Hell Hook and Cedar Creek) of the Chesapeake Bay in Dorchester County, Maryland, USA, and used this data to develop a model of carbon sequestration by coastal marshes. They found "coastal marsh soils are accreting vertically and migrating laterally over the [adjacent] low-lying forest soils to keep pace with sea-level rise," and during the past 150 years, the rate of carbon sequestration by the marsh soils averaged 83.5 ± 23 g $m^{-2}$ $yr^{-1}$, whereas prior to that period it had averaged 29.2 ± 5.35 g $m^{-2}$ $yr^{-1}$.

These sequestration rates are much greater than those of either local forest or agricultural soils. In addition, the three scientists report, "carbon sequestration in mineral soils of agro- and upland-forest ecosystems is generally of limited capacity and tends to reach steady-state condition within relatively short time," but "in coastal marsh soils, carbon sequestration will continue to occur with time by accumulation in the organic horizons, and with increasing storage capacity." Based on a model they developed from their data, for example, Hussein *et al*. project sea-level rise will cause carbon sequestration by coastal marsh ecosystems over the next 100 years to average 400 ± 162 g $m^{-2}$ $yr^{-1}$. Thus they conclude, "coastal marsh ecosystems tend to sequester carbon continuously with increasing storage capacity as marsh age progresses," and "carbon sequestration in coastal marsh ecosystems under positive accretionary balance acts as a negative feedback mechanism to global warming."

Returning to the Chesapeake Bay wetland study at the 17-year point of its progression, Rasse *et al*. (2005) evaluated the long-term effects of atmospheric $CO_2$ enrichment on the net CO2 exchange, shoot density, and shoot biomass of the wetland sedge, *Scirpus olneyi*, as well as how these effects have been influenced by salinity, one of the main environmental stressors of the wetland. In every year of the past 17 years, they found 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 those of the plants growing in ambient air. The extra $CO_2$ also boosted the net $CO_2$ exchange rate 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, but whereas the $CO_2$-induced stimulation of the net $CO_2$ exchange rate remained essentially constant over the last 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. In addition, the trends in shoot density and biomass do not appear to be leveling off, leading one to wonder just how high the $CO_2$-induced stimulations ultimately will rise.

Salinity was closely correlated with net $CO_2$ exchange, shoot density, and shoot biomass, such that the higher the salinity, the more detrimental were its effects on these variables. Nevertheless, even at the highest levels of salinity reported, atmospheric $CO_2$ enrichment was able to produce a positive, albeit reduced, stimulatory effect on 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, in the words of Rasse *et al*., "circumstantial evidence suggesting that salinity stress increased the stimulation of shoot density by elevated atmospheric $CO_2$ concentration."

This experiment demonstrates several important things. 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, given that 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 much more long-term research needs to be carried out if we are to ascertain the full and correct impacts of atmospheric $CO_2$ enrichment on plants. In the case of the wetland sedge of this study, for example, it took about ten growing seasons before an increasing trend in the shoot density could be recognized. Finally, there is the researchers' "most important finding"—"that a species response to elevated atmospheric $CO_2$ concentration can continually increase when [it] is under stress and declining in its natural environment."

Erickson *et al*. (2007) present data "on 18 years of measurement of above and belowground biomass, tissue N concentration and total standing crop of N for a *Scirpus olneyi*-dominated ($C_3$ sedge) community, a *Spartina patens*-dominated ($C_4$ grass) community and a $C_3$-$C_4$-mixed species community exposed to ambient and elevated (ambient + 340 ppm) atmospheric $CO_2$ concentration [via open-top chamber technology] in natural salinity and sea level conditions of a Chesapeake Bay wetland." This report shows "elevated atmospheric $CO_2$ enhancement of $C_3$ biomass was sustained through time in the *S. olneyi*-dominated community, averaging about 40% for shoots and 26% for roots, whereas elevated $CO_2$ had no significant overall effect on biomass production in the $C_4$ grass community." In addition, the authors state, "the greatest amount of carbon was added to the *S. olneyi*-dominated community during years when shoot N concentration was reduced the most, suggesting that the availability of N was not the most or even the main limitation to elevated $CO_2$ stimulation of carbon accumulation in this ecosystem." These findings, the four researchers conclude, "demonstrate that elevated $CO_2$ effects on biomass production can be sustained through time," even when N availability is at the lowest of levels typically encountered in the wetland. They note similar $CO_2$-induced "sustained enhancement of growth has been found in a scrub oak ecosystem (Dijkstra *et al*., 2002; Hymus *et al*., 2002), a tallgrass prairie (Owensby *et al*., 1999) and several forested ecosystems (Norby *et al*., 2005), indicating that increased productivity of many ecosystems will follow global increases in atmospheric $CO_2$ concentration."

Working with *Phragmites australis*—a wetland plant found in every U.S. state and numerous other places around the world—in a study with very different implications, Scholefield *et al*. (2004) measured isoprene emissions from plants growing at different distances from a natural $CO_2$ spring located in central Italy, where atmospheric $CO_2$ concentrations of approximately 350, 400, 550, and 800 ppm likely had prevailed for the entire lifetimes of the plants. They found as long-term atmospheric $CO_2$ concentrations rose, plant isoprene emissions dropped: Over the first 50 ppm increase in the air's $CO_2$ concentration, they were reduced to approximately 65% of what they were at ambient $CO_2$, and for $CO_2$ increases of 200 and 450 ppm, they were respectively reduced to only about 30% and 7% of what they were in ambient-$CO_2$ air, as best we can determine from the bar graph of the authors' data.

These $CO_2$-induced reductions in plant isoprene emissions are significant because isoprene, a highly reactive non-methane hydrocarbon (NMHC) emitted by vegetation in copious quantities at current atmospheric $CO_2$ concentrations, is responsible for the production of vast amounts of plant- and animal-harming ozone (Chameides *et al*., 1988; Harley *et al*., 1999). Poisson *et al.* (2000), for example, calculated current concentrations of NMHC emissions (the vast majority of which are isoprene) increase surface ozone concentrations by 50–60% over land and by as much as 40% over the world's oceans. In addition, biogenic NMHCs (with isoprene being the most important) play a major role in the global tropospheric chemistry of methane, one of the atmosphere's most powerful greenhouse gases, boosting methane's atmospheric lifetime by approximately 14% above what it would be without isoprene (Poisson *et al.*, 2000). This being the case, if other plants behave similarly—and much evidence suggests they do (Monson and Fall, 1989; Loreto and Sharkey, 1990; Sharkey *et al.*, 1991; Loreto *et al.*, 2001; Rosenstiel *et al.*, 2003)—the ongoing rise in the air's $CO_2$ content can be expected to enhance plant productivity, mitigate the deleterious consequences of one of Earth's worst air pollutants (ozone), and reduce the atmospheric lifetime of one of the planet's most powerful greenhouse gases (methane).

As background for their work, Langley *et al.* (2009) note "tidal wetlands experiencing increased rates of sea-level rise (SLR) must increase rates of soil elevation gain to avoid permanent conversion to open water." As for how that might happen, they note "root zone expansion by accumulation of plant material is essential to maintaining a constant surface elevation relative to rising sea level." Against this backdrop, in Kirkpatrick Marsh—a microtidal sub-estuary of Chesapeake Bay, where each of several 200-$m^2$ plots was outfitted with a surface elevation table (SET) to measure soil elevation change—Langley *et al.* exposed half of the plots to an extra 340 ppm of $CO_2$ for two years. Data "from a greenhouse mesocosm experiment (Cherry *et al.*, 2009) were used to examine how elevated $CO_2$ might affect elevation response under simulated SLR scenarios."

The five researchers report the extra $CO_2$ of their marsh experiment increased fine root productivity by an average of 36% over the two-year study, and aboveground biomass production was increased by as much as 30%, "consistent with a 20-year record of elevated $CO_2$ treatment in a previous $CO_2$ study on the same marsh (Erickson *et al.*, 2007)." In addition, they say the elevated $CO_2$ caused an increase in root zone thickness of 4.9 mm/year compared with only 0.7 mm/year in the ambient $CO_2$ treatment, so there was "a slight loss of elevation in ambient $CO_2$ (-0.9 mm/year) compared with an elevation gain (3.0 mm/year) in the elevated $CO_2$ treatment." Furthermore, they report the greenhouse mesocosm experiment of Cherry *et al.* (2009) "revealed that the $CO_2$ effect was enhanced under salinity and flooding conditions likely to accompany future SLR."

Langley *et al.* conclude, "by stimulating biogenic contributions to marsh elevation, increases in the greenhouse gas, $CO_2$, may paradoxically aid some coastal wetlands in counterbalancing rising seas." They say their findings "bear particular importance given the threat of accelerating SLR to coastal wetlands worldwide," citing the recent EPA report of Reed *et al.* (2008) which suggests "a 2-mm increase in the rate of SLR will threaten or eliminate a large portion of mid-Atlantic marshes." Once again, however, the proven and positive growth-promoting effect of atmospheric $CO_2$ enrichment more than compensates for its hypothetical and negative global-warming effect.

Kirwan *et al.* (2009) write, "when subjected to future [projected] rates of sea level rise, numerical models and statistical projections predict that marshland worldwide will decline on the order of 10–50% during the next 50–100 years," and "such a decline could represent a catastrophic loss of ecosystem services by one of Earth's most valuable coastal environments." To explore this subject further, Kirwan *et al.* "compiled 56 measurements of aboveground annual productivity for *Spartina alterniflora*, the dominant macrophyte in North American coastal wetlands," along the Gulf Coast and Eastern Seaboard of the United States, as well as the east coast of Canada.

The researchers report, "despite local and temporal variability, a significant ($r = 0.83$; $P < 0.000001$) latitudinal gradient of 25 g $m^{-2}$/year per degree of latitude exists across the entire geographic range of the compilation." In addition, "the latitudinal gradient in productivity appears to be driven by temperature," noting "annual productivity most significantly correlates with mean annual temperature and the annual number of growing degree days." Consequently, Kirwan *et al.* estimate the response of *S. alterniflora* productivity to future increases in global temperature, noting their results suggest "an increase in global temperature of 2–4°C by 2100 (IPCC, 2007) would cause productivity to increase by about 50–100 g $m^{-2}$/year." For mid-Atlantic and northern marshes with current productivities ranging from 450 to 250 g $m^{-2}$/year, they say the result they obtained "represents approximately a 10–40% increase in annual productivity," which they describe as being of "a magnitude similar to that of marsh lost due to sea level change (10–50%)," as calculated by numerical models for the same time period. They therefore conclude, "increased growth under a warming climate may compensate for the amount of productivity lost by eroding marshland."

The increase in atmospheric $CO_2$ concentration expected for the current century likely will boost marsh productivity even more, further strengthening this conclusion. In addition, it is widely recognized, as Kirwan *et al*. state, "increased vegetation growth will tend to promote higher marsh accretion rates, stabilize channel expansion, and decrease the ability for waves to erode the marsh platform." As a result, they conclude, "the combined impacts of future global change (e.g. sea level, temperature, $CO_2$) could actually increase the total productivity of marshland."

Mateos-Naranjo *et al*. (2010) obtained 15 cm-diameter clumps of *S. maritima* from a low-marsh site along the southwest coast of Spain in April 2007, which they transplanted into individual plastic pots filled with pearlite that rested on shallow trays filled with Hoagland's solution of three different salinities (0, 170, or 510 mM NaCl). The research team maintained the plants in controlled environment chambers having atmospheric $CO_2$ concentrations of either 380 ppm or 700 ppm (an increase of 84%) for periods of 30 days, during which time they measured a number of plant properties and processes. The four researchers report the 84% increase in the atmosphere's $CO_2$ concentration stimulated the growth of *S. maritima* by about 65% in all three salinity treatments; the graphical representation of the halophyte's water use efficiency indicates this important property of the plant was enhanced by approximately 10%, 100%, and 160% in the 0, 170, and 510 mM salinity treatments, respectively, because "increasing $CO_2$ concentration has a positive effect on the photochemical apparatus, helping to counteract salt stress experienced by plants at current $CO_2$ concentrations." The UK and Spanish scientists say their results suggest the productivity of *S. maritima* "might increase in a future scenario of rising atmospheric $CO_2$ concentration in environments with salinities as high as that of seawater," good news for what they describe as "an important pioneer and ecosystem engineer in salt marshes."

Kathilankal *et al*. (2011) made a series of physiological measurements on smooth cordgrass, which is believed to possess $C_4$ physiology, at two locations in the Virginia Coast Reserve's Long Term Ecological Research area—Fowling Point Marsh (a lagoon salt marsh) and Oyster Marsh (a mainland fringing marsh)—to investigate how light, temperature, and intercellular $CO_2$ concentration affected the marsh plant's rate of photosynthesis. They used the functional relationships between these environmental variables and *S. alterniflora's* physiological responses to improve $C_4$-leaf photosynthesis models ultimately employed to determine the net impact of potential increases in air temperature and atmospheric $CO_2$ concentration on the productivity of smooth cordgrass in a $CO_2$-enriched and warmer world.

Instead of acting like a $C_4$ plant, the modeling studies and field measurements indicate "*S. alterniflora* exhibited physiological traits similar to $C_3$-$C_4$ intermediate plants," so one could expect "atmospheric warming in conjunction with an increase in atmospheric $CO_2$ would enhance photosynthesis in *S. alterniflora*," the six scientists discovered. In further support of this conclusion, they note "McKee and Rooth (2008) reported a significant stimulation in *S. alterniflora* biomass in plants grown under elevated $CO_2$," and "warming experiments in New England (Charles and Dukes, 2009) demonstrated that *S. alterniflora* increased productivity with increasing temperature," while the plant's optimum temperature for photosynthesis also will "likely increase in response to enriched $CO_2$ conditions," citing Simon *et al*. (1984).

In the concluding paragraph of their report, Kathilankal *et al*. declare "in a scenario of atmospheric warming and increased atmospheric $CO_2$ levels, *S. alterniflora* will likely respond positively to both changes," and they suggest these responses "will result in increased *S. alterniflora* productivity," which should be beneficial for western Atlantic intertidal marshes and the many beneficial services that smooth cordgrass provides to those ecosystems.

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## 1.2.5 Soils

### *1.2.5.1 Bacteria*

- Rising atmospheric $CO_2$ concentrations likely will allow greater numbers of beneficial bacteria (those that help sequester carbon and nitrogen) to exist in soils and anaerobic water environments. This two-pronged phenomenon would be a great boon to terrestrial and aquatic ecosystems.

Nearly all of Earth's plant life responds favorably to increases in the air's $CO_2$ content by exhibiting enhanced rates of photosynthesis and biomass production. Consequently, these phenomena tend to increase soil carbon contents by increasing root exudation of organic compounds and the amount of plant litter returned to the soil. Thus, it can be expected that $CO_2$-mediated increases in soil carbon content will affect soil bacterial communities. This section explores the findings of several scientists who have studied the effects of elevated $CO_2$ on bacteria.

Regarding beneficial terrestrial bacteria, Ronn *et al*. (2003) grew wheat (*Triticum aestivum* L. cv. Minaret) in open-top chambers fumigated with either ambient air or air enriched with an extra 320 ppm of $CO_2$; on two occasions during the growing season they assessed various plant and soil characteristics, total protozoan numbers, and numbers of culturable bacteria. They found "higher numbers of bacterivorous protozoa in soil under plants grown at elevated $CO_2$ and larger amounts of root-derived substrates in the soil at plant maturity." Ronn *et al*. note "protozoan grazing generally enhances carbon and nitrogen mineralization in soil," which typically results in more nitrogen being made available to plants. This phenomenon, in turn, enables plants to increase their biomass (as was observed in the $CO_2$-enriched plants in this experiment) without suffering reductions in tissue nitrogen concentration (as also was observed in the $CO_2$-enriched plants in this experiment). The end result of these linked phenomena was thus more high-quality wheat production in response to atmospheric $CO_2$ enrichment.

Montealegre *et al*. (2002) obtained similar results by growing white clover (*Trifolium repens* L.) and perennial ryegrass (*Lolium perenne* L.) in free-air $CO_2$ enrichment (FACE) plots maintained at atmospheric $CO_2$ concentrations of 350 and 600 ppm for three years and then sampling the soil to determine the effects of elevated $CO_2$ on its bacterial populations. Although elevated $CO_2$ increased the total number of bacteria and respiring bacteria in the bulk soil beneath white clover by 40 and 70%, respectively, it had no significant impact on bulk-soil bacterial numbers beneath perennial ryegrass. When the total bacterial numbers in the *rhizosphere* soil—which lies within about 1.5 mm of plant roots and is characterized by heightened biological activity and chemical weathering of minerals—were expressed on a per unit land area basis, the scientists found elevated $CO_2$ increased the total number of bacteria and respiring bacteria beneath white clover by about 100 and 250%, respectively, and it increased the total number of bacteria and respiring bacteria beneath perennial ryegrass by approximately 85 and 125%, respectively.

In a related study from the same FACE clover and ryegrass plots, Marilley *et al*. (1999) report atmospheric $CO_2$ enrichment also altered the profile of bacterial communities in a plant species-dependent manner. In ryegrass, for example, elevated $CO_2$ increased the dominance of *Pseudomonas* species, which enhance plant growth by many different mechanisms. In white clover, it increased the dominance of *Rhizobium* species, which enhance plant growth by making atmospheric nitrogen available for utilization. After three years of differential $CO_2$ treatment in the same FACE experiment, Montealegre *et al*. (2000) determined the genetic structure of 120 isolates of the symbiotic bacterium *Rhizobium leguminosarum* associated with roots of white clover, finding atmospheric $CO_2$ enrichment favored some of the isolates over others. When these isolates were mixed with isolates favored in ambient air and the resulting combination was exposed to $CO_2$-enriched air, the isolates favored by elevated $CO_2$ produced 17% more nodules on roots than the isolates favored in ambient air.

Zak *et al*. (2000) grew six genotypically different aspen (*Populus tremuloides*) cuttings in open-top chambers for 2.5 growing seasons in Michigan, USA, at atmospheric $CO_2$ concentrations of 350 and 700 ppm under adequate and inadequate supplies of soil nitrogen, reporting the effects of elevated $CO_2$ and soil nitrogen on soil microbial composition, biomass, and functioning. Although atmospheric $CO_2$ enrichment had no effect on soil microbial biomass, even after 2.5 years of treatment, high soil nitrogen supply increased it fivefold over that observed in low soil nitrogen plots. Similarly, elevated $CO_2$ did not significantly impact microbial community composition, whereas high soil nitrogen supply did. Atmospheric $CO_2$ did not influence microbial rates of nitrogen mineralization, nor did it alter the microbial demand for inorganic nitrogen.

The several observations of Zak *et al*. suggest the increased fine root biomass and turnover, which led to greater carbon inputs to the soils of the $CO_2$-enriched plots, were not significant enough to elicit any responses in microbial community composition, biomass, and functioning, likely due to the enormous amount of background organic carbon present in the experimental soils, which was approximately 1,000-fold greater than that contributed by the aspen roots. Notwithstanding this observation, the authors conducted an eloquent review of the scientific literature pertaining to this topic, and they conclude when root-associated soil carbon inputs are sufficiently large, relative to native soil organic carbon contents, they can influence microbial community composition, biomass, and functioning.

Therefore, as atmospheric $CO_2$ concentrations rise, it is likely aspen trees will exhibit significant increases in growth, regardless of soil nitrogen availability. These growth increases will occur both above- and below-ground, stimulating greater carbon inputs to soils. Because most forest soils are already relatively rich in organic carbon, however, it is likely the extra carbon inputs resulting from the increasing $CO_2$ content of the air will have little impact on soil microbial composition, biomass, and functioning.

Fu *et al*. (2008) employed semi-continuous culturing methods that used filtered, microwave-sterilized surface Sargasso seawater enriched with phosphate and trace nutrients to examine the physiological responses of steady-state iron (Fe)-replete and Fe-limited cultures of the biogeochemically critical marine unicellular diazotrophic cyanobacterium *Crocosphaera watsonii* at 380 ppm and 750 ppm $CO_2$ levels. When the seawater was replete with iron, they found daily primary production at 750 ppm $CO_2$ was 21% greater than it was at 380 ppm, but when the seawater was iron-limited, daily primary production at 750 ppm $CO_2$ was 150% greater than it was at 380 ppm. With respect to $N_2$ fixation, rates varied little between the two $CO_2$ treatments when the seawater was iron-limited, but when the seawater was replete with iron, $N_2$ fixation at 750 ppm $CO_2$ was 60% greater than it was at 380 ppm.

In discussing their findings, Fu *et al*. write "several studies examining the marine diazotrophic cyanobacterium *Trichodesmium* have shown significant increases in $N_2$ fixation and photosynthesis in response to elevated $CO_2$ concentration (Hutchins *et al*., 2007; Levitan *et al*., 2007; Ramos *et al*., 2007)," and they say their data "extend these findings to encompass the marine unicellular $N_2$-fixing cyanobacterium *Crocosphaera*." This group, they add, "is now recognized as being perhaps equally as important as *Trichodesmium* to the ocean nitrogen cycle (Montoya *et al*., 2004)." Consequently, they conclude, "anthropogenic $CO_2$ enrichment could substantially increase global oceanic $N_2$ and $CO_2$ fixation," which would be a boon to the marine biosphere.

Feng *et al*. (2009) measured a number of characteristics of purple phototrophic bacteria (PPB) within the rhizosphere and bulk soils of a rice/wheat rotation system at the Nianyu Experimental Station in Jiangsu Province, China, under two $CO_2$ treatments. Rice fields, in their words, "represent the most important agricultural ecosystems in Asia, since rice and wheat are the main source for food supply, and more than 90% of rice fields around the world are located in Asia," and "purple phototrophic bacteria (PPB) are thought to be crucial in the nutrient cycling of rice fields." The Chinese researchers say PPB "thrive in the anaerobic portions of all kinds of aquatic environments, and have long been recognized as one of the key players in global carbon and nitrogen cycles." The researchers grew rice plants (*Oryza sativa* L.) under standard paddy culture at two levels of soil nitrogen (N) fertility (low and high) and two levels of atmospheric $CO_2$ concentrations (ambient and ambient +200 ppm).

Throughout this period they measured a number of PPB characteristics. Feng *et al.* report, "based on denaturant gradient gel electrophoresis (DGGE) analysis of *pufM* gene encoding the M subunit of anoxygenic PPB light reaction center, elevated $CO_2$ appeared to enhance the biodiversity of PPB in flooded paddy soils." They continue, "this was further supported by canonical correspondence analysis (CCA) of DGGE fingerprinting pattern of *pufM* genes in paddy soils as well as Shannon diversity indices." They also note "real-time quantitative PCR analysis of *pufM* gene further indicated that PPB abundance was stimulated by elevated $CO_2$ in bulk soil," and "N fertilization enhanced the biodiversity of PPB under elevated atmospheric $CO_2$." Feng *et al.* state the significance of these findings by noting "PPB inoculation into the flood water [in rice paddy culture] could lead to grain yield increase by 29% (Elbadry *et al*., 1999; Harada *et al*., 2005)," and "PPB are thought to be capable of fixing nitrogen." Feng *et al.* (2011) expressed similar sentiments in discussing the results of the same experiment, acknowledging the importance of elevated $CO_2$ concentrations on PPB to "enhance the microbial food chain and promote the growth and yield of crops."

The above observations suggest rising atmospheric $CO_2$ levels likely will allow similar or greater numbers of bacteria to exist in terrestrial environments, enhancing carbon and nitrogen sequestration, which in turn will stimulate the growth and productivity of the surrounding environments.

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### *1.2.5.2 Carbon Sequestration*

- The aerial fertilization effect of atmospheric $CO_2$ enrichment likely will result in greater soil carbon stores due to increased carbon-input into soils, even in nutrient-poor soils and in spite of predicted increases in temperature. In addition, the soil-carbon-sequestering capability of Earth's vegetation likely will act as a significant brake on the rate of rise of the air's $CO_2$ content and thereby help to mute any $CO_2$-induced impetus for global warming.

As the $CO_2$ content of the air increases, nearly all plants respond favorably by increasing their photosynthetic rates and producing greater amounts of biomass. Invariably, this phenomenon leads to greater inputs of carbon to the soil in the form of roots, root exudates, and senesced plant material. Much research has been conducted to determine whether these biological inputs will increase the carbon sequestering abilities of soils, particularly if air temperatures rise, which some scientists have predicted will enhance plant litter decomposition rates to the point they will exacerbate global warming. This section summarizes research that has addressed this subject.

Atmospheric $CO_2$ enrichment typically has but a small effect on the decomposition rates of senesced plant materials present in soils. Nonetheless, $CO_2$ enrichment often leads to significantly greater soil carbon sequestration, as demonstrated by De Angelis *et al.* (2000), who report a 4% reduction in the decomposition rate of leaf litter beneath stands of 30-year-old Mediterranean forest species enriched with air of 710 ppm $CO_2$, concluding, "if this effect is coupled to an increase in primary production [which nearly always occurs in response to elevated $CO_2$] there will be a net rise of C-storage in the soils of forest ecosystems." Similarly, in a study of soybean and sorghum plant residues grown at 705 ppm $CO_2$, where decomposition rates were not affected by elevated $CO_2$, Henning *et al.* (1996) concluded "the possibility exists for increased soil C storage under field crops in an elevated $CO_2$ world," due to the greater residue production resulting from $CO_2$-enhanced plant growth.

In a study that revealed how these phenomena once manifested themselves in a field of clover (*Trifolium repens* L.) at the Swiss Federal Institute of Technology near Zurich, a 71% increase in atmospheric $CO_2$ concentration increased aboveground growth by 146%, and it increased the pumping of newly fixed carbon into the soil of the $CO_2$-enriched plots by approximately 50% (Nitschelm *et al.* 1997). In addition, root decomposition in the $CO_2$-enriched plots was found to be 24% less than in the ambient-treatment plots. The researchers conclude, "the occurrence at elevated $CO_2$ of both greater plant material input, through higher yields, and reduced residue decomposition rates would be expected to impact soil carbon storage significantly." In a similar study of the effects of a doubling of the air's $CO_2$ concentration on three grass species, Cotrufo and Gorissen (1997) conclude "elevated $CO_2$ could result in greater soil carbon stores due to increased carbon-input into soils."

One year later, Verburg *et al.* (1998) grew one-year-old heather plants (*Calluna vulgaris* L.) for two months in greenhouses maintained at atmospheric $CO_2$ concentrations of 380 and 580 ppm in combination with low and high levels of soil nitrogen before exposing them to $^{14}CO_2$ for one day, to study the fate of recently fixed carbon in their experimental plant-soil system. They found the extra $CO_2$ increased net $^{14}C$ uptake in heather by approximately 43%, irrespective of soil nitrogen content. In addition, soil $^{14}C$ increased in elevated $CO_2$ plots by 17% and 25% at low and high soil nitrogen levels, respectively. Also, although total soil respiration initially was higher in the $CO_2$-enriched plots (for two days post $^{14}CO_2$ labeling), it declined and became significantly lower than the soil respiration rate displayed by plots exposed to ambient air within two weeks. That trend persisted throughout the remaining four weeks of the study. Thus it would appear soil carbon sequestration beneath heather communities likely will increase in the future with further increases in the air's $CO_2$ concentration.

Similar results have been reported for other shrubs and trees that possess the ability to store more carbon in their associated soils than do grasses, as noted by Gill and Burke (1999). Pregitzer *et al.*

(2000), for example, grew aspen seedlings for 2.5 years at 700 ppm $CO_2$ and observed fine root biomass was 65 and 17% greater than that produced by seedlings growing at ambient $CO_2$ concentration on nitrogen-rich and nitrogen-poor soils, respectively. The researchers state such increases in soil carbon inputs "can be substantial," even under low soil nitrogen conditions. Rouhier and Reed (1999) also note soil carbon was significantly greater beneath seedlings of birch grown at 700 ppm $CO_2$ than it was beneath seedlings grown at 350 ppm $CO_2$. Leavitt *et al.* (1994) found 10% of the organic carbon present in soils beneath $CO_2$-enriched cotton plants grown for only three years at 550 ppm $CO_2$ came from the extra $CO_2$, which was stable-isotope labeled to trace its path through this woody agricultural species and into the soil.

In a study that included air temperature as a variable, Casella and Soussana (1997) grew perennial ryegrass (*Lolium perenne* L.) in ambient and elevated (700 ppm) $CO_2$ at two different levels of soil nitrogen and at ambient and elevated (+3°C) temperature for two years. They found "a relatively large part of the additional photosynthetic carbon is stored below-ground during the two first growing seasons after exposure to elevated $CO_2$, thereby increasing significantly the below-ground carbon pool." At the low and high levels of soil nitrogen supply, for example, the elevated $CO_2$ increased soil carbon storage by 32 and 96%, respectively, "with no significant increased temperature effect," which led the two scientists to conclude, in spite of predicted increases in temperature, "this stimulation of the below-ground carbon sequestration in temperate grassland soils could exert a negative feed-back on the current rise of the atmospheric $CO_2$ concentration." Along these same lines, van Ginkel and Gorissen (1998) and van Ginkel *et al.* (1999)—who performed similar experiments using *Lolium perenne*—conclude the effects of atmospheric $CO_2$ enrichment on increasing plant growth and decreasing decomposition rates of plant litter are "more than sufficient to counteract the positive feedback [on decomposition rates] caused by [an] increase in air temperature."

Fitter *et al.* (1999) heated upland grass ecosystem soils by nearly 3°C and found root production and root death were increased by equivalent amounts. Hence, they conclude elevated temperatures "will have no direct effect on the soil carbon store [in upland grass communities]." Similarly, Johnson *et al.* (2000) warmed Arctic tundra ecosystems by nearly 6°C for eight years, reporting warming had no significant effect on ecosystem respiration. In addition, Liski *et al.* (1999) showed carbon storage in soils of both high- and low-productivity boreal forests increased with temperature along a temperature gradient in Finland. Thus it is clear any warming likely will have little or no impact on soil carbon sequestration rates, and if there is an impact, it may be positive.

Increased soil carbon storage occurring from the ongoing rise in the air's $CO_2$ content should have wide-ranging positive influences on agriculture. In considering soil carbon storage in the context of global climate change, Rosenzweig and Hillel (2000) state "our management of the soil should be aimed at enhancing soil organic matter for the multiple complementary purposes of improving soil fertility and soil structure, reducing erosion, and helping to mitigate the greenhouse effect." In an experiment where soybeans were grown at an atmospheric $CO_2$ concentration of 500 ppm, Islam *et al.* (1999) report soil particulate organic carbon content was significantly increased, as were the amounts of dissolved carbon, humic, and fulvic acids. These findings led them to conclude "one of the main benefits arising from the greater supply of organic residues to soils under $CO_2$ enrichment is an improvement of soil structure." In a similar study, Insam *et al.* (1999) note fumigation of artificial tropical ecosystems with 610 ppm $CO_2$ for about 1.5 years increased humic substances in their soils by nearly 30%.

Ross *et al.* (2000) collected soil samples from around a natural $CO_2$ vent in New Zealand to determine the effects of elevated $CO_2$ (510–900 ppm vs. 440–460 ppm) on soil carbon and nitrogen contents. The soil at the site was considered to be a gley, and the overlying vegetation was typical of native grasslands in the area, consisting of both $C_3$ and $C_4$ species. They found several decades of exposure to elevated atmospheric $CO_2$ significantly increased the soil's organic carbon and total nitrogen contents by 24%, and it increased microbial carbon and nitrogen contents by 116%. These results led Ross *et al.* to conclude storage of C and N in gley soils "can increase under prolonged exposure to elevated $CO_2$" and "increased storage of soil organic matter at such springs can occur, even when soil C concentrations are already high." Thus, as the air's $CO_2$ content rises, vegetated gley soils will sequester increasingly greater amounts of both carbon and nitrogen, and they will exhibit enhanced biological activity both above- and below-ground.

Hu *et al.* (2001) studied carbon and nitrogen relations in the plants and moderately fertile soil of a sandstone grassland at Stanford University's Jasper Ridge Biological Preserve in central California near the conclusion of a five-year study conducted between 1992 and 1997, where two $CO_2$ treatments (360 and 720 ppm) were maintained in 20 open-top chambers (ten replicates per treatment). This effort revealed the rise in atmospheric $CO_2$ increased both soil microbial biomass and plant nitrogen uptake, the net effect being less nitrogen was left in the soil for microbes to use, which resulted in decreased microbial respiration per unit biomass and, hence, decreased microbial decomposition and increased ecosystem carbon accumulation.

King *et al*. (2001) grew $O_3$-sensitive and $O_3$-tolerant aspen (*Populus tremuloides* Michx.) clones alone and in mixed stands of paper birch (*Betula papyrifera* Marsh.) for two years in 30m-diameter free-air $CO_2$ enrichment (FACE) plots in Rhinelander, Wisconsin, which they maintained at $CO_2$ concentrations of 360 and 560 ppm with and without exposure to elevated $O_3$ (1.5 times ambient concentrations), to study the interactive effects of these parameters on fine-root production and belowground carbon cycling in the soils associated with these stands. They found the elevated $CO_2$ significantly enhanced the production of fine root biomass by 133 and 83% for aspen and aspen-birch mixed stands, respectively. In contrast, elevated $O_3$ had no effect on fine-root biomass, but simultaneous exposure to elevated $O_3$ and $CO_2$ increased fine-root biomass by approximately 66% for both types of stands. And when averaged across both stands, elevated $CO_2$ also increased dead root biomass by 140%, but another example of elevated $CO_2$ increasing carbon inputs to soils.

In August 1996, Andrews and Schlesinger (2001) and a number of other researchers established circular FACE plots (30 meters in diameter) that they exposed to air of either 360 or 560 ppm $CO_2$. This modest increase in the air's $CO_2$ content increased the weathering rate of parent rock material, as indicated by a 271% increase in soil mineral cation concentration and a 162% increase in soil alkalinity after the second year of $CO_2$ enrichment. In addition, the elevated $CO_2$ increased the flux of dissolved inorganic carbon compounds to the groundwater by 33%. Extrapolating this phenomenon to the global land area covered by forests, the two researchers remark the observed increase in the efflux of dissolved inorganic carbon compounds to groundwater "may act to buffer the rate of $CO_2$ increase in the atmosphere over geologic time periods."

Working in the same plots at the same time, Pritchard *et al*. (2001) studied the effects of elevated $CO_2$ on belowground root dynamics as assessed by mini-rhizotrons inserted into the low-nutrient (nitrogen and phosphorus) soils of the experimental plots. After one year of treatment, they report total standing root length and root numbers per minirhizotron were 16 and 34% greater, respectively, in the $CO_2$-enriched plots than in the ambient-air plots. In addition, the elevated $CO_2$ increased the diameter of living and dead roots by 8 and 6%, respectively, and annual root production and root mortality were 26 and 46% greater in the $CO_2$-enriched plots than in the control plots. All of these phenomena would be expected to result in enhanced carbon sequestration in the soils in which the trees were rooted.

In another contemporaneous paper, Cardon *et al*. (2001) write, "soil organic carbon (SOC) is the largest reservoir of organic carbon in the terrestrial biosphere." They affirm this in introducing their experimental study of the potential effects of the ongoing rise in the air's $CO_2$ content on this vast store of material, which was once the "C" in the $CO_2$ of much of Earth's atmosphere, where it was freely wafted about prior to being assimilated by plants and sequestered in the soil.

Occupying such a pivotal position as it does in the planetary carbon cycle, SOC is of great interest to scientists who worry about its stability. Among other things, Cardon *et al*. wanted to know whether allowing more $CO_2$ to be emitted to the atmosphere would lead to even more carbon being sequestered in the soil (a logical hypothesis), or if it would somehow cause a reduction in what was already there (a less logical hypothesis but one that cannot be ignored).

Cardon *et al*. studied soil carbon income and outgo in a number of small microcosms of two annual $C_3$ grassland communities (sandstone and serpentine) of contrived high and low soil-nutrient availability maintained out-of-doors in open-top chambers at the Jasper Ridge Biological Preserve in Stanford, California, from October 1994 through August 1996. Key to their study was the utilization of isotopic tracer techniques to determine the sizes of the various SOC pools through time. They grew the $C_3$ plants in a soil obtained from a $C_4$ grassland in Colorado, which ensured that the original organic carbon of their experimental soil would have a different isotopic signature from the organic carbon that would be injected into it by the $C_3$ plants that grew upon it. In addition, the carbon of the fossil fuel-derived $CO_2$ supplied to the $CO_2$-enriched chambers had yet a third unique isotopic signature.

They found the extra $CO_2$ supplied to half of the mini-ecosystems increased the total root biomass in the serpentine grassland microcosms by a factor of three in both high and low soil-nutrient availability treatments, and it increased total root biomass in the sandstone grassland microcosms by a factor of four in both the high and low soil-nutrient availability treatments. Thus there was a tremendous $CO_2$-induced increase in the amount of organic material that eventually would become available for incorporation into the soils of both grassland microcosms.

With so much new organic matter being added to the soils of the $CO_2$-erniched microcosms, Cardon *et al.* hypothesized previously carbon-limited microbes in these soils would alter their survival strategy and turn from breaking down older, more recalcitrant soil organic matter to attack the more abundant and labile rhizodeposits being laid down in the newly carbon-rich soils of the $CO_2$-enriched microcosms. This rhizodeposition, as they christened it, consists of "all deposition of organic carbon from living root systems to soils, including compounds lost through root exudation, sloughing of dead cells during root growth, and fine root turnover," which, as noted above, was dramatically enhanced by atmospheric $CO_2$ enrichment.

The upshot of this scenario—which seems thoroughly vindicated in light of the observations about to be described—is that the experimentally imposed increase in atmospheric $CO_2$ concentration actually retarded the decomposition of the older SOC of the imported soil. Also, this phenomenon effectively increased the turnover time of the original SOC, significantly increasing its stability.

"If this reduction in breakdown of older SOC is sustained," write Cardon *et al.*, "an increased retention of carbon in older SOC pools might be expected under elevated relative to ambient $CO_2$." Therefore, not only does atmospheric $CO_2$ enrichment lead to higher rates of carbon input to soils, it likely also leads to slower rates of carbon withdrawal from them. That allows ever-more carbon to be locked away in Earth's soil bank as the air's $CO_2$ content rises. And that phenomenon appears to keep the air's rate of $CO_2$ rise from accelerating too greatly, even in the face of yearly increases in anthropogenic $CO_2$ emissions.

Since biological activity generally increases with rising temperatures—especially when the initial temperature is below the freezing point of water—it might be reasoned global warming would enhance rates of soil microbial respiration, leading to increases in the soil-to-air flux of $CO_2$. However, as Neilsen *et al.* (2001) noted, "over-winter processes account for a significant portion (20–70%) of annual ecosystem carbon and nitrogen cycling and soil-atmosphere trace gas fluxes." Therefore, it was not immediately apparent what the ultimate consequences of warming-induced reductions in the frequency and severity of freezing would be.

To find the answer, Neilsen *et al.* collected samples of soil from a northern hardwood-dominated forest in New Hampshire, USA. These samples, from nearly pure stands of sugar maple (*Acer saccharum* Marshall) and yellow birch (*Betula alleghaniensis* Britton), were placed in small vessels and either maintained at the normal laboratory temperature of 20–25°C or subjected to mild and severe freezes of -3 and -13°C, respectively, for ten days, after which all samples were kept at the normal laboratory temperature for 23 additional days. Neilsen *et al.* measured the evolution of $CO_2$ from the soils at the beginning and end of the full 33-day period, as well as at three other times during the course of the experiment.

They found freezing had a significant effect on $CO_2$ evolution from the soils. Cumulative 33-day totals of respiration (in units of mg carbon per kg of soil) for the soil samples taken from the maple stand were 1,497, 2,120, and 3,882 for the control and -3 and -13°C temperature treatments, respectively, which represent carbon loss enhancements (relative to the control) of 42 and 159% for the -3 and -13°C treatments, respectively, an increased carbon loss of 13 ± 1% for each degree C below freezing. For the soil samples taken from the birch stand, the corresponding respiration numbers were 1,734, 2,866, and 5,063, representing carbon loss enhancements of 65 and 192% for the -3 and -13°C treatments, respectively, or an increased carbon loss of 18 ± 3% for each degree C below freezing.

It can be readily appreciated how these research results relate to the subject of global warming effects on soil carbon sequestration. As temperatures gradually warm over the course of many years and climate zones move poleward in latitude and upward in elevation, regions that experienced many hard freezes in the past will experience fewer of them in the future, and other regions will undergo a shift from hard freezes to mild freezes. Still other regions that experienced mild freezes in the past will experience fewer—or none—in the future. And in all of these situations, together with every permutation that falls somewhere between them, there will be a tendency for less carbon to be released to the atmosphere, which means more will remain sequestered in the soil.

The great deserts of Africa and Asia have a huge potential for sequestering carbon, because they are currently so barren their soil carbon contents have essentially nowhere to go but up. The problem with this scenario, however, is that their soils blow away with every wisp of wind that disturbs their surfaces. The ongoing rise in the air's $CO_2$ content could do much to reverse this trend. At higher atmospheric $CO_2$ concentrations, nearly all plants are more efficient at utilizing water (Morison, 1985). Hence, as the air's $CO_2$ content rises, the vegetation that rings Earth's deserts should be able to encroach upon them and more effectively protect their surfaces from the ravages of wind, thereby reducing soil and carbon losses due to erosion. Also, rising atmospheric $CO_2$ concentrations should increase the stability of surface soil crusts held together by lichens and/or algae (Tuba *et al*., 1998; Brostoff *et al*., 2002), which also should help to reduce the deleterious effects of wind erosion (Evans and Johansen, 1999). In addition, many of the algal components of desert soil crusts are nitrogen-fixers (Evans and Belnap, 1999), and their $CO_2$-enhanced presence should lead to more nitrogen being made available to other plants, which should accelerate the development of soil-protecting ecosystems even more.

The end result of all these phenomena working together is greater carbon storage, both above- and below-ground, in what was previously little more than a source of dust for the rest of the world. And therein lies one of the great unanticipated benefits of the $CO_2$-induced greening of the globe's deserts: less airborne dust to spread havoc across Earth.

To better understand this phenomenon, it is helpful to refer to an article in the *American Scientist* magazine titled "The Global Transport of Dust." Griffin *et al*. (2002) began their essay with a description of the magnitude of soil materials wafted about by the wind. "By some estimates," they write, "as much as two billion metric tons of dust are lifted into the Earth's atmosphere every year." Riding along on those particles are "pollutants such as herbicides and pesticides and a significant number of micro-organisms—bacteria, viruses and fungi." The four scientists calculate there are easily enough bacteria thus moved about the planet each year "to form a microbial bridge between Earth and Jupiter."

And although it does not traverse interplanetary space, dust from Africa and Asia does cross both the Atlantic and Pacific Oceans. Griffin *et al*. report, for example, dust storms originating in North Africa "routinely affect the air quality in Europe and the Middle East" and millions of tons of African sediment "fall on the North Amazon Basin of South America every year." Likewise, Prospero (2001) notes everyone in the United States living east of the Mississippi River is affected by dust of African origin. And in April 2001, Griffin *et al*. report, a large dust cloud originating over the Gobi Desert of China "moved eastward across the globe, crossing Korea, Japan, the Pacific (in five days), North America (causing sporadic reports of poor air quality in the United States), the Atlantic Ocean and then Europe."

Many of the biological entities associated with the dust particles that are thus dispersed about the planet have serious consequences for plants, animals, and humans. Airborne fungi from Africa that frequently make their way to the Americas, for example, cause sugar cane rust, coffee rust, and banana leaf spot. Griffin *et al*. also describe how the scourge of Caribbean sea fans—*Aspergillus sydowii*—"is also found in the Caribbean atmosphere during African dust events," noting the region's "sea fans and other coral reef organisms have experienced a steady decline since the late 1970s," when worsening drought in Africa predisposed increasing amounts of soil there to wind erosion (Prospero, 2001). They also state they expect "future research will show that many other coral diseases are spread by dust from both Africa and Asia."

As to human health effects, Griffin *et al*. note "African dust is reported to be a vector for the meningococcal meningitis pathogen *Neisseria meningitis* in sub-Saharan Africa," and outbreaks of the disease often followed localized or regional dust events that resulted in many fatalities. They also report a 17-fold increase in the incidence of asthma on the island of Barbados since 1973, "which corresponds to the period when the quantities of African dust in the region started to increase."

Because the dust clouds that reach the Americas from Africa and Asia have traveled such long distances, most of the larger particles they originally contained generally fall out along the way. The particles that remain, therefore, are typically very small—so small, in fact, that Griffin *et al*. report, "once they are inhaled into the lungs they cannot be exhaled." What makes this situation especially serious is the tiny dust particles typically are heavily coated with iron, and a substantial fraction of that iron is released to the lung tissue when the particles are deposited there. And iron, as Prospero notes, is "particularly efficient in producing an inflammatory response in the lungs."

In light of these observations, it is clear the slow but steady acceleration of carbon sequestration in the deserts of Africa and Asia, which is being provided by the ongoing rise in the air's $CO_2$ content, is producing more than just local benefits. Plants and animals far and wide, on land and in the sea, together with people everywhere, will ultimately benefit, if they are not already doing so, from the reduced airborne-dispersal of pathogens responsible for many debilitating diseases, as source-region soils become better protected against the erosive power of the wind. And if natural carbon sequestration tendencies can bring about these ancillary benefits, so too can those of man. Consequently, citizens involved in local carbon sequestration projects can take satisfaction their efforts are having a positive impact on the global environment in more ways than one. Even if rising concentrations of atmospheric $CO_2$ have no substantial impact on the world's climate, there are many other reasons to be involved in projects designed to enhance the productivity of the planet's managed and natural ecosystems, not the least of which is the reduction of airborne dust caused by wind-induced soil erosion.

Moving from desert to tropical isle, Dilustro *et al.* (2002) note soils store approximately three times more carbon than plants do, but almost all of that carbon is transferred to the soil through plants. They also note plant root responses to elevated $CO_2$ have been largely overlooked in this regard, and they thus conclude some of the carbon missing from current global carbon cycle models may be sequestered belowground. Intrigued by the possibility that enhanced carbon transfer to soils via plants responding to the aerial fertilization effect of atmospheric $CO_2$ enrichment may account for much of the carbon that exits the atmosphere each year, the four researchers designed an experiment to provide some potential answers to this important question.

On a small barrier island in the northern part of the Kennedy Space Center, Florida, USA, the group of scientists erected 16 open-top chambers around clumps of evergreen scrub oaks and associated saw palmetto shrubs that comprised a fire-adapted ecosystem that historically had been maintained by natural fire cycles of 10- to 15-year intervals, which had last been burned in February 1996, just prior to the start of their experiment. They maintained half of the chambers at the $CO_2$ concentration of the ambient air, and the other half—starting on 15 May 1996—at $CO_2$ concentrations approximately 350 ppm above ambient. In addition, in the soils of each of the 16 chambers, the scientists inserted two mini-rhizotron tubes to a depth of 101 cm, through which they viewed the growth and development of the ecosystem's fine-roots at three-month intervals, from March 1996 to December 1997, via tiny video camera systems.

Dilustro *et al.* write "our hypothesis that elevated atmospheric $CO_2$ would increase fine-root density, productivity, mortality and turnover was demonstrated." By the end of the 21-month study period, the fine-root length density of the re-sprouting trees and shrubs in the ambient-air chambers had attained a mean of 7.53 mm $cm^{-2}$ in the top 101 cm of soil, and the re-sprouting plants in the $CO_2$-enriched chambers had attained a mean of 21.36 mm $cm^{-2}$, indicating a $CO_2$-induced increase of 184% in this important root property. Concomitantly, there was also a 55% increase in ecosystem aboveground biomass, and all this happened, the scientists note, "despite water and nutrient limited conditions."

Dilustro *et al.* state "the increased rates of fine root growth coupled with no change in decomposition rate suggest a potential increased rate of carbon input into the soil." Furthermore, their detailed fine-root data for June 1997 indicate a mean $CO_2$-induced increase in fine-root length density of approximately 75% in the top three-fourths of the soil profile, and an increase on the order of 125% in the bottom quarter. Hence, there are strong indications the bottom layer of soil was being supplied with a greater proportion of extra carbon than were the upper soil layers.

Ritchie and McCarty (2003) write, "recent studies indicate that soil erosion and redeposition may establish an ecosystem disequilibrium that will promote carbon sequestration in the biosphere (Stallard, 1998; Harden *et al.*, 1999)." In this scenario, they continue, "soil erosion on the uplands moves soil carbon to deposition sites on the landscape and promotes soil carbon replacement at the eroded sites from the production of vegetative biomass." Often, these deposition sites are riparian systems with high net primary productivity, which also leads to increased onsite storage of carbon. As to the validity of these concepts, Ritchie and McCarty note "the capacity of riparian and flood plain systems to capture sediments has been documented (Ritchie *et al.*, 1975; Walling *et al.*, 1999) as well as the ability of these systems to store carbon has been documented (Lal *et al.*, 1998)."

The two researchers collected and analyzed for carbon content profiles of soils obtained from an upland area and adjacent riparian system into which the upland area drained. Results indicated the riparian system acted as a filter, removing eroded soil materials from the overland flow before they reached the stream that drained the area, so that soil carbon content was significantly greater in the riparian soils than in the upland soils. Ritchie and McCarty report carbon storage in the riparian soils was 3.8 times greater than in the upland soils in the upper 20 cm of the soil profile and 4.7 times greater in the upper 30 cm, and they report the earlier work of Ritchie and McCarty (2001) suggests "there may be as much as 10–15 times more carbon in the total profile (0–200 cm) of the riparian soils." These results put a bright new face on what was long believed to be a phenomenon of no virtue whatsoever—precipitation-driven soil erosion. In addition, they provide a new reason for protecting Earth's wetlands: preserving an important sink for atmospheric $CO_2$.

Working concurrently, Jongmans *et al.* (2003) carried out a micro-morphological study of structural development and organic matter distribution in two calcareous marine loam soils on which pear trees had been grown for the prior 45 years. The soil of one of these Dutch orchards exhibited little or no earthworm activity, and the soil of the other orchard exhibited high earthworm activity, a difference resulting from different levels of heavy metal contamination of the soils of the two orchards due to the prior use of different amounts of fungicides.

The absence of earthworms in the first orchard led to topsoil compaction, restricted litter incorporation into the mineral portion of the soil, less fragmentation of particulate organic matter, and restricted mixing of organic matter with the mineral soil's clay fraction. Furthermore, without earthworms there were no earthworm casts, and the five researchers point out "the rate of organic matter decomposition can be decreased in worm casts compared to bulk soil aggregates," citing Martin (1991) and Haynes and Fraser (1998).

Thus, based on their own findings and others, Jongmans *et al.* conclude "earthworms play an important role in the intimate mixing of organic residues and fine mineral soil particles and the formation of organic matter-rich micro-aggregates and can, therefore, contribute to physical protection of organic matter, thereby slowing down organic matter turnover and increasing the soil's potential for carbon sequestration." These points take on added significance when we consider elevated levels of atmospheric $CO_2$ tend to increase earthworm populations and activities, as has been demonstrated by Zaller and Arnone (1997, 1999). Thus, the ongoing rise in the air's $CO_2$ content likely will help more of the extra organic matter that is produced under $CO_2$-enriched conditions to remain in the soil even longer than it otherwise would remain due to the organic-matter-conserving nature of the increased activities of the increased earthworm populations shown to occur as a consequence of increases in the atmosphere's $CO_2$ concentration.

Prior *et al.* (2004) speculate "enhanced aboveground crop growth under elevated $CO_2$, leading to more soil surface residue and greater percent ground cover (Prior *et al.*, 1997) coupled with positive shifts in crop root systems (Prior *et al.*, 2003), may have the potential to alter soil structural characteristics." To see whether this inference was correct, and if it was, to see whether elevated atmospheric $CO_2$ concentrations tend to enhance or degrade soil physical properties, Prior *et al.* grew soybean (*Glycine max* (L.) Merr. cv. Stonewall) and sorghum (*Sorghum bicolor* (L.) Moench cv. Savanna 5) plants from seed to maturity for five consecutive growing seasons in open-top chambers maintained at atmospheric $CO_2$ concentrations of either 360 or 720 ppm. The soil in which the plants grew had been fallow for more than 25 years prior to the start of the study and was located in a huge outdoor bin, where at the end of each growing season aboveground non-yield residues (stalks, soybean pod hulls, and sorghum chaff), including 10% (by weight) of the grain yield, were allowed to remain on the surfaces of the plots to simulate no-tillage farming, after which measurements of soil properties made at the beginning of the experiment were compared with similar measurements made at its conclusion.

The elevated $CO_2$ had no effect on soil bulk density in the sorghum plot, but lowered it in the soybean plot by approximately 5%. The elevated $CO_2$ also had no effect on soil saturated hydraulic conductivity in the sorghum plot, but increased it in the soybean plot by about 42%. Soil aggregate stability was increased in both plots, but by a greater amount in the soybean plot, and total soil carbon content was increased by 16% in the sorghum plot and 29% in the soybean plot. Consequently, the soils of both plots experienced some improvements in response to the experimental doubling of the air's $CO_2$ content, although there were more and greater improvements in the soybean plot than in the sorghum plot. Prior *et al.* conclude their findings indicate a significant "potential for improvements in soil carbon storage, water infiltration and soil water retention, and reduced erosion," valuable positive consequences they describe as "$CO_2$-induced benefits."

Krull *et al.* (2005) report "colonization of grasslands or savannas by trees over the last 50–100 years, often described as 'thickening,' has received attention due to the large potential for carbon sequestration in woody biomass." It was a hot topic because many studies have attributed thickening to "the increase in atmospheric $CO_2$, causing $CO_2$ fertilization and resulting in increased water use efficiency in $C_3$ plants," as discussed by Berry and Roderick (2002) and Grunzweig *et al.* (2003). In addition, they write, "much of the change in atmospheric $CO_2$ occurred over the last 50 years [1953–2003 = 64 ppm] with the most significant changes being in the last 20 years [1983–2003 = 33 ppm]."

Working at a site some 40 km northwest of Longreach, Queensland, Australia, Krull *et al.* measured vertical profiles of $\delta^{13}C$ and $^{14}C$ of bulk and size-separated soil organic matter to infer the time course of changes in these parameters along a transect spanning the dynamic transition zone between $C_4$-dominated grassland and $C_3$-dominated woodland, an ecotone that comprised different-age specimens of leguminous gidyea trees (*Acacia cambagei*) interspersed with occasional whitewood trees (*Atalaya hemiglauca*). Then, since the longtime landholder reported thickening by the Acacia trees occurred "at least since the 1950s," they tested whether the observed changes in soil carbon stocks could be reproduced by the Roth-Carbon turnover model over a 50-year time period.

The eight researchers conclude "much of the vegetation change at this site occurred over the last 50 years." In addition, they found approximately twice as much total organic carbon in the soil beneath the fully established woodland as in the soil beneath the pristine grassland. They conclude their findings "stress the importance of viewing soils as dynamic systems and indicating the potential for soil organic carbon sequestration in grazed semi-arid woodlands." Such land use represents a form of agroforestry, the virtues of which were touted by Mutuo *et al.* (2005).

Also, the findings of Krull *et al.* suggest the operation of an important negative feedback that can slow the rate-of-rise of the air's $CO_2$ content. The ongoing enrichment of the air with $CO_2$ from the burning of fossil fuels enables woody species to colonize less-productive grasslands more readily and thereby extract greater amounts of $CO_2$ from the atmosphere, meanwhile providing many benefits to the soil in which the trees are rooted.

Parenthetically, it is important to note papers published in journals such as *Science* and *Nature* typically attract much attention, especially when they deal with high-profile subjects such as global warming, which some have described as a threat worse than nuclear warfare or global terrorism. When a study describes a phenomenon that could exacerbate that threat, it behooves its authors and the editors of the journal in which it is published to be especially careful in the way they describe what was found and what its implications may be.

A case in point is the report of Heath *et al.* (2005), who studied soil sequestration of root-derived carbon from seedlings of six European tree species and found it to decline in response to atmospheric $CO_2$ enrichment. This finding led them to write, "should similar processes operate in forest ecosystems, the size of the annual terrestrial carbon sink may be substantially reduced, resulting in a positive feedback on the rate of increase in atmospheric carbon dioxide concentration." This outcome was parroted by the journal's editors, who state the new findings "raise the possibility that the future rise in atmospheric $CO_2$ concentrations could be higher than expected."

How reasonable are these speculations? To answer this question, it is important to know how closely—or not—the experimental setting of Heath *et al.*'s study reproduced real-world forests or orchards. Was their study a FACE experiment, such as that conducted in the Duke University Forest, where multiple 30m-diameter plots of initially 13-year-old loblolly pine trees had been exposed continuously to ambient and elevated concentrations of atmospheric $CO_2$ each growing season since August 1996? Or was it an out-of-doors open-top chamber study, such as the Phoenix, Arizona sour orange tree experiment, where trees were grown from the sapling stage to mature adults for 17 years of continuous $CO_2$ enrichment? It was in fact neither of these.

The Heath *et al.* experiment was only a 15-month study conducted in small greenhouses, where seedlings were grown in vertical sections of 16cm-diameter polyethylene tubes supplied with only 10 liters of soil, and their results are not consistent with more comprehensive experiments such as the Duke University FACE experiment. To their credit, Heath *et al.* readily acknowledge the many deficiencies of their study. They state, for example, "young trees, grown in mesocosms in a semi-controlled environment and protected from major herbivores, may respond differently from mature trees growing in a natural forest." They also note their experiment "ran for only two growing seasons" and "the input of leaf litter to the soil was excluded." With respect to these latter two points, they also state "the possibility that longer term increased inputs of leaf litter under elevated $CO_2$ could counteract the effect on the sequestration of root-derived carbon cannot be ruled out." And they admit, "although soil microbial respiration increased under elevated $CO_2$, the effect of this on the decomposition of native soil carbon is not known."

That these deficiencies likely precluded the discovery of the truth sought by Heath *et al.* in their experiment is revealed by their acknowledgment, "in contrast to our experiment, $CO_2$ enrichment caused an increase in soil carbon sequestration beneath *Betula* seedlings over the course of one growing season (Ineson *et al.*, 1996)," and "free-air $CO_2$ enrichment (FACE) also caused an increase in the sequestration of new carbon in $C_4$ soil cores transplanted into former agricultural ground beneath 2- to 3-year-old *Populus* saplings (Hoosbeek *et al.*, 2004)." Consequently, and after reviewing the results of still other pertinent experiments, they ultimately conclude "there is insufficient evidence to predict with certainty whether plant responses to elevated $CO_2$ will result in increased or decreased sequestration of new carbon in the soils of forest ecosystems."

In light of these observations, which were made in Heath *et al.*'s own paper and which suggest there is no compelling reason to conclude their results bear any resemblance to what will actually occur in the real world as the air's $CO_2$ content climbs, one wonders why their paper was accepted for publication in so prestigious a journal as *Science*. It seems all too likely it was not for scientific reasons at all but more likely for the support the paper could be seen as providing for the political views of the journal's editor, who strongly supported Kyoto-type regulations of anthropogenic $CO_2$ emissions.

In a contemporary study suffering from some of the same problems as Heath *et al.*, Bellamy *et al.* (2005) measured soil carbon contents at 2,179 locations across England and Wales between 1994 and 2003, adjacent to points where similar measurements had been made between 1978 and 1983, after which rates of change of soil carbon content were calculated for the quarter-century period 1978–2003. They report "carbon was lost from soils across England and Wales over the survey period at a mean rate of 0.6% $yr^{-1}$," which they attribute to "climate change," noting over the period of study "the mean temperature across England and Wales increased by about 0.5°C."

Bellamy *et al.* thus conclude, "losses of soil carbon in the UK, and by inference in other temperate regions, are likely to have been offsetting absorption by terrestrial sinks." Associated Press writer Michael McDonough begins his review of the study (7 September 2005) by stating, "rising temperatures resulting from climate change are likely causing soil in England and Wales to lose large amounts of carbon, possibly further contributing to the greenhouse gas effect." These conclusions are not as well supported as they were portrayed to be.

Bellamy *et al.* resampled only 38.5% of the original sites sampled between 1978 and 1983, so the vast majority of England and Wales, much less "other temperate regions" of the globe, was not assessed for changes in soil organic carbon (SOC) content. In addition, the five researchers claim "the relationship between rate of carbon loss and carbon content is irrespective of land use," which was key to their being able to claim "a link to climate change." However, in an accompanying article that raised several other concerns, Schulze and Freibauer (2005) write, in "re-inspecting the results, we think that the land-use factor has played a role—for example, only alteration in land use and gradual changes in land management can explain why croplands lost more carbon than other areas." They also note studies conducted in China, Finland, and Flanders "attribute most of the SOC loss to changes in land use and management." Even Bellamy *et al.* admit "various changes in land use will have contributed to carbon losses from soils across England and Wales over the survey period, both under agricultural uses (drainage schemes, post-war grassland conversion, increased stocking rates) and non-agricultural uses (afforestation on wet soils, increased erosion, increased burning of upland vegetation)." However, they state they did "not have sufficient data at the scale of the National Soil Inventory to explore these effects," so they really did *not* know the role played by land use, which meant they really did not know the role played by climate change.

Schulze and Friebauer also note the SOC losses observed by Bellamy *et al.* "occurred independently of soil properties, challenging our knowledge about SOC stability," as this observation was at odds with what had been learned about the subject over the years. They also point out the carbon losses were proportional to SOC concentration, which implies "a first-order decay of a homogeneous pool" which "contradicts the view that SOC in carbon-rich soils contains a higher fraction of stable carbon than does that in carbon-poor soils."

Finally, Schulze and Friebauer note SOC contents may have changed in deeper soil layers than the top 15 cm layer measured by Bellamy *et al.*, possibly in compensating ways, and they are firm in their opinion "increased temperature alone seems to be too weak a driver" to have caused the observed changes in SOC. Thus, Bellamy *et al.* merely scratched the surface of the controversial topic in a way that failed to reveal the truth.

Callesen *et al.* (2003) measured SOC contents of forest floors and mineral soils to a depth of 100 cm in 234 well-drained Danish, Finnish, Norwegian, and Swedish forests between latitudes 55° and 68°N and longitudes 6° and 28°E. They then performed a number of analyses with the data, the first of which they say revealed "soil organic carbon in forest floors and mineral soil + forest floors was positively correlated with temperature and precipitation in the study region." They also report "a similar increase in SOC with temperature and precipitation was found in nine pine stands on sandy soils in the same latitude range but between 22° and 29°E (Vucetich *et al.*, 2000) representing the same temperature gradient but a lower precipitation range." And they affirm the positive correlation with temperature was greatest for coarse-textured soils, less for medium-textured soils, and negligible for fine-textured soils.

The Nordic scientists write, "the increase in SOC with temperature and precipitation is interpreted as an indirect effect of higher net primary production," further noting in Europe "increasing site productivity has been reported in both nemoral forests and in boreal forests at higher latitudes (Eriksson and Karlsson, 1996; Skovsgaard and Henriksen, 1996; Cannell *et al.*, 1998)," and this increase "could be attributed to increased atmospheric $CO_2$ concentrations along with the fertilizer effect of nitrogen deposition, and management regimes optimizing forest production." These broad-based findings suggest just the opposite of what Bellamy *et al.* had claimed to be occurring in the top 15 cm of soils in England and Wales had actually been happening in the top 100 cm of soils throughout much of Europe, producing a negative feedback to both rising air temperatures and atmospheric $CO_2$ concentrations.

Lichter *et al.* (2005) reviewed what had been learned to that point in time about the effects of an atmospheric $CO_2$ enrichment of 200 ppm on the soil carbon dynamics of the Duke Forest (an aggrading loblolly pine stand near Chapel Hill, North Carolina, USA) during the first six years of the long-term FACE experiment being conducted there. Over this period, they report, organic C accumulated in the forest floor of the elevated $CO_2$ plots at a rate 52 ± 16 g C $m^{-2}$ $yr^{-1}$ greater than what would have been expected during reforestation under ambient $CO_2$ conditions, as represented by the rate of C accumulation in the forest floor of the ambient $CO_2$ plots.

This additional C sink, in their words, "resulted from increased C inputs of 50 ± 30 g C $m^{-2}$ $yr^{-1}$ to the forest floor in response to $CO_2$ enhancement of primary production." And since there was "no evidence that the overall rate of decomposition of the forest floor decreased under the elevated $CO_2$ treatment," they conclude "the additional C sink in the forest floor of the elevated $CO_2$ treatment ... is wholly dependent on the net primary production enhancement and increased C inputs," which after six years had increased the forest floor's organic C content by approximately 27%, as best as could be determined from their plotted data. The data gave no indication this trend will decline anytime soon.

With respect to the underlying mineral soil, Lichter *et al.* report they detected no statistically significant treatment effects on the C content of the bulk mineral soil or the intra-aggregate particulate organic matter and mineral-associated organic matter fractions after six years of $CO_2$ enrichment. Nevertheless, there was a nearly statistically significant ($P = 0.11$) increase of 18.5% in the free light fraction of the organic matter in the top 15 cm of the soil profile, and a 3.9% increase in the total intra-aggregate particulate organic matter there. The sum of the organic C in these two categories plus the mineral-associated organic C was 11.5% greater in the $CO_2$-enriched plots than in the ambient treatment plots.

Although Lichter *et al.* expressed pessimism and a belief "forest soils are unlikely to sequester significant additional quantities of atmospheric C associated with $CO_2$ fertilization because of the low rates of C input to refractory and protected soil organic matter pools," the $CO_2$-enriched trees of their study continued to demonstrate a large and unabated growth advantage over the ambient-$CO_2$ trees, and both the forest floor and the surface soil horizon beneath the $CO_2$-enriched trees continued to accumulate more organic C than the forest floor and surface soil horizon beneath the ambient-$CO_2$ trees. And, therefore, the un-stimulated refractory and protected soil organic matter pools of which Lichter *et al.* write could yet begin to show increased carbon accumulation.

In addition to the naturally occurring phenomena that tend to mute the rate of rise of the anthropogenic-driven increase in the atmosphere's $CO_2$ concentration, there are others that owe their existence to human ingenuity. Prior *et al*. (2005) describe a multifaceted field management system developed to help farmers conserve resources and increase crop yields while simultaneously stimulating carbon sequestration in their fields.

Unlike a conventional cropping system, this conservation system employed little to no tillage and used special crop rotations. In the southern United States, where Prior *et al*. had been testing the two approaches for the prior five years, the conventional cropping system consisted of a rotation cycle where grain sorghum and soybean were rotated each year with spring tillage after winter fallow that produced only a light growth of weeds. In the conservation cropping system, grain sorghum and soybean were also rotated, but in the place of weeds were three cover crops: crimson clover, sunn hemp, and wheat, which were similarly rotated but without tillage.

To see how the two management systems compared in terms of crop production and soil carbon sequestration, and how well they might fare in the high-$CO_2$ world expected to prevail a half-century or so from now, the five U.S. Department of Agriculture scientists employed the systems for four years (two complete cropping cycles) in 7-meter-wide x 76-meter-long x 2-meter-deep bins filled with a silt loam soil, upon which they constructed a number of clear-plastic-wall open-top chambers they maintained at atmospheric $CO_2$ concentrations that averaged either 375 ppm (ambient) or 683 ppm (enriched) over the four years of their study.

In terms of the cumulative residue produced over the two cropping cycles, the scientists found little interaction between management practices and atmospheric $CO_2$ concentration, with conservation practices increasing this parameter by about 90% in both $CO_2$ treatments, elevated $CO_2$ increasing it by approximately 30% in both of the management treatments, and conservation practices and elevated $CO_2$ together increasing it by 150%. In terms of the carbon retained and incorporated into the first 5 cm of the soil at the end of the two cropping cycles, however, there were significant interactions. The elevated $CO_2$ increased this important soil property by about 10% in the conventional system, but by 45% in the conservation system, and the application of conservation practices increased 0–5 cm soil carbon storage by close to 45% in ambient-$CO_2$ air but by nearly 90% in elevated-$CO_2$ air. Together, the two treatments increased surface soil carbon storage by close to 110%.

Clearly, increasing atmospheric $CO_2$ concentrations and best-management conservation practices work hand-in-hand to boost crop yields and residue production while increasing soil carbon storage, with each factor bringing out the best in the other. In addition, as Prior *et al*. note, "in an elevated $CO_2$ environment there will be larger amounts of crop residue and consequently more ground cover," so "accumulation of additional surface litter may improve water infiltration (and storage) and help ameliorate water quality problems by reducing runoff and soil erosion."

Jastrow *et al*. (2005) write many field-scale $CO_2$-enrichment studies "have failed to detect significant changes in soil C against the relatively large, spatially heterogeneous pool of existing soil organic matter, leading to the general conclusion that the potential for increased soil C is limited (Hungate *et al*., 1997; Gill *et al*., 2002; Hagedorn *et al*., 2003; Lichter *et al*., 2005)." And an additional long-held opinion, as they relate it, is, "if $CO_2$-stimulated increases in soil organic C do occur, they will be allocated to rapidly cycling, labile pools with little, if any, long-term stabilization," citing Hungate *et al*. (1997) and Lichter *et al*. (2005). By the time of Jastrow *et al*.'s writing, however, after many long and arduous experiments had been conducted and their data properly analyzed, the truth was beginning to be seen to be quite different.

The long-awaited confirmation of the more optimistic view of the subject was firmly established by Jastrow *et al*. (2005). They describe and further analyze the findings of the first five years of the deciduous forest FACE study being conducted at Oak Ridge, Tennessee (Norby *et al*., 2001); the entire eight years of the prairie grassland open-top chamber study at Manhattan, Kansas (Owensby *et al*., 1993); and 35 other similar studies.

They found atmospheric $CO_2$ enrichment to approximately 200 ppm above ambient "increased C stocks in the forest soil at an average rate of 44 ± 9 g C $m^{-2}$ $yr^{-1}$," and "in the prairie, the incremental increase in C stocks corresponded to an average accrual rate of 59 ± 19 g C $m^{-2}$ $yr^{-1}$." This happened because "both systems responded to $CO_2$ enrichment with large increases in root production," and "even though native C stocks were relatively large, over half of the accrued C at both sites was incorporated into micro-aggregates, which protect C and increase its longevity." Likewise, their meta-analysis of the 35 independent experimental observations indicated $CO_2$ enrichment ranging from 200 to 350 ppm over periods ranging from two to nine years increased soil C over soil depths ranging from 5 to 20 cm by 5.6%

(95% CI = 2.8–8.4%), "supporting the generality of the accrual measured in the forest and prairie experiments."

The seven scientists say their findings "clearly demonstrate that mineral soil C, including micro-aggregate protected pools, can increase measurably in response to a step-function increase in atmospheric $CO_2$ concentrations," and "the C storage capacities of mineral soils—even those with large organic matter stocks—are not necessarily saturated at present and may be capable of serving as C sinks if inputs increase as a result of passive $CO_2$ fertilization." In addition, they write "the meta-analysis, which included some multifactor studies and data collected over a wide range of climatic conditions, suggests that soil C accrual ... is likely to be a general response to $CO_2$ enrichment."

This response, Jastrow *et al.* state, "is not insignificant." They note, "if mineral soil C in the surface 20 cm of the world's temperate forests, temperate grasslands, shrublands, and croplands (234 Pg C ... according to Jobbagy and Jackson, 2000) were to increase by 5.6% or at a rate of 19 g C $m^{-2}$ $yr^{-1}$, then 8–13 Pg of C might be accumulated within a 10-year period." That suggests the amount of carbon found in the soils of these biomes could be doubled over a period of 180 years (234 Pg C divided by 1.3 Pg C per year = 180 years).

These several observations demonstrate the soil-carbon-sequestering capability of Earth's vegetation can indeed act as a significant brake on the rate of rise of the air's $CO_2$ content and thereby help mute any $CO_2$-induced impetus for global warming.

At the Sky Oaks $CO_2$ enrichment site of San Diego State University in California, located in chaparral vegetation dominated by chemise (*Adenostoma fasciulatum*) shrubs, researchers constructed 12 2-m by 2-m by 2-m closed chambers so as to contain a central individual *Adenostoma* shrub and its surrounding herbaceous plants. Beginning in December 1995, they maintained the chambers continuously at six atmospheric $CO_2$ concentrations ranging from 250 to 750 ppm in 100-ppm increments. At various times throughout 1999, they took measurements of net ecosystem exchange of $CO_2$ and collected soil samples for analyses of arbuscular mycorrhizal (AM) fungi and sequestered carbon found in both bulk soil and water-stable aggregates.

Treseder *et al.* (2003) report "plants and soils within the chambers took up more carbon under $CO_2$ enrichment." Specifically, the chambers exposed to 250 to 550 ppm $CO_2$ released an average of 703 g C $m^{-2}$ $year^{-1}$, and the chambers in the 650–750-ppm treatments absorbed an average of 160 g C $m^{-2}$ $year^{-1}$. Likely driven by these dramatic $CO_2$-induced differences in net ecosystem exchange of $CO_2$, it was not surprising, as they describe it, "pools of total carbon in bulk soil and in water-stable aggregates increased 1.5- and three-fold, respectively, between the 250- and 650-ppm treatments." In addition, they found "the abundance of live AM hyphae and spores rose markedly over the same range of $CO_2$." Thus Treseder *et al.* conclude the augmentation of the carbon pools found in their study, "if common in other ecosystems, appears substantial enough to influence sequestration of $CO_2$ originating from fossil fuel burning and deforestation."

In another study from the same location utilizing the identical experimental chambers, Allen *et al.* (2005) assessed the various ways carbon entered the soil and was sequestered there. They found the "total allocation of carbon to soil increased significantly through the study period with elevated $CO_2$," as did "new carbon inputs into macro-aggregates." This latter observation is very important, as these aggregates, in their words, "have increasing concentrations of glomalin, a glycoprotein produced by arbuscular mycorrhizal fungi (Rillig *et al.*, 1999)," a substance that acts to create and stabilize soil aggregates and protect the carbon they contain. In addition, the scientists report $CO_2$ effects on soil bacteria "were not detectable." They report microbial mass was "negatively affected by increasing $CO_2$," noting, "under extended nitrogen limitation the plants ultimately garner the nitrogen," and the plants "ultimately outcompete microbes for these scarce soil resources," citing Hu *et al.* (2001).

In concluding the discussion of their findings, Allen *et al.* remark, "undisturbed arid shrublands may not fix comparatively large amounts of carbon, but they may sequester a large fraction of that carbon." Noting "carbon allocated to arbuscular mycorrhizal fungi forms a large part of the macro-aggregate structure in the form of glomalin (Rillig *et al.*, 2002)," and those aggregates "may be protected from decomposition," they conclude the enhanced formation of such aggregates in $CO_2$-enriched air forms "an important [carbon] sequestration pathway" in chaparral ecosystems.

Working in the Mojave Desert at the FACE facility located near Mercury, Nevada, USA, where various shrubs and perennial grasses grow, Billings and Schaeffer (2004) examined the effects of atmospheric $CO_2$ enrichment (to 550 ppm throughout each growing season since April 1997) on soil nitrogen (N) dynamics via measurements of foliage C and N contents and isotope composition, and by measuring resin-available N and rates of soil respiration in the field in conjunction with assessments of potential C evolution and net N mineralization derived from long-term soil incubations. Their findings showed the "effects of elevated $CO_2$ on soil C and N dynamics are variable and complex, with many competing processes," and "changes in soil microbial activity with elevated $CO_2$ ... could affect both mineralizing and immobilizing microbial processes." Nevertheless, the bulk of their observations suggest "elevated $CO_2$ may increase root and/or soil microbial activity," which more often than not "can result in periodic increases in resin-available N, particularly when soil moisture is available." They say these several interrelated phenomena "may translate into more plant available N at these times." The two researchers thus conclude "if increases in plant-available N are maintained, particularly when soil moisture is available, arid ecosystems may be able to sustain any increases in productivity induced by elevated $CO_2$."

In studying the potential for the long-term storage of carbon in Earth's soils, Lagomarsino *et al*. (2006) note an increase of labile carbon below ground, such as is typically provided by atmospheric $CO_2$ enrichment, "could induce two mechanisms acting in opposite ways: (1) an enhanced soil organic matter decomposition due to the stimulation of microbial activity through the so-called *priming effect* (Kuzyakov *et al*., 2000); and (2) a retarded mineralization of native soil organic carbon due to the preference of microbes for easily decomposable substrates (Cardon *et al*., 2001)."

In a study designed to determine which mechanism is likely the stronger of the two, Lagomarsino *et al*. conducted physical and chemical analyses of soils they sampled in June and October 2004 at the POPFACE experimental plantation in central Italy, where clones of *Populus alba*, *Populus nigra,* and *Populus x euramericana* had been grown since 1999 with nitrogen fertilization throughout the 2002–2004 growing seasons. Hoosbeek *et al*. (2004) observed a priming effect of the newly incorporated litter in the first rotation cycle of trees exposed to air containing an approximate 50% increase in atmospheric $CO_2$ concentration, but in the second rotation cycle Hoosbeek *et al*. (2006) observed an accumulation of carbon in the soil of that treatment. In harmony with this latter observation, Lagomarsino *et al*.'s 2004 data reveal no increase in carbon mineralization activity under elevated $CO_2$, but rather a decrease of microbial basal respiration in the non-rhizospheric soil of the $CO_2$-enriched treatment. And noting "microbial carbon immobilization was the dominant process under elevated $CO_2$, limiting the carbon losses from soil," Lagomarsino *et al*. conclude their results suggest "a possible positive trend for carbon storage on the long term, independent of soil nitrogen availability."

Cheng *et al*. (2007) conducted a two-year FACE study of sorghum (*Sorghum bicolor* (L.) Moench) near Phoenix, Arizona (USA), where they studied the dynamics of soil organic carbon (SOC) pools comprised of labile and recalcitrant SOC of short and long mean residence time (MRT), respectively, under control conditions (360 ppm $CO_2$) and FACE conditions (560 ppm $CO_2$), together with water-adequate (wet) and water-deficient (dry) treatments. They note it is difficult to measure changes in total SOC content over periods of only a few years because soils typically contain large amounts of carbon compared to what they sequester annually. Their study proved no exception to this rule, as no significant differences in total SOC could be detected between the control and FACE treatments over the two years of the sorghum experiment.

Nevertheless, they learned much by other means, such as stable-carbon isotopic ($\delta^{13}C$) tracing, which revealed 53% of the final SOC in the FACE plot was in the recalcitrant or long MRT carbon pool and 47% in the labile or short MRT pool, whereas in the control plot 46% and 54% of the final SOC was in the recalcitrant and labile pools, respectively. This indicates "elevated $CO_2$ transferred more SOC into the slow-decay carbon pool," the ten researchers write. In addition, they report "isotopic mixing models revealed that increased new sorghum residue input to the recalcitrant pool mainly accounts for this change, especially for the upper soil horizon (0–30 cm) where new carbon in recalcitrant soil pools of FACE wet and dry treatments was 1.7 and 2.8 times as large as that in respective Control recalcitrant pools." In addition, Cheng *et al*. state "old C in the recalcitrant pool under elevated $CO_2$ was higher than that under ambient $CO_2$, indicating that elevated $CO_2$ reduces the decay of the old C in [the] recalcitrant pool."

Therefore, because "higher recalcitrant C content and lower labile C content in the soils were detected under elevated $CO_2$ relative to ambient $CO_2$ treatments, suggesting that SOC under elevated $CO_2$ becomes more stable against chemical and biological degradation," the ten scientists say their results imply terrestrial agro-ecosystems may play a critical role in sequestering $CO_2$ under future atmospheric conditions.

Bockheim (2007) explains "cryoturbation is a dominant process in permafrost regions and refers collectively to all soil movements due to frost action," and reports several prior studies suggested cryoturbation "was particularly active during mid-Holocene warming periods in the arctic." Bockheim thus studied the effect sustained warming will have on redistribution of soil organic carbon, and whether this redistribution will exacerbate or mitigate the release of $CO_2$ to the atmosphere. The study focused on the amount of soil organic carbon (SOC) incorporated via cryoturbation into the active layer and near-surface permafrost of 21 sites in northern Alaska, 10 of which were located in the Arctic Coastal Plain and 11 of which were in the Arctic Foothills. Based on data acquired from the 21 sites, the University of Wisconsin researcher determined "55% of the SOC density of the active layer and near-surface permafrost could be attributed to redistribution from cryoturbation," listing "five lines of evidence suggesting that increased cryoturbation from arctic warming will result in increased storage of SOC."

First, Bockheim states "once cryoturbation has moved SOC to the cold, deeper soil layers, little or no biological decomposition will take place." Second, "major organic horizons that are cryoturbated ... are 10 to 50% more dense than the equivalent uncryoturbated horizons," and "low-density SOC may be more susceptible to decomposition than high-density SOC." Third, "low-molecular-weight neutrally charged organic compounds are more biodegradable than high-molecular fractions." Fourth, "Kaiser *et al*. (2007) reported lower decomposition rates of redistributed SOC in Siberian subsoils than in equivalent material collected from the surface." And fifth, "mechanistic models (Waelbroeck *et al*., 1997) predict that sustained arctic warming will result in permafrost thawing and a delayed long-lasting increase in SOC storage."

Bockheim concludes, "these results suggest that continued warming of the arctic may accelerate cryoturbation," and "this, in turn, will increase the incorporation of dense, high-molecular-weight SOC at depth, thereby enabling the soil to store more SOC than at present and reducing the loss of $CO_2$ to the atmosphere from soil respiration"—essentially just the opposite of what IPCC contends.

Pendall and King (2007) conducted a series of long-term (170–330 days) laboratory incubation experiments to examine changes in soil organic matter pool sizes and turnover rates in soil collected from an open-top chamber (OTC) atmospheric $CO_2$ enrichment study in the shortgrass steppe of northeastern Colorado, USA, where the air in the ambient $CO_2$ chambers (ACs) and elevated $CO_2$ chambers (ECs) had atmospheric $CO_2$ concentrations of 360 and 720 ppm, respectively, and where this degree of $CO_2$ enrichment enhanced both above- and below-ground plant growth by 15–35%. They also discovered "active pool carbon increased in EC relative to AC treatments systematically over the first 3 years of exposure to elevated $CO_2$ in topsoils and to a lesser degree in subsoils," and they remark, "these results are consistent with independent results from the same OTC study showing that rhizo-deposition rates doubled and root production increased under elevated $CO_2$." In addition, they report "new carbon turnover was not enhanced by elevated $CO_2$," confirming "new carbon inputs under elevated $CO_2$ are not simply lost to mineralization" and "pool sizes may continue to increase under elevated $CO_2$." The two researchers conclude, "these results suggest that soil carbon storage may increase in semi-arid grasslands under elevated $CO_2$," and they opine this phenomenon, in turn, would tend to mitigate the global warming thought by many to accompany increases in the air's $CO_2$ content.

Marhan *et al*. (2008) studied undisturbed soil cores with and without visible wheat residues extracted at the conclusion of the third year of a mini-FACE experiment conducted in a field near Hohenheim, Germany planted annually to spring wheat (*Triticum aestivum* L.). The researchers examined the effect of elevated atmospheric $CO_2$ concentration (an extra 160 ppm) on the decomposition of the wheat residues present in the soil by measuring $CO_2$ evolution from the cores, as well as the leaching of inorganic and organic carbon from them, during 191 days of core incubations in the laboratory. They found cumulative residue decomposition was not affected by elevated $CO_2$ when no wheat residues were visible in the cores. When such residues were visible, however, decomposition was "significantly lower" (by 19%) in the elevated compared to the ambient $CO_2$ treatment, which for the more common 300 ppm degree of atmospheric $CO_2$ enrichment roughly translates to a decomposition reduction of 36%. In addition, they report more dissolved inorganic carbon (DIC) was leached from the elevated $CO_2$ treatment cores, both with and without visible plant residues, than from similar cores from the ambient $CO_2$ treatment (47.2% and 29.5%, respectively, for their degree of $CO_2$ enrichment, which equates to about 88% and 55%, respectively, for a 300 ppm increase in atmospheric $CO_2$ concentration). These extra amounts of DIC represent "an additional possible mechanism for carbon sequestration in soils of arable cropping systems under future elevated $CO_2$ concentrations," they note. They also report stubble and root biomass was higher by 12.0 and 9.44%, respectively, in soil cores taken from the elevated $CO_2$ plots at the end of the study, which equates to approximate stubble and root biomass enhancements of 22% and 18%, respectively, for a 300 ppm increase in atmospheric $CO_2$ concentration. With respect to the potential for enhanced carbon sequestration in wheat (and other cereal-crop) fields in a $CO_2$-enriched world of the future, therefore, the six scientists conclude, "increased input of plant residues and reduced decomposition of plant-derived carbon" are "possible mechanisms for enhanced carbon sequestration under elevated atmospheric $CO_2$ concentration."

Hopkins *et al.* (2009) write there were "two sets of long-term experimental plots which have been under constant and known management for over a century and for which historical data exist that allow comparison over recent decades to determine what, if any, changes in SOC have occurred." These unique plots were the Palace Leas Meadow Hay Plots in northeast England, established in 1897, and the plots of the Park Grass Continuous Hay Experiment established in 1856 at Rothamsted in southeast England. In studying them, Hopkins *et al.* say they determined "there were no significant differences between 1982 and 2006 for the Palace Leas plots or between 1959 and 2002 for the Park Grass plots," leading them to conclude, "there has been no consistent decrease in SOC stocks in surface soils under old, permanent grassland in England in recent decades, even though meteorological records for both sites indicate significant warming of the soil and air between 1980 and 2000." They theorize "the lack of a consistent decline in SOC content linked to increased soil temperature since 1980 may be due to a compensatory increase in primary production," citing Jenkinson *et al.* (1991).

Martens *et al.* (2009) write, "the generally higher above and belowground productivity of $C_3$ plants under elevated $CO_2$ leads to the conclusion that more rhizo-depositions (roots and exudates) are transferred into soils, potentially increasing soil carbon content," but they note most FACE and outdoor chamber studies have failed to detect significant changes in soil organic carbon (SOC) due to the typically large amount and spatially heterogeneous nature of preexisting SOC. In an attempt to overcome these difficulties, Martens *et al.* cultivated well-watered and well-fertilized spring wheat (cv. Minaret) in stainless steel cylinders forced into the soil of control and free-air $CO_2$-enriched (to 180 ppm above ambient) plots at the experimental farm of the Federal Research Institute in Braunschweig, Germany, where between stem elongation and beginning of ripening the plants were repeatedly pulse-labeled with $^{14}CO_2$ and thereafter monitored daily for soil-borne total $CO_2$ and $^{14}CO_2$ until harvest, after which the distribution of $^{14}C$ was analyzed in all plant parts, soil, soil mineral fractions, and soil microbial biomass.

The four researchers found "in comparison to ambient conditions, 28% more $^{14}CO_2$ and 12% more total $CO_2$ was evolved from soil under elevated $CO_2$," and "in the root-free soil 27% more residual $^{14}C$ was found in the free-air $CO_2$-enriched soil than in the soil from the ambient treatment." In addition, they say, in soil samples from both treatments about 80% of residual $^{14}C$ was "integrated into the stable, clay bound soil organic matter pool," which suggests, "under FACE conditions a considerable contribution was made to the long-term storage of soil carbon in this soil." Thus Martens *et al.* were able to "show for the first time," as they describe it, "that a crop plant grown under FACE conditions deposited significantly more carbon to soil than those grown under ambient $CO_2$ in the field," and "the additional carbon input under elevated $CO_2$ did not induce an accelerated degradation of pre-existing soil organic matter (no positive priming effect)." Those findings demonstrate "wheat plants grown under elevated $CO_2$ can contribute to an additional net carbon gain in soils," which is especially beneficial to the biosphere.

Springsteen *et al.* (2010) write "woody plant expansion within grassland ecosystems is a worldwide phenomenon, and dramatic vegetation shifts from grassland to savanna/woodlands have occurred over the past 50–100 years in North America," noting one of the chief factors contributing to this phenomenon is believed to be the concomitant historical increase in the air's carbon dioxide concentration, as suggested by Archer *et al.* (1995), Polley (1997), Bond and Midgley (2000), and Bond *et al.* (2003). They also state once shrublands are established, they tend to persist for a number of possible reasons, one of which is a type of feedback phenomenon referred to as *islands of fertility*, which "occurs when resources accumulate in soils beneath woody plants due to litterfall, interception of wet and dry deposition, nitrogen fixation, and animal droppings," as described by Schlesinger *et al.* (1990), Archer *et al.* (1995), Reynolds *et al.* (1999), and Lopez-Pintor *et al.* (2006). They report, "changes in soil attributes under woody vegetation have been documented in the arid grasslands of the southern Great Plains, including increases in soil carbon and nitrogen," citing Reynolds *et al.* (1999), Hibbard *et al.* (2001, 2003), McCulley *et al.* (2004), Schade and Hobbie (2005), and Liao *et al.* (2006).

In their work at the USDA-ARS Northern Great Plains Research Laboratory near Mandan, North Dakota (USA), Springsteen *et al.* examined near-surface (upper 15 cm) soil biogeochemistry along a 42-year (1963–2005) chrono-sequence, which encompassed grassland, woodland, and grassland-woodland transition zones in a northern Great Plains grassland, to determine the influence of woody plant expansion on soil carbon and nitrogen contents. The four researchers report total soil carbon content rose by 26% across the chrono-sequence from grassland to woodland within the 0–15 cm soil depth, and total soil nitrogen content rose by 31%. In addition, they report, the rate of woody shrub expansion from 1963 to 1988 (25 years) was ~1,800 $m^2$ per year at their study site, and from 1988 to 2005 (17 years) it was ~3,800 $m^2$ per year, or just a little more than doubled.

Yang *et al.* (2010) write, "soil stores more than twice as much carbon than does vegetation or the atmosphere," citing Schlesinger (1997), and they note many people believe "climate warming is likely to accelerate the decomposition of soil organic carbon which could lead to increased carbon release from soils, providing a positive feedback to climate change (Davidson and Janssens, 2006)." To test that belief, Yang *et al.* "conducted five consecutive regional soil surveys in China's grasslands during 2001–2005 and sampled 981 soil profiles from 327 sites across the northern part of the country," comparing their results "with data of 275 soil profiles derived from China's National Soil Inventory during the 1980s." The seven scientists report the organic carbon stock in the upper 30 cm of soil in northern China's grasslands "did not show significant association with mean annual temperature," and "grassland soil organic carbon stock did not change significantly over the past two decades."

Yang *et al.* conclude, "it has been often asserted that soil will act as a carbon source because of its sensitivity to global environmental change (e.g., Melillo *et al*., 2002; Bellamy *et al*., 2005; Schipper *et al*., 2007)," but "in contrast to these previous reports, our results indicate that soil organic carbon stock in northern China's grasslands has not experienced significant changes during the past two decades, despite measureable climate change."

Iversen *et al.* (2012) explored the fate of carbon (C) and nitrogen (N) in the soil of a sweetgum tree (*Liquidambar styraciflua* L.) plantation in Oak Ridge, Tennessee (USA) at the conclusion of a nearly 12-year FACE study. The four researchers report net primary productivity increased in response to atmospheric $CO_2$ enrichment "even though production in the sweetgum stand was limited by soil N availability." In addition, they write, "the majority of the additional C fixed under elevated $CO_2$ was allocated belowground to the production of fine roots," with the largest increases in root biomass production and mortality being "at relatively deep soil depths (i.e., below 30 cm)," with the end result "soil C and N contents were greater throughout the soil profile under elevated $CO_2$ at the conclusion of the experiment." With respect to carbon, for example, "soil C content was ~19% greater throughout the soil profile after more than 11 years of $CO_2$ enrichment."

Iversen *et al.* conclude, "the greater residence time of C in deeper soil indicates that inputs from deep roots under elevated $CO_2$ may increase the potential for long-term storage of C and N in forested ecosystems." They add, "this finding suggests greater C accrual in elevated $CO_2$ compared with ambient $CO_2$ during the experiment, consistent with the conclusion of a meta-analysis that indicated increased ecosystem C storage under elevated $CO_2$ (Luo *et al*., 2006)." These observations presage "the potential of future forests to store C and mitigate some portion of rising atmospheric $CO_2$," as they state in the concluding sentence of their report.

Zhou *et al.* (2013) took advantage of a long-term field experiment with increased temperature and precipitation, established in late April 2005 in a semiarid temperate steppe in Duolun County, Inner Mongolia, China, "to investigate the effects of warming, increased precipitation and their interactions on SOC [soil organic carbon] fraction" by quantifying "labile SOC, recalcitrant SOC and stable SOC at 0–10 and 10–20 cm depths." They found "neither warming nor increased precipitation affected total SOC and stable SOC at either depth," but "increased precipitation significantly increased labile SOC at the 0–10 cm depth" and "warming decreased labile SOC and marginally but significantly increased recalcitrant SOC at the 10–20 cm depth." They also found "significant interactive effects of warming and increased precipitation on labile SOC and recalcitrant SOC at the 0–10 cm depths."

Zhou *et al.* conclude, "given that the absolute increase of SOC in the recalcitrant SOC pool was much greater than the decrease in labile SOC, and that the mean residence time of recalcitrant SOC is much greater, our results suggest that soil C storage at 10–20 cm depth may increase with increasing temperature in this semiarid grassland," which represents a net negative feedback on predicted global warming and a tremendous benefit for the terrestrial biosphere.

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### *1.2.5.3 Erosion*

- The historical increase in the atmosphere's $CO_2$ concentration has significantly reduced the erosion of Earth's valuable topsoil over the past several decades, and the continuing increase in atmospheric $CO_2$ can maintain this trend, and perhaps even accelerate it, throughout the foreseeable future.

More than two decades ago, Idso (1989) predicted, "as a result of the direct effects of atmospheric $CO_2$ enrichment upon the primary plant processes of photosynthesis and transpiration ... many plants will greatly expand their ranges with augmented water use efficiencies, stabilizing the soil and protecting it from erosion." Prior to that time (and continuing well past it), study after study had concluded (and continued to conclude) soil erosion by both wind and water was running at a high sustained rate. In an article published in *Science*, Trimble and Crosson (2000) wrote, "some sources have suggested that recent erosion is as great as or greater than that of the 1930s."

Remarkably, this long-held belief in continued high or even increasing soil erosion "was based mostly on models," write Trimble and Crosson. Enlarging on this thesis, the two researchers report little physical field-based evidence other than anecdotal statements has been offered to verify the high soil erosion estimates. They note, "it is questionable whether there has ever been another perceived public problem for which so much time, effort, and money were spent in light of so little scientific evidence." The good news, according to Trimble and Crosson, is "available field evidence suggests declines of soil erosion, some very precipitous, during the past six decades."

The problem was largely a failure to realize most of the soil particles removed from one part of the land, by either wind or water, were later deposited in nearby areas, so the net loss of soil was only a very small portion of the total that was moved about by the forces of nature.

Over the course of the data-driven shift in the public's perception of U.S. soil erosion, it has become evident perceptions of several ancillary phenomena also need adjusting. Trimble and Crosson note, for example, certain studies once warned "increasingly eroded soil profiles will allow less rainfall to be infiltrated and stored," leading to "increased overland flow, erosion, and flooding." However, they note, detailed hydrologic studies indicate just the opposite was occurring: "runoff is decreasing, flood peaks are smaller, and in some places, the base flow is greater." In addition, they write, "these field studies show that more water is infiltrating into the soil and, in some cases ... significantly more water is being transpired by plants."

These real-world observations follow what would be expected on the basis of Idso's 1989 prediction. With gradually increasing atmospheric $CO_2$ concentrations gradually enhancing plant water use efficiencies, more plants should have gradually been spreading over the surface of the land, reducing rates of surface runoff and allowing more water to infiltrate the soil, thereby providing more water to be extracted from the soil by more plants for subsequent transpiration. These hydrologic improvements, in turn, should have improved the status of still other aspects of the planet's natural resource base, for example by increasing the stability of streams.

A pair of photographs in the Trimble and Crosson article provided a visual testament to the reality of this phenomenon. Both photos showed the same view of a portion of Bohemian Creek in La Crosse County, Wisconsin, USA. The first of the pictures, taken in 1940, showed an "eroded, shallow channel composed of gravel and cobbles, with coarse sediment deposited by overflows on the floodplain." The second, taken 34 years later in 1974, indicates the stream channel was "narrower, smaller, and more stable." In addition, Trimble and Crosson note, "the coarse sediment has been covered with fine material, and the flood plain is vegetated to the edge of the stream." And conditions improved even more over the following quarter-century, they observe.

In addition to this broad introduction to the issue of soil erosion, a number of scientific studies have focused on other specific effects of rising temperatures and atmospheric $CO_2$ concentrations on soil erosion.

Allen *et al.* (1999) analyzed sediment cores extracted from a lake in southern Italy and from the Mediterranean Sea, deriving a high-resolution climate and vegetation dataset for this region that covered the last 102,000 years. Rapid changes in vegetation were found to be correlated with rapid changes in climate, such that complete shifts in natural ecosystems sometimes occurred over periods of less than 200 years. Throughout the warmest portion of this record—the current interglacial or Holocene—the total organic carbon content of the vegetation reached its highest level, more than doubling values experienced over the rest of the record. Other proxy indicators revealed the increased vegetative cover typically was associated with less soil erosion during the more productive woody plant period of the Holocene.

Rillig *et al.* (2000) examined several characteristics of beneficial arbuscular mycorrhizal fungi (AMF) associated with the roots of plants growing for at least 20 years along a natural $CO_2$ gradient near a $CO_2$-emitting spring in New Zealand. Enriching the air's $CO_2$ concentration from 370 to 670 ppm increased percent root colonization by AMF in a linear fashion—and by nearly fourfold. Similarly, fungal hyphal length experienced a more-than-threefold linear increase along the same $CO_2$ gradient, and total soil glomalin (a protein secreted by fungal hyphae that increases soil aggregation and stability) experienced a linear increase of approximately fivefold. Consequently, as the air's $CO_2$ concentration rises, the positive responses of AMF identified in this study likely will become increasingly pronounced, significantly reducing soil losses via wind and water erosion by way of $CO_2$-induced glomalin-mediated increases in soil aggregate stability, which should benefit terrestrial ecosystems throughout the world.

In a closely allied free-air $CO_2$-enrichment (FACE) study of adequately fertilized sorghum, where daylight atmospheric $CO_2$ concentration was increased by approximately 50%, Rillig *et al.* (2001) studied plants grown under both well-watered and water-stressed irrigation treatments, focusing on the effects of elevated $CO_2$ on the hyphal growth of AMF, two fractions of glomalin, and the production of water-stable soil aggregates. They found the 50% increase in the air's $CO_2$ concentration dramatically increased fungal hyphae lengths—by about 120% in the wet irrigation treatment and 240% in the dry treatment. The biological effects of the extra $CO_2$ in the air also increased the mass of water-stable soil aggregates—by 40% in the wet treatment and 20% in the dry treatment. In addition, the researchers write, the "two fractions of glomalin and AMF hyphal lengths were all positively correlated with soil aggregate water stability." Hence they say their study "demonstrated for the first time that elevated $CO_2$ can affect soil aggregation in an agricultural system," where "a soil stabilizing effect of $CO_2$ would be clearly advantageous."

Knox (2001) determined how the conversion of the United States' Upper Mississippi River Valley from prairie and forest to crop and pasture land by settlers in the early 1800s influenced subsequent watershed runoff and soil erosion rates. They found conversion of the region's natural landscape to agricultural uses boosted surface erosion rates to values three to eight times greater than those characteristic of pre-settlement times. In addition, the land-use conversion increased peak discharges from high-frequency floods by 200 to 400%. Since the late

1930s, however, surface runoff has been decreasing; but this decrease was "not associated with climatic causes," Knox writes, as "an analysis of temporal variation in storm magnitudes for the same period showed no statistically significant trend."

It is important to note the decreases in soil erosion rates and extreme streamflow conditions that began in the late 1930s in the Upper Mississippi River Valley were the exact opposite of predictions, which suggest these phenomena should have been increasing as a result of unprecedented $CO_2$-induced global warming. However, they likely were not related to climate factors, Knox argues, instead attributing them to the introduction of soil conservation measures such as contour plowing, strip-cropping, terracing, and minimum tillage, to which list could be added the concomitant rise in atmospheric $CO_2$ concentration and its impacts on the various beneficial phenomena discussed in this subsection.

Olafsdottir and Gudmundsson (2002) studied spatial and temporal patterns of land degradation in northeastern Iceland over the past 7,500 years based on data from excavations of 67 soil profiles, comparing their results with climatic variations known to have occurred over the same period. These activities revealed, in their words, "the deterioration in vegetation and soil cover noted coincides with the recorded deterioration in climate." During every major cold period of their record, land degradation was classified as "severe." During every major warm period, however, this condition was reversed, and soils were built up as vegetation cover expanded.

The primary implication of these findings, according to the two researchers, is "climate has a significant role in altering land cover *per se* and may trigger land degradation without the additional influence of men." Thus they conclude, "in Iceland severe land degradation could commence without anthropogenic influence—simply as a result of the cold periods."

In a FACE study conducted on the North Island of New Zealand, Newton *et al.* (2003) measured the water repellency of a grassland soil—which contained about 20 species of legumes, $C_3$ grasses, $C_4$ grasses, and forbs, and was grazed periodically by adult sheep—after five years of exposure to an extra 100 ppm of $CO_2$. They found a significant reduction in the water repellency of the soil in the elevated $CO_2$ treatment. The researchers note, "at field moisture content the repellence of the ambient soil was severe and significantly greater than that of the elevated [$CO_2$] soil."

Newton *et al.* say water repellency "is a soil property that prevents free water from entering the pores of dry soil (Tillman *et al.*, 1989)," and they report it "has become recognized as a widespread problem, occurring under a range of vegetation and soil types (agricultural, forestry and amenity; sand, loam, clay, peat and volcanic) (Bachmann *et al.*, 2001) and over a large geographical range (Europe, USA, Asia, Oceania) (Bauters *et al.*, 1998)." Specifically, they note water-repellency-induced problems for land managers include "increased losses of pesticides and fertilizers, reduced effectiveness of irrigation, increased rates of erosion, and increased runoff," and there are water-repellency-induced problems "in the establishment and growth of crops (Bond, 1972; Crabtree and Gilkes, 1999) and implications for the dynamics of natural ecosystems, particularly those subject to fire (DeBano, 2000)." The $CO_2$-induced reduction of soil water repellency discovered in this study portends a wide range of very important benefits for both agro- and natural ecosystems as the air's $CO_2$ content rises in the future.

Prior *et al.* (2004) note "enhanced aboveground crop growth under elevated $CO_2$, leading to more soil surface residue and greater percent ground cover (Prior *et al.*, 1997), coupled with positive shifts in crop root systems (Prior *et al.*, 2003), may have the potential to alter soil structural characteristics." They decided to see whether this inference was indeed true, and if true, whether elevated atmospheric $CO_2$ concentrations tend to enhance or degrade soil physical properties.

The researchers grew plots of soybean and sorghum plants from seed to maturity for five consecutive growing seasons in open-top chambers maintained at atmospheric $CO_2$ concentrations of either 360 or 720 ppm. The soil in which the plants grew had been fallow for more than 25 years prior to the start of the study and was located in a huge outdoor bin. There, at the end of each growing season, the researchers allowed aboveground non-yield residues (stalks, soybean pod hulls, and sorghum chaff), including 10% of the grain yield, to remain on the surfaces of the plots to simulate no-tillage farming. Measurements of various soil properties made at the beginning of the experiment were compared with similar measurements conducted at its conclusion.

They found elevated $CO_2$ had no effect on soil bulk density in the sorghum plot, but lowered it in the soybean plot by approximately 5% Elevated $CO_2$ also had no effect on soil saturated hydraulic conductivity in the sorghum plot, but increased it in the soybean plot by about 42%. Soil aggregate stability was increased in both plots, but by a greater amount in the soybean plot, and total soil carbon content was increased by 16% in the sorghum plot and 29% in the soybean plot. Consequently, the soils of both plots experienced some improvements in response to the experimental doubling of the atmosphere's $CO_2$ concentration, although there were more and greater improvements in the soybean plot than in the sorghum plot. Prior *et al.* conclude their results "indicate potential for improvements in soil carbon storage, water infiltration and soil water retention, and reduced erosion," which are positive consequences they described as "$CO_2$-induced benefits."

Zhang and Liu (2005) report using the general circulation model of the UK Meteorological Office's Hadley Centre to calculate expected changes in temperature and precipitation throughout the Chinese Loess Plateau over the next century. They found 2.3–4.3°C increases in daily maximum temperature, 3.6–5.3°C increases in daily minimum temperature, and 23–37% increases in annual precipitation. They used a stochastic weather generator to downscale these monthly projections to daily values, after which they ran the Water Erosion Prediction Project model of Flanagan and Nearing (1995), as modified to account for $CO_2$ effects on evapotranspiration and biomass production by Favis-Mortlock and Savabi (1996), for a wheat-wheat-corn rotation utilizing either conventional or conservation tillage.

Zhang and Liu determined the climate-change scenarios they investigated led to 29–79% more water runoff and 2–81% greater soil loss under conventional tillage practices, but "adoption of conservation tillage could reduce runoff by 18–38% and decrease soil loss by 56–68% as compared to the conventional tillage under the present climate." They conclude "the use of the conservation tillage would be sufficient to maintain low runoff and erosion levels and thus protect agro-ecosystems under projected climate changes." As for crop productivity, they determined the warmer, wetter, $CO_2$-enriched environment projected to prevail on the Chinese Loess Plateau a hundred years from now would boost yields by significant amounts: 15–44% for wheat and 40–58% for corn. Zhang and Liu express great optimism about the future, noting "the significant increases in predicted wheat and maize yields [that] were results of increased precipitation and $CO_2$ concentration ... outweighed the negative effect of temperature rise on crop growth."

Shifting from the physiological effects of atmospheric $CO_2$ enrichment on groundcover plants to the immediate impacts of certain climatic phenomena on soil erosivity, D'Asaro *et al.* (2007) begin the report of their study by stating "warmer atmospheric temperatures associated with greenhouse warming are expected to lead to a more variable hydrological cycle, including more extreme rainfall events (IPCC, 1995)," adding "this change is expected to influence the erosive power, or erosivity, of rainfall and, hence, soil erosion rates (Nearing, 2001)." As a test of this "expectation," D'Asaro *et al.* set out "to assess changes in annual and seasonal rainfall erosivity that occurred in Sicily during the twentieth century," the hundred-year period typically described by IPCC and others as having experienced an increase in global temperature unprecedented over the past two millennia (Mann and Jones, 2003; Mann *et al.*, 2003) or more (Hansen *et al.* 2006). The scientists generated long-term series (from 1916 to 1999 in most cases) of a storm erosion index based on storm rainfall amounts and intensities and then applied that index at 17 Sicilian locations (representative of different climatic zones) where the latter two parameters were routinely measured. The three Italian researchers found "the annual erosivity did not increase during the twentieth century." In fact, they write, it "decreased at a few locations."

Diodato *et al.* (2008) conducted a detailed analysis of Calore River Basin (South Italy) erosive rainfall using data from 425-year-long series of both observations (1922–2004) and proxy-based reconstructions (1580–1921). The more recent of these two series was based on a scheme that employed the Revised Universal Soil Loss Equation; documentary descriptions provided the basis for the earlier series. They write the results of this work revealed pronounced interdecadal variations, with "multi-decadal erosivity reflecting the mixed population of thermo-convective and cyclonic rainstorms with large anomalies." In addition, they report, "the so-called Little Ice Age (16th to mid-19th centuries) was identified as the stormiest period, with mixed rainstorm types and high frequency of floods and erosive rainfall."

In the concluding section of their paper, the three researchers note, "in recent years, climate change (generally assumed as synonymous with global warming) has become a global concern and is widely reported in the media." One of the chief of these concerns is that extreme weather phenomena, such as droughts and floods, will become both more frequent and more severe as the planet warms, which would lead to more soil erosion. However, Diodato *et al.* say their study indicates "climate in the Calore River Basin has been largely characterized by naturally occurring weather anomalies in past centuries (long before industrial $CO_2$ emissions), not only in recent years," and there has been a "relevant smoothing" of such events during the modern era.

Stankoviansky (2003) employed topographical maps and aerial photographs, field geomorphic investigation, and the study of historical documents, including those from local municipal and church sources, to determine the spatial distribution of gully landforms and the temporal history of their creation in the Myjava Hill Land of Slovakia, situated in the western part of the country near its border with the Czech Republic. This work revealed "the central part of the area, settled between the second half of the 16th and the beginning of the 19th centuries, was affected by gully formation in two periods, the first between the end of the 16th century and the 1730s and the second roughly between the 1780s and 1840s." Stankoviansky notes the gullies were formed "during periods of extensive forest clearance and expansion of farmland," and "the triggering mechanism of gullying was extreme rainfalls during the Little Ice Age." More specifically, he writes, "the gullies were formed relatively quickly by repeated incision of ephemeral flows concentrated during extreme rainfall events, which were clustered in periods that correspond with known climatic fluctuations during the Little Ice Age."

From the mid-nineteenth century to the present, Stankoviansky affirms, "there has been a decrease in gully growth because of the afforestation of gullies and especially climatic improvements since the termination of the Little Ice Age." These observations suggest extreme and destructive rainfall events were much more common in the Myjava Hill Land of Slovakia during the Little Ice Age than they have been subsequently. This view, in his words (and in many of the references he cites), "is often regarded as generally valid for Central Europe." This evidence-derived view runs counter to that of most climate alarmists, who tend to blame global warming for such destructive precipitation events and the erosive flooding they cause.

In the course of a long-term field experiment at the Kessler Farm Field Laboratory in McClain County, Oklahoma, USA, Xue *et al.* (2011) explored how annual clipping for biofuel feedstock production and warming caused soil erosion and accompanying carbon and nitrogen losses in tallgrass prairie. The researchers provided warming by infrared heaters suspended 1.5 m above the ground, as described by Kimball (2005), raising air temperatures by an average of 1.47°C and soil temperatures in the clipping plots by 1.98°C. The results of this experiment revealed the average relative depth of erosion caused by clipping was 1.65 and 0.54 mm/year, respectively, in the warmed and control plots from November 21, 1999 to April 21, 2009; the soil erosion rate was 2148 $g/m^2$/year in the warmed plots and 693 $g/m^2$/year in the control plots; soil organic carbon was lost at a rate of 69.6 $g/m^2$/year in the warmed plots and 22.5 $g/m^2$/year in the control plots; and total nitrogen was lost at a rate of 4.6 $g/m^2$/year in the warmed plots and 1.4 $g/m^2$/year in the control plots. Xue *et al.* note, "the amount of carbon and nitrogen loss caused by clipping is equivalent to, or even larger than, changes caused by global change factors."

The five researchers state their results indicate "clipping for biofuel harvest results in significant soil erosion and accompanying losses of soil carbon and nitrogen, which is aggravated by warming." Also, "soil erosion is one of the most pressing global environmental challenges facing the world today, causing declining soil productivity and crop yields, which may create difficulties in meeting the rising demand for food and energy (Brink *et al*., 1977; Brown, 1981; Lal, 2004; MEA, 2005)." Consequently, the biofuel "cure" for the global warming "disease" might be worse than the malady itself.

Tape *et al.* (2011) state "recent changes in the climate of Arctic Alaska, including warmer temperatures and a lengthened growing season (Chapin *et al*., 2005; Serreze and Francis, 2006; Shulski and Wendler, 2007), are linked with ... increased vegetation productivity, as measured using time series of satellite vegetation indices such as Normalized Difference Vegetation Index (NDVI)," as documented by Myneni *et al.* (1997), Jia *et al.* (2003), Goetz *et al.* (2005), and Bhatt *et al*., 2010). This phenomenon, they note, "has been partly attributed to the expansion of shrubs, which has been documented using time series of aerial photography (Sturm *et al*., 2001; Tape *et al*., 2006), plot studies (Joly *et al*., 2007), and shrub growth ring chronologies (Forbes *et al*., 2010; Hallinger *et al*., 2010)." In light of these observations they ask, "Is the current warming and concurrent shrub expansion on older Arctic landscapes associated with increased or decreased erosion?"

Working with time series imagery from Landsat thematic mapper data covering the period 1986–2009, Tape *et al.* (2011) examined the landscape pattern of tall shrub distribution and expansion in the Arctic foothills, located on the north side of the Brooks Range, Alaska, and they studied sediments obtained from cores of four lakes near the Chandler River on the central North Slope of Alaska (where shrub expansion is occurring), to compare relationships among shrub cover, erosion, and runoff over the past quarter-century. Their results reveal "a background decline in erosion since 1980, superimposed by episodic erosional events," and "the background decline in erosion is associated with trends of increasing shrubs and declining peak runoff events."

The results of the many studies discussed in this review suggest the historical increase in the atmosphere's $CO_2$ concentration has reduced significantly the erosion of valuable topsoil worldwide over the past several decades, and the continuing increase in atmospheric $CO_2$ can maintain this trend, and perhaps even accelerate it, throughout the foreseeable future.

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