

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

In light of these contradictory results, the most reasonable conclusion is that atmospheric CO<sub>2</sub> enrichment may either increase or decrease woody-plant respiration, but not to any great degree, and that in the mean, the net result for the conglomerate of earth's trees would likely be something of little impact.

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

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## 7.7. Carbon Sequestration

As the CO<sub>2</sub> content of the air continues to rise, nearly all of earth's plants respond by increasing their photosynthetic rates and producing more biomass. This results in more carbon being captured and stored, or sequestered, in plant fibers and soil, which counterbalances some of the CO<sub>2</sub> emissions produced by mankind's use of fossil fuels.

In this section we begin with a research review of what is known about forest and forest-species responses to atmospheric CO<sub>2</sub> enrichment and subsequent carbon sequestration. Then we survey research on how temperatures affect sequestration and whether CO<sub>2</sub> enhancement offsets the rate at which carbon is re-released from soil (decomposition).

### 7.7.1. CO<sub>2</sub> Enhancement and Carbon Sequestration

#### 7.7.1.1 Forests

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

In an open-top chamber experiment conducted in Switzerland, Nitschelm *et al.* (1997) reported that a 71 percent increase in the atmospheric CO<sub>2</sub> concentration above white clover monocultures led to a 50 percent increase in soil organic carbon content. Related studies on wheat and soybean agroecosystems (Islam *et al.*, 1999) provided similar results, as did a free-air CO<sub>2</sub> enrichment (FACE) experiment on cotton, which documented a 10 percent increase in soil organic carbon content in plots receiving 550 ppm CO<sub>2</sub> relative to those receiving 370 ppm (Leavitt *et al.*, 1994). These phenomena will allow long-lived perennial species characteristic of forest ecosystems to sequester large amounts of carbon within their wood for extended periods of time (Chambers *et al.*, 1998).

In reviewing studies that have been conducted on individual trees, it is clear that elevated levels of atmospheric CO<sub>2</sub> increase photosynthesis and growth

in both broad-leaved and coniferous species. When broad-leaved trembling aspen (*Populus tremuloides*) were exposed to twice-ambient levels of atmospheric CO<sub>2</sub> for 2.5 years, for example, Pregitzer *et al.* (2000) reported 17 and 65 percent increases in fine root biomass at low and high levels of soil nitrogen, respectively; while Zak *et al.* (2000) observed 16 and 38 percent CO<sub>2</sub>-induced increases in total tree biomass when subjected to the same respective levels of soil nitrogen.

Similar results have been reported for coniferous trees. When branches of Sitka spruce (*Picea sitchensis*) were fumigated with air of 700 ppm CO<sub>2</sub> for four years, rates of net photosynthesis in current and second-year needles were 100 and 43 percent higher, respectively, than photosynthetic rates of needles exposed to ambient air (Barton and Jarvis, 1999). In addition, ponderosa pine (*Pinus ponderosa*) grown at 700 ppm CO<sub>2</sub> for close to 2.5 years exhibited rates of net photosynthesis in current-year needles that were 49 percent greater than those of needles exposed to air containing 350 ppm CO<sub>2</sub> (Houpis *et al.*, 1999).

Elevated CO<sub>2</sub> also enhances carbon sequestration by reducing carbon losses arising from plant respiration. Karnosky *et al.* (1999) reported that aspen seedlings grown for one year at 560 ppm CO<sub>2</sub> displayed dark respiration rates that were 24 percent lower than rates exhibited by trembling aspen grown at 360 ppm CO<sub>2</sub>. Also, elevated CO<sub>2</sub> has been shown to decrease maintenance respiration, which it did by 60 percent in western hemlock seedlings exposed to an atmospheric CO<sub>2</sub> concentration of nearly 1600 ppm (McDowell *et al.*, 1999).

In a thorough review of these topics, Drake *et al.* (1999) concluded that, on average, a doubling of the atmospheric CO<sub>2</sub> concentration reduces plant respiration rates by approximately 17 percent. This finding contrasts strikingly with the much smaller effects reported by Amthor (2000), who found an average reduction in dark respiration of only 1.5 percent for nine deciduous tree species exposed to 800 ppm CO<sub>2</sub>. The period of CO<sub>2</sub> exposure in his much shorter experiments, however, was a mere 15 minutes. If the air's CO<sub>2</sub> content doubles, plants will likely sequester something on the order of 17 percent more carbon than ambiently grown plants, solely as a consequence of CO<sub>2</sub>-induced reductions in respiration. And it is good to remember that this stored carbon is in addition to that sequestered as a result of CO<sub>2</sub>-induced increases in plant photosynthetic rates.

Based upon several different types of empirical data, a number of researchers have concluded that current rates of carbon sequestration are robust and that future rates will increase with increasing atmospheric CO<sub>2</sub> concentrations. In the study of Fan *et al.* (1998) based on atmospheric measurements, for example, the broad-leaved forested region of North America between 15 and 51°N latitude was calculated to possess a current carbon sink that can annually remove all the CO<sub>2</sub> emitted into the air from fossil fuel combustion in both Canada and the United States. On another large scale, Phillips *et al.* (1998) used data derived from tree basal area to show that average forest biomass in the tropics has increased substantially over the past 40 years and that growth in the Neotropics alone (south and central South America, the Mexican lowlands, the Caribbean islands, and southern Florida) can account for 40 percent of the missing carbon of the entire globe. And in looking to the future, White *et al.* (2000) have calculated that coniferous and mixed forests north of 50°N latitude will likely expand their northern and southern boundaries by about 50 percent due to the combined effects of increasing atmospheric CO<sub>2</sub>, rising temperature, and nitrogen deposition.

The latter of these factors, nitrogen deposition, is an important variable. As indicated in the study of White *et al.*, it can play an interactive role with increasing atmospheric CO<sub>2</sub> to increase plant growth and carbon sequestration. However, the magnitude of that role is still being debated. Nadelhoffer *et al.* (1999), for example, concluded that nitrogen deposition from human activities is "unlikely to be a major contributor" to the large CO<sub>2</sub> sink that exists in northern temperate forests. Houghton *et al.* (1998), however, feel that nitrogen deposition holds equal weight with CO<sub>2</sub> fertilization in the production of terrestrial carbon sinks; and Lloyd (1999) demonstrated that when CO<sub>2</sub> and nitrogen increase together, modeled forest productivity is greater than that predicted by the sum of the individual contributions of these two variables. Thus, anthropogenic nitrogen deposition can have anywhere from small to large positive effects on carbon sequestration, as well as everything in between.

In conclusion, as the air's CO<sub>2</sub> content continues to rise, the ability of earth's forests to sequester carbon should also rise. With more CO<sub>2</sub> in the atmosphere, trees will likely exhibit greater rates of photosynthesis and reduced rates of respiration. Together, these observations suggest that biologically fixed carbon will experience greater residency times

within plant tissues. And if this carbon is directed into wood production, which increases substantially with atmospheric CO<sub>2</sub> enrichment, some of it can be kept out of circulation for a *very* long time, possibly even a millennium or more.

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

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### 7.7.1.2. Old Forests

In addition to enhancing the growth and production of young forests, available research indicates that rising atmospheric CO<sub>2</sub> concentrations will also increase the productivity and growth of older forests. For most of the past century it was believed that old-growth forests, such as those of Amazonia, should be close to dynamic equilibrium. Just the opposite, however, has been repeatedly observed over the past two decades.

In one of the first studies to illuminate this reality, Phillips and Gentry (1994) analyzed the turnover rates—which are close correlates of net productivity (Weaver and Murphy, 1990)—of 40 tropical forests from all around the world. They found that the growth rates of these already highly productive forests had been rising ever higher since at least 1960, and that they had experienced an apparent acceleration in growth rate sometime after 1980. Commenting on these findings, Pimm and Sugden (1994) reported that the consistency and simultaneity of the forest growth trends that Phillips and Gentry had documented on several continents led them to conclude that “enhanced productivity induced by increased CO<sub>2</sub> is the most plausible candidate for the cause of the increased turnover.”

A few years later, Phillips *et al.* (1998) analyzed forest growth rate data for the period 1958 to 1996 for several hundred plots of mature tropical trees scattered around the world, finding that tropical forest biomass, as a whole, increased substantially over the period of record. In fact, the increase in the Neotropics was equivalent to approximately 40 percent of the missing terrestrial carbon sink of the entire globe. Consequently, they concluded that

tropical forests “may be helping to buffer the rate of increase in atmospheric CO<sub>2</sub>, thereby reducing the impacts of global climate change.” And, again, they identified the aerial fertilization effect of the ongoing rise in the air’s CO<sub>2</sub> content as one of the primary factors likely to be responsible for this phenomenon.

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

Expanding upon this theme, Laurance *et al.* (2005) say they “interpreted these changes as being consistent with an ecological ‘signature’ expected from increasing forest productivity (cf., Phillips and Gentry, 1994; Lewis *et al.* 2004a,b; Phillips *et al.*, 2004).” They note, however, that they have been challenged in this conclusion by Nelson (2005), and they thus go on to consider his arguments in some detail, methodically dismantling them one by one.

Evidence of increasing dynamism and productivity of intact tropical forests continued, with Lewis *et al.*, (2004a) reporting that among 50 old-growth plots scattered across tropical South America, “stem recruitment, stem mortality, and biomass growth, and loss, *all* increased significantly.” In summarizing these and other findings, Lewis (2006) reports that over the past two decades, “these forests have shown concerted changes in their ecology, becoming, on average, faster growing—more productive—and more dynamic, and showing a net increase in above-ground biomass,” all of which rates of increase are greater than the previously documented increases in the rates of these phenomena. What is more, Lewis says that “preliminary analyses also suggest the African and Australian forests are showing structural changes similar to South American forests.”

So why should we care about growth trends of old forests? People who seek to address the issue

solely on the basis of forced reductions in anthropogenic CO<sub>2</sub> emissions claim that carbon sequestration by forests is viable only when forests are young and growing vigorously. (Pearce, 1999) As forests age, as claimed by the IPCC, they gradually lose their carbon-sequestering prowess, such that forests more than one hundred years old become essentially useless for removing CO<sub>2</sub> from the air, as they claim such ancient and decrepit stands yearly lose as much CO<sub>2</sub> via respiration as they take in via photosynthesis.

Although demonstrably erroneous, with repeated telling the twisted tale actually begins to sound reasonable. After all, doesn't the metabolism of every living thing slow down as it gets older? We grudgingly admit that it does—even with trees—but some trees live a remarkably long time. In Panama (Condit *et al.*, 1995), Brazil (Chambers *et al.*, 1998; Laurance *et al.*, 2004; Chambers *et al.*, 2001), and many parts of the southwestern United States (Graybill and Idso, 1993), for example, individuals of a number of different species have been shown to live for nearly one and a half millennia. At a hundred years of age, these super-slurpers of CO<sub>2</sub> are mere youngsters. And in their really old age, their appetite for the vital gas, though diminished, is not lost. In fact, Chambers *et al.* (1998) indicate that the long-lived trees of Brazil continue to experience protracted slow growth even at 1,400 years of age. And protracted slow growth (evident in yearly increasing trunk diameters) of very old and *large* trees can absorb a huge amount of CO<sub>2</sub> 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 percent of their above-ground biomass is contained in less than the largest 10 percent of their trees. Consequently, since the life span of these massive long-lived trees is considerably greater than the projected life span of the entire "Age of Fossil Fuels," their cultivation and preservation represents an essentially permanent, though only partial, solution to the perceived problem of the anthropogenic global warming.

Another important fact about forests and their ability to sequester carbon over long periods of time is that the forest itself is the unit of primary importance when it comes to determining the amount of carbon that can be sequestered on a unit area of land. Cary *et al.* (2001) note most models of forest carbon sequestration wrongly assume that "age-related growth trends of individual trees and even-aged, monospecific stands can be extended to natural

forests." When they compared the predictions of such models against real-world data they gathered from northern Rocky Mountain subalpine forests that ranged in age from 67 to 458 years, for example, they found that above-ground net primary productivity in 200-year-old natural stands was almost twice as great as that of modeled stands, and that the difference between the two increased linearly throughout the entire sampled age range.

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

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

Another study relevant to the ability of forests to act as long-term carbon sinks was conducted by Luo *et al.* (2003), who analyzed data obtained from the Duke Forest FACE experiment, in which three 30-meter-diameter plots within a 13-year-old forest (composed primarily of loblolly pines with sweetgum and yellow poplar trees as sub-dominants, together with numerous other trees, shrubs, and vines that occupy still smaller niches) began to be enriched with an extra 200 ppm of CO<sub>2</sub> in August 1996, while three similar plots were maintained at the ambient atmospheric CO<sub>2</sub> concentration. A number of papers describing different facets of this still-ongoing long-term study have been published; and as recounted by Luo *et al.*, they have revealed the existence of a CO<sub>2</sub>-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<sub>2</sub> than at ambient CO<sub>2</sub> [Schlesinger and Lichter, 2001].”

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

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

To see if these claims had any merit, Paw U *et al.* used an eddy covariance technique to estimate the CO<sub>2</sub> exchange rate of the oldest forest ecosystem (500 years old) in the AmeriFlux network of carbon-flux measurement stations—the Wind River old-growth forest in southwestern Washington, USA, which is composed mainly of Douglas fir and western hemlock—over a period of 16 months, from May 1998 to August 1999. Throughout this period, the 14 scientists report “there were no monthly averages with net release of CO<sub>2</sub>,” and that the cumulative net ecosystem exchange showed “remarkable sequestration of carbon, comparable to many younger forests.” They concluded that “in contrast to frequently stated opinions, old-growth forests can be significant carbon sinks,” noting that “the old-growth forests of the Pacific Northwest can contribute to

optimizing carbon sequestration strategies while continuing to provide ecosystem services essential to supporting biodiversity.”

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

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

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

These observations about forests are remarkably similar to recent findings regarding humans; i.e., that nongenetic interventions, even late in life, can put one

on a healthier trajectory that extends productive lifespan. So what is the global “intervention” that has put the planet’s trees on the healthier trajectory of being able to sequester significant amounts of carbon in their old age, when past theory (which was obviously based on past observations) decreed they should be in a state of no-net-growth or even negative growth? The answer is probably CO<sub>2</sub> enhancement. For any tree of age 250 years or more, the greater portion of its life (at least two-thirds of it) has been spent in an atmosphere of reduced CO<sub>2</sub> content. Up until 1920, for example, the air’s CO<sub>2</sub> concentration had never been above 300 ppm throughout the lives of such trees, whereas it is currently 375 ppm or 25 percent higher. And for older trees, even greater portions of their lives have been spent in air of even lower CO<sub>2</sub> concentration. Hence, the “intervention” that has given new life to old trees would appear to be the aerial fertilization effect produced by the CO<sub>2</sub> that resulted from the Industrial Revolution and is being maintained by its ever-expanding aftermath (Idso, 1995).

Based on these many observations, as well as the results of the study of Greenep *et al.* (2003), which strongly suggest, in their words, that “the capacity for enhanced photosynthesis in trees growing in elevated CO<sub>2</sub> is unlikely to be lost in subsequent generations,” it would appear that earth’s forests will remain strong sinks for atmospheric carbon well into the distant future. A wealth of scientific data confirms the reality of the ever-increasing productivity of earth’s older forests, especially those of Amazonia, concomitant with the rise in the air’s CO<sub>2</sub> content. An even greater wealth of laboratory and field data demonstrates that rising forest productivity is what one would expect to observe in response to the stimulus provided by the ongoing rise in the atmosphere’s CO<sub>2</sub> concentration.

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

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### 7.7.2. Decomposition

What is the fate of the extra carbon that is stored within plant tissues as a consequence of atmospheric CO<sub>2</sub> enrichment? Is it rapidly returned to the atmosphere following tissue senescence and decomposition? Or is it locked away for long periods of time? Experiments and real-world observations reveal that atmospheric CO<sub>2</sub> enrichment typically reduces, or has no effect upon, decomposition rates of senesced plant material.

#### 7.7.2.1. Processes and Properties

Atmospheric CO<sub>2</sub> enrichment stimulates photosynthesis and growth in nearly all plants, typically producing more non-structural carbohydrates, which can be used to manufacture more carbon-based secondary compounds (CBSCs) or phenolics. This observation is important because phenolics tend to inhibit the decomposition of the organic matter in which they are found (Freeman *et al.*, 2001). If elevated levels of atmospheric CO<sub>2</sub> lead to the production of more of these decay-resistant substances, one would expect the ongoing rise in the air's CO<sub>2</sub> content to lead to the enhanced

sequestration of plant-litter-derived carbon in the world's soils, producing a negative feedback phenomenon that would tend to slow the rate of rise of the air's CO<sub>2</sub> content and thereby moderate CO<sub>2</sub>-induced global warming.

For a long time, research on this matter was rather muddled. Many studies reported the expected increases in CBSC concentrations with experimentally created increases in the air's CO<sub>2</sub> content. Others, however, could find no significant plant phenolic content changes; a few even detected CO<sub>2</sub>-induced decreases in CBSC concentrations. Penuelas *et al.* (1997) finally brought order to the issue when they identified the key role played by soil nitrogen.

In analyzing the results of several different studies, Penuelas *et al.* noticed that when soil nitrogen supply was less than adequate, some of the CBSC responses to a doubling of the air's CO<sub>2</sub> content were negative, i.e., a portion of the studies indicated that plant CBSC concentrations declined as the air's CO<sub>2</sub> content rose. When soil nutrient supply was more than adequate, however, the responses were almost all positive, with plant CBSC concentrations rising in response to a doubling of the air's CO<sub>2</sub> concentration. In addition, when the CO<sub>2</sub> content of the air was tripled, *all* CBSC responses, under both low and high soil nitrogen conditions, were positive.

The solution to the puzzle was thus fairly simple. With a tripling of the air's CO<sub>2</sub> content, nearly all plants exhibited increases in CBSC production; but with only a doubling of the atmospheric CO<sub>2</sub> concentration, adequate nitrogen is needed to ensure a positive CBSC response.

What makes these observations exciting is that atmospheric CO<sub>2</sub> enrichment, in addition to enhancing plant growth, typically stimulates nitrogen fixation in both woody (Olesniewicz and Thomas, 1999) and non-woody (Niklaus *et al.*, 1998; Dakora and Drake, 2000) legumes. As the air's CO<sub>2</sub> content continues to rise, earth's nitrogen-fixing plants should become ever more proficient in this important enterprise. In addition, some of the extra nitrogen thus introduced into earth's ecosystems will likely be shared with non-nitrogen-fixing plants. Also, since the microorganisms responsible for nitrogen fixation are found in nearly all natural ecosystems (Gifford, 1992), and since atmospheric CO<sub>2</sub> enrichment can directly stimulate the nitrogen-fixing activities of these microbes (Lowe and Evans, 1962), it can be appreciated that the ongoing rise in the air's CO<sub>2</sub> content will likely provide more nitrogen for the

production of more CBSCs in all of earth's plants. And with ever-increasing concentrations of decay-resistant materials being found throughout plant tissues, the plant-derived organic matter that is incorporated into soils should remain there for ever longer periods of time.

On the other hand, in a meta-analysis of the effects of atmospheric CO<sub>2</sub> enrichment on leaf-litter chemistry and decomposition rate that was based on a total of 67 experimental observations, Norby *et al.* (2001) found that elevated atmospheric CO<sub>2</sub> concentrations—mostly between 600 and 700 ppm—reduced leaf-litter nitrogen concentration by about 7 percent. But in experiments where plants were grown under as close to natural conditions as possible, such as in open-top chambers, free-air CO<sub>2</sub> enrichment (FACE) plots, or in the proximity of CO<sub>2</sub>-emitting springs, there were no significant effects of elevated CO<sub>2</sub> on leaf-litter nitrogen content.

In addition, based on a total of 46 experimental observations, Norby *et al.* determined that elevated atmospheric CO<sub>2</sub> concentrations increased leaf-litter lignin concentrations by an average of 6.5 percent. However, these increases in lignin content occurred in woody but not in herbaceous species. And again, the lignin concentrations of leaf litter were not affected by elevated CO<sub>2</sub> when plants were grown in open-top chambers, FACE plots, or in the proximity of CO<sub>2</sub>-emitting springs.

In an analysis of a total of 101 observations, Norby *et al.* found elevated CO<sub>2</sub> had no consistent effect on leaf-litter decomposition rate in any type of experimental setting. As the air's CO<sub>2</sub> content continues to rise, it will likely have little to no impact on leaf-litter chemistry and rates of leaf-litter decomposition. Since there will be more leaf litter produced in a high-CO<sub>2</sub> world of the future, however, that fact alone will ensure that more carbon is sequestered in the world's soils for longer periods of time.

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

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#### 7.7.2.2. Agricultural Crops

In the study by Booker *et al.* (2000), leaves from defoliated cotton plants grown at an atmospheric CO<sub>2</sub> concentration of 720 ppm displayed significantly greater amounts of starch and soluble sugars and significantly lower concentrations of nitrogen than the leaves of plants grown in ambient air. These changes in the quality of the leaf litter produced under high CO<sub>2</sub> likely affected its subsequent decomposition rate, which was 10 to 14 percent slower than that observed for leaf litter collected from plants grown in air of normal CO<sub>2</sub> concentration. Likewise, when crop residues from soybean and sorghum plants that were raised in twice-ambient CO<sub>2</sub> environments were mixed with soils to study their decomposition rates, Torbert *et al.* (1998) noted they lost significantly less carbon – up to 40 percent less – than similarly treated crop residues from ambiently grown crops.

In contrast to the aforementioned studies, neither Van Vuuren *et al.* (2000), for spring wheat, nor Henning *et al.* (1996), for soybean and sorghum, found any significant differences in the decomposition rates of the residues of crops grown under conditions of high or normal atmospheric CO<sub>2</sub> concentration.

As the air's CO<sub>2</sub> content continues to rise, therefore, and agricultural crops grow more robustly and return greater amounts of litter to the soil, it is likely that greater amounts of carbon will be sequestered in the soil in which they grew, as crop residue decomposition rates are significantly decreased or remain unchanged.

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

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#### 7.7.2.3. Grassland Species

In the study of Nitschelm *et al.* (1997), white clover exposed to an atmospheric CO<sub>2</sub> concentration of 600 ppm for one growing season channeled 50 percent more newly fixed carbon compounds into the soil than similar plants exposed to ambient air. In addition, the clover's roots decomposed at a rate that was 24 percent slower than that observed for roots of control plants, as has also been reported for white clover by David *et al.* (2001). These observations suggest that soil carbon sequestration under white clover ecosystems will be greatly enhanced as the air's CO<sub>2</sub> content continues to rise, as was also shown for moderately fertile sandstone grasslands (Hu *et al.*, 2001).

Similar results have been observed with mini-ecosystems comprised entirely of perennial ryegrass. Van Ginkel *et al.* (1996), for example, demonstrated that exposing this species to an atmospheric CO<sub>2</sub> concentration of 700 ppm for two months caused a 92 percent increase in root growth and 19 percent and 14 percent decreases in root decomposition rates one and two years, respectively, after incubating ground roots within soils. This work was later followed up by Van Ginkel and Gorissen (1998), who showed a 13 percent reduction in the decomposition rates of CO<sub>2</sub>-enriched perennial ryegrass roots in both disturbed and undisturbed root profiles. This and other work led the authors to calculate that CO<sub>2</sub>-induced reductions in the decomposition of perennial ryegrass litter, which enhances soil carbon sequestration, could well be large enough to remove over half of the anthropogenic CO<sub>2</sub> emissions that may be released in the next century (Van Ginkel *et al.*, 1999).

In some cases, atmospheric CO<sub>2</sub> enrichment has little or no significant effect on litter quality and subsequent rates of litter decomposition, as was the case in the study of Hirschel *et al.* (1997) for lowland

calcareous and high alpine grassland species. Similar non-effects of elevated CO<sub>2</sub> on litter decomposition have also been reported in a California grassland (Dukes and Field, 2000).

In light of these experimental findings, it would appear that as the air's CO<sub>2</sub> concentration increases, litter decomposition rates of grassland species will likely decline, increasing the amount of carbon sequestered in grassland soils. Since this phenomenon is augmented by the aerial fertilization effect of atmospheric CO<sub>2</sub> enrichment, which leads to the production of greater amounts of litter, there is thus a double reason for expecting more carbon to be removed from the atmosphere by earth's grasslands in the future.

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

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### 7.7.2.4. Woody Plants

The sequestering of carbon in the soils upon which woody plants grow has the potential to provide a powerful brake on the rate of rise of the air's CO<sub>2</sub> content if the plant litter that is incorporated into those soils does not decompose more rapidly in a CO<sub>2</sub>-enriched atmosphere than it does in current ambient air. It is important to determine if this latter constraint is true or false. In this section we review this question with respect to litter produced by conifers and deciduous trees.

Scherzel *et al.* (1998) exposed seedlings of two eastern white pine genotypes to elevated concentrations of atmospheric CO<sub>2</sub> and O<sub>3</sub> in open-top chambers for four full growing seasons, finding no changes in the decomposition rates of the litter of either genotype to the concentration increases of either of these two gases. Likewise, Kainulainen *et al.* (2003) could find no evidence that the litter of 22-year-old Scots pine trees that had been exposed to elevated concentrations of CO<sub>2</sub> and O<sub>3</sub> for three full years decomposed any faster or slower than litter produced in ambient air. In addition, Finzi and Schlesinger (2002) found that the decomposition rate of litter from 13-year-old loblolly pine trees was unaffected by elevated CO<sub>2</sub> concentrations maintained for a period of two full years in a FACE study.

In light of these observations, plus the fact that Saxe *et al.* (1998) have determined that a doubling of the air's CO<sub>2</sub> content leads to more than a doubling of the biomass production of coniferous species, it logically follows that the ongoing rise in the atmosphere's CO<sub>2</sub> concentration is increasing carbon sequestration rates in the soils upon which conifers grow and producing a significant negative feedback phenomenon that slows the rate of rise of the air's CO<sub>2</sub> content.

What about deciduous trees? Scherzel *et al.* (1998) exposed seedlings of yellow poplar trees to elevated concentrations of atmospheric CO<sub>2</sub> and O<sub>3</sub> in

open-top chambers for four full growing seasons, finding that rates of litter decomposition were similar for all treatments for the first five months of the study. Thereafter, however, litter produced in the elevated O<sub>3</sub> and CO<sub>2</sub> treatment decomposed at a significantly slower rate, such that after two years had passed, the litter from the elevated O<sub>3</sub> and CO<sub>2</sub> treatment contained approximately 12 percent more biomass than the litter from any other treatment.

Cotrufo *et al.* (1998) grew two-year-old ash and sycamore seedlings for one growing season in closed-top chambers maintained at atmospheric CO<sub>2</sub> concentrations of 350 and 600 ppm. The high-CO<sub>2</sub> 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<sub>2</sub>-enriched chambers. After one year of incubation, for example, litter bags from the CO<sub>2</sub>-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<sub>2</sub> than when fed litter generated from seedlings grown in ambient air.

De Angelis *et al.* (2000) constructed large open-top chambers around 30-year-old mixed stands of naturally growing Mediterranean forest species (dominated by *Quercus ilex*, *Phillyrea augustifolia*, and *Pistacia lentiscus*) near the coast of central Italy. Half of the chambers were exposed to ambient air of 350 ppm CO<sub>2</sub>, while half were exposed to air of 710 ppm CO<sub>2</sub>; and after three years, the lignin and carbon concentrations of the leaf litter of all three species were increased by 18 and 4 percent, respectively, while their nitrogen concentrations were reduced by 13 percent. These changes resulted in a 20 percent CO<sub>2</sub>-induced increase in the carbon-to-nitrogen ratio of the leaf litter, which parameter is commonly used to predict decomposition rates, where larger ratios are generally associated with less rapid decomposition than smaller ratios. This case was no exception, with 4 percent less decomposition occurring in the leaf litter gathered from beneath the CO<sub>2</sub>-enriched trees than in the litter collected from beneath the trees growing in ambient air.

Cotrufo and Ineson (2000) grew beech seedlings for five years in open-top chambers fumigated with air containing either 350 or 700 ppm CO<sub>2</sub>. Subsequently, woody twigs from each CO<sub>2</sub> treatment were collected and incubated in native forest soils for 42 months, after which they determined there was no significant effect of the differential CO<sub>2</sub> exposure

during growth on subsequent woody twig decomposition, although the mean decomposition rate of the CO<sub>2</sub>-enriched twigs was 5 percent less than that of the ambient-treatment twigs.

Conway *et al.* (2000) grew two-year-old ash tree seedlings in solardomes maintained at atmospheric CO<sub>2</sub> 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<sub>2</sub> significantly reduced the amount of nitrogen in the senesced leaves, thus giving the CO<sub>2</sub>-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<sub>2</sub>-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<sub>2</sub> concentrations of 350 and 700 ppm. At the end of this period, naturally senesced leaf litter was collected, analyzed, and allowed to decompose under ambient conditions for 111 days. Although the elevated CO<sub>2</sub> slightly lowered leaf litter nitrogen content, it had no effect on litter sugar, starch, or tannin concentrations. With little to no CO<sub>2</sub>-induced effects on leaf litter quality, there was no CO<sub>2</sub>-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<sub>2</sub> concentrations of either 350 or 700 ppm, after which they incubated ambient- and elevated-CO<sub>2</sub>-produced fine roots for 2.2 years in the chamber soils, which were nutrient-poor and often water-stressed. They found the elevated CO<sub>2</sub> did not significantly affect the decomposition rates of the fine roots originating from either the ambient or CO<sub>2</sub>-enriched environments.

Of these seven studies of deciduous tree species, five are suggestive of slight reductions in litter decomposition rates under CO<sub>2</sub>-enriched growth conditions, while two show no effect. With deciduous trees exhibiting large growth enhancements in response to atmospheric CO<sub>2</sub> enrichment, we can expect to see large increases in the amounts of carbon they sequester in the soils on which they grow as the air's CO<sub>2</sub> content continues to rise. And this phenomenon should slow the rate of rise of the

atmosphere's CO<sub>2</sub> concentration and thereby reduce the impetus for CO<sub>2</sub>-induced global warming.

To summarize, scientific theory and empirical research show that the ongoing rise in the air's CO<sub>2</sub> content will not materially alter the rate of decomposition of the world's soil organic matter. This means the rate at which carbon is sequestered in the world's soils should continue to increase, a joint function of the rate at which the productivity of earth's plants is increased by the aerial fertilization effect of the rising atmospheric CO<sub>2</sub> concentration and the rate of expansion of the planet's vegetation into drier regions of the globe that is made possible by the concomitant CO<sub>2</sub>-induced increase in vegetative water use efficiency.

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

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## 7.7.3. Temperature and Carbon Sequestration

### 7.7.3.1. General

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

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

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

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

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

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

Rising CO<sub>2</sub> levels tend to maintain (Henning *et al.*, 1996) or decrease (Torbert *et al.*, 1998; Nitschelm *et al.*, 1997) CO<sub>2</sub> fluxes from agricultural soils. Consequently, these phenomena tend to increase the carbon contents of most soils in CO<sub>2</sub>-enriched atmospheres. However, it is sometimes suggested that rising air temperatures, which can accelerate the breakdown of soil organic matter and increase biological respiration rates, could negate this CO<sub>2</sub>-induced enhancement of carbon sequestration,

possibly leading to an even greater release of carbon back to the atmosphere.

Casella and Soussana (1997) grew perennial ryegrass in controlled environments receiving ambient and elevated (700 ppm) atmospheric CO<sub>2</sub> concentrations, two levels of soil nitrogen, and ambient and elevated (+3°C) air temperatures for a period of two years, finding that “a relatively large part of the additional photosynthetic carbon is stored below-ground during the two first growing seasons after exposure to elevated CO<sub>2</sub>, thereby increasing significantly the below-ground carbon pool.” At the low and high levels of soil nitrogen supply, for example, the elevated CO<sub>2</sub> increased soil carbon storage by 32 and 96 percent, respectively, “with no significant increased temperature effect.” The authors thus concluded that in spite of predicted increases in temperature, “this stimulation of the below-ground carbon sequestration in temperate grassland soils could exert a negative feed-back on the current rise of the atmospheric CO<sub>2</sub> concentration.”

Much the same conclusion was reached by Van Ginkel *et al.* (1999). After reviewing prior experimental work that established the growth and decomposition responses of perennial ryegrass to both atmospheric CO<sub>2</sub> enrichment and increased temperature, these researchers concluded that, at both low and high soil nitrogen contents, CO<sub>2</sub>-induced increases in plant growth and CO<sub>2</sub>-induced decreases in plant decomposition rate are more than sufficient to counteract any enhanced soil respiration rate that might be caused by an increase in air temperature. In addition, after reconstructing carbon storage in the terrestrial vegetation of Northern Eurasia as far back as 125,000 years ago, Velichko *et al.* (1999) determined that plants in this part of the world were more productive and efficient in sequestering carbon at higher temperatures than they were at lower temperatures. Similarly, Allen *et al.*, (1999) used sediment cores from a lake in southern Italy and from the Mediterranean Sea to conclude that, over the past 102,000 years, warmer climates have been better for vegetative productivity and carbon sequestration than have cooler climates.

In conclusion, research conducted to date strongly suggests that the CO<sub>2</sub>-induced enhancement of vegetative carbon sequestration will not be reduced by any future rise in air temperature, regardless of its cause. The rest of this section looks more closely at research regarding forests and peatlands.

Additional information on this topic, including reviews of newer publications as they become

available, can be found at <http://www.co2science.org/subject/c/carbonco2xtemp.php>.

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### 7.7.3.2. Forests

Liski *et al.* (1999) studied soil carbon storage across a temperature gradient in a modern-day Finnish boreal forest, determining that carbon sequestration in the soil of this forest increased with temperature. In deciduous forests of the eastern United States, White *et al.* (1999) also determined that persistent increases

in growing season length (due to rising air temperatures) may lead to long-term increases in carbon storage, which tend to counterbalance the effects of increasing air temperature on respiration rates.

A data-driven analysis by Fan *et al.* (1998) suggests that the carbon-sequestering abilities of North America's forests between 15 and 51°N latitude are so robust that they can yearly remove from the atmosphere all of the CO<sub>2</sub> annually released to it by fossil fuel consumption in both the United States and Canada (and this calculation was done during a time touted as having the warmest temperatures on record). Moreover, Phillips *et al.* (1998) have shown that carbon sequestration in tropical forests has increased substantially over the past 42 years, in spite of any temperature increases that may have occurred during that time.

Similarly, King *et al.* (1999) showed that aspen seedlings increased their photosynthetic rates and biomass production as temperatures rose from 10 to 29°C, putting to rest the idea that high-temperature-induced increases in respiration rates would cause net losses in carbon fixation. White *et al.* (2000) showed that rising temperatures increased the growing season by about 15 days for 12 sites in deciduous forests located within the United States, causing a 1.6 percent increase in net ecosystem productivity per day. Thus, rather than exerting a negative influence on forest carbon sequestration, if air temperatures rise in the future they will likely have a positive effect on carbon storage in forests and their associated soils.

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### 7.7.3.3. Peatlands

Putative CO<sub>2</sub>-induced global warming has long been predicted to turn boreal and tundra biomes into major sources of carbon emissions. Until just a few short years ago it was nearly universally believed that rising air temperatures would lead to the thawing of extensive areas of permafrost and the subsequent decomposition of their vast stores of organic matter, which, it was thought, would release much of the peatlands' tightly held carbon, enabling it to make its way back to the atmosphere as CO<sub>2</sub>.

Improved soil drainage and increased aridity were also envisioned to help the process along, possibly freeing enough carbon at a sufficiently rapid rate to rival the amount released to the atmosphere as CO<sub>2</sub> by all anthropogenic sources combined. The end result was claimed to be a tremendous positive feedback to the ongoing rise in the air's CO<sub>2</sub> content, which was envisioned to produce a greatly amplified atmospheric greenhouse effect that would lead to catastrophic global warming.

This scenario was always too bad to be true. Why? Because it did not begin to deal with the incredible complexity of the issue, several important neglected aspects of which have been briefly described by Weintraub and Schimel (2005).

One of the first cracks in the seemingly sound hypothesis was revealed by the study of Oechel *et al.* (2000), wherein long-term measurements of net ecosystem CO<sub>2</sub> exchange rates in wet-sedge and moist-tussock tundra communities of the Alaskan Arctic indicated that these ecosystems were gradually changing from carbon sources to carbon sinks. The transition occurred between 1992 and 1996, at the apex of a regional warming trend that culminated with the highest summer temperature and surface water deficit of the previous four decades.

How did this dramatic and unexpected biological transformation happen? The answer of the scientists who documented the phenomenon was "a previously undemonstrated capacity for ecosystems to

metabolically adjust to long-term changes in climate." Just as people can change their behavior in response to environmental stimuli, so can plants. And this ecological acclimation process is only one of several newly recognized phenomena that have caused scientists to radically revise the way they think about global change in Arctic regions.

Camill *et al.* (2001) investigated (1) changes in peat accumulation across a regional gradient of mean annual temperature in Manitoba, Canada, (2) net above-ground primary production and decomposition for major functional plant groups of the region, and (3) soil cores from several frozen and thawed bog sites that were used to determine long-term changes in organic matter accumulation following the thawing of boreal peatlands. In direct contradiction of earlier thinking on the subject, but in confirmation of the more recent findings of Camill (1999a,b), the researchers discovered that above-ground biomass and decomposition "were more strongly controlled by local succession than regional climate." In other words, they determined that over a period of several years, natural changes in plant community composition generally "have stronger effects on carbon sequestration than do simple increases in temperature and aridity." Their core-derived assessments of peat accumulation over the past two centuries demonstrated that rates of biological carbon sequestration can almost double following the melting of permafrost, in harmony with the findings of Robinson and Moore (2000) and Turetsky *et al.* (2000), who found rates of organic matter accumulation in other recently thawed peatlands to have risen by 60-72 percent.

Griffis and Rouse (2001) drew upon the findings of a number of experiments conducted over the past quarter-century at a subarctic sedge fen near Churchill, Manitoba, Canada, in order to develop an empirical model of net ecosystem CO<sub>2</sub> exchange there. The most fundamental finding of this endeavor was that "carbon acquisition is greatest during wet and warm conditions," such as is generally predicted for the world as a whole by today's most advanced climate models. However, since regional climate change predictions are not very dependable, the two scientists investigated the consequences of a 4°C increase in temperature accompanied by both a 30 percent increase and decrease in precipitation; and "in all cases," as they put it, "the equilibrium response showed substantial increases in carbon acquisition." One of the reasons behind this finding, as explained by Griffis and Rouse, is that "arctic ecosystems

photosynthesize below their temperature optimum over the majority of the growing season,” so that increasing temperatures enhance plant growth rates considerably more than they increase plant decay rates.

In summing up their findings, Griffis and Rouse say “warm surface temperatures combined with wet soil conditions in the early growing season increase above-ground biomass and carbon acquisition throughout the summer season.” Indeed, they note that “wet spring conditions can lead to greater CO<sub>2</sub> acquisition through much of the growing period even when drier conditions persist.” They thus conclude that if climate change plays out as described by current climate models—i.e., if the world becomes warmer and wetter—“northern wetlands should therefore become larger sinks for atmospheric CO<sub>2</sub>.”

In a somewhat different type of study, Mauquoy *et al.* (2002) analyzed three cores obtained from a raised peat bog in the UK (Walton Moss) and a single core obtained from a similar bog in Denmark (Lille Vildmose) for macro- and micro-fossils (pollen), bulk density, loss on ignition, carbon/nitrogen ratios, and humification, while they were <sup>14</sup>C dated by accelerator mass spectrometry. Among a variety of other things, it was determined, in their words, that “the lowest carbon accumulation values for the Walton Moss monoliths between ca. cal AD 1300 and 1800 and between ca. cal AD 1490 and 1580 for Lille Vildmose occurred during the course of Little Ice Age deteriorations,” which finding they describe as being much the same as the observation “made by Oldfield *et al.* (1997) for a Swedish ‘aapa’ mire between ca. cal AD 1400 and 1800.” They also report that carbon accumulation before this, in the Medieval Warm Period, was higher, as was also the case following the Little Ice Age, as the earth transitioned to the Modern Warm Period. Consequently, whereas the IPCC claims that warming will hasten the release of carbon from ancient peat bogs, these real-world data demonstrate that just the opposite is more likely.

In a somewhat similar study, but one that concentrated more on the role of nitrogen than of temperature, Turunen *et al.* (2004) derived recent (0-150 years) and long-term (2,000-10,000 years) apparent carbon accumulation rates for several ombrotrophic peatlands in eastern Canada with the help of <sup>210</sup>Pb- and <sup>14</sup>C-dating of soil-core materials. This work revealed that the average long-term apparent rate of C accumulation at 15 sites was  $19 \pm 8$  g C m<sup>-2</sup> yr<sup>-1</sup>, which is comparable to long-term rates observed in Finnish bogs by Tolonen and Turunen

(1996) and Turunen *et al.* (2002). Recent C accumulation rates at 23 sites, on the other hand, were much higher, averaging  $73 \pm 17$  g C m<sup>-2</sup> yr<sup>-1</sup>, which results, in their words, are also “similar to results from Finland (Tolonen and Turunen, 1996; Pitkanen *et al.*, 1999) and for boreal *Sphagnum* dominated peat deposits in North America (Tolonen *et al.*, 1988; Wieder *et al.*, 1994; Turetsky *et al.*, 2000).” Noting that recent rates of C accumulation are “strikingly higher” than long-term rates, Turunen *et al.* suggested that increased N deposition “leads to larger rates of C and N accumulation in the bogs, as has been found in European forests (Kauppi *et al.*, 1992; Berg and Matzner, 1997), and could account for some of the missing C sink in the global C budget.”

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

In a study of experimental warming of Icelandic plant communities designed to see if the warming of high-latitude tundra ecosystems would result in significant losses of species and reduced biodiversity, Jonsdottir *et al.* (2005) conducted a field experiment to learn how vegetation might respond to moderate warming at the low end of what is predicted by most climate models for a doubling of the air’s CO<sub>2</sub> content. Specifically, they studied the effects of 3-5 years of modest surface warming (1°-2°C) on two widespread but contrasting tundra plant communities, one of which was a nutrient-deficient and species-poor moss heath and the other of which was a

species-rich dwarf shrub heath. At the conclusion of the study, no changes in community structure were detected in the moss heath. In the dwarf shrub heath, on the other hand, the number of deciduous and evergreen dwarf shrubs increased more than 50 percent, bryophytes decreased by 18 percent, and canopy height increased by 100 percent, but with the researchers reporting they “detected no changes in species richness or other diversity measures in either community and the abundance of lichens did not change.” Although Jonsdottir *et al.*'s study was a relatively short-term experiment as far as ecosystem studies go, its results indicate a rise in temperature need not have a negative effect on the species diversity of high-latitude tundra ecosystems and may have a positive influence on plant growth.

In a study that included an entirely new element of complexity, Cole *et al.* (2002) constructed 48 small microcosms from soil and litter they collected near the summit of Great Dun Fell, Cumbria, England. Subsequent to “defaunating” this material by reducing its temperature to  $-80^{\circ}\text{C}$  for 24 hours, they thawed and inoculated it with native soil microbes, after which half of the microcosms were incubated in the dark at  $12^{\circ}\text{C}$  and half at  $18^{\circ}\text{C}$  for two weeks, in order to establish near-identical communities of the soils' natural complement of microflora in each microcosm. The former of these temperatures was chosen to represent mean August soil temperature at a depth of 10 cm at the site of soil collection, while the latter was picked to be “close to model predictions for soil warming that might result from a doubling of  $\text{CO}_2$  in blanket peat environments.”

Next, 10 seedlings of *Festuca ovina*, an indigenous grass of blanket peat, were planted in each of the microcosms, while 100 enchytraeid worms were added to each of half of the mini-ecosystems, producing four experimental treatments: ambient temperature, ambient temperature plus enchytraeid worms, elevated temperature, and elevated temperature plus enchytraeid worms. Then, the 48 microcosms—sufficient to destructively harvest three replicates of each treatment four different times throughout the course of the 64-day experiment—were arranged in a fully randomized design and maintained at either  $12^{\circ}$  or  $18^{\circ}\text{C}$  with alternating 12-hour light and dark periods, while being given distilled water every two days to maintain their original weights.

So what did the researchers learn? First, they found that elevated temperature reduced the ability of the enchytraeid worms to enhance the loss of carbon

from the microcosms. At the normal ambient temperature, the presence of the worms enhanced dissolved organic carbon (DOC) loss by 16 percent, while at the elevated temperature expected for a doubling of the air's  $\text{CO}_2$  content they had no effect on DOC. In addition, Cole *et al.* note that “warming may cause drying at the soil surface, forcing enchytraeids to burrow to deeper subsurface horizons;” and since the worms are known to have little influence on soil carbon dynamics below a depth of about 4 cm (Cole *et al.*, 2000), the researchers concluded that this additional consequence of warming would further reduce the ability of enchytraeids to enhance carbon loss from blanket peatlands. In summing up their findings, Cole *et al.* concluded that “the soil biotic response to warming in this study was negative,” in that it resulted in a reduced loss of carbon to the atmosphere.

But what about the effects of elevated  $\text{CO}_2$  itself on the loss of DOC from soils? Freeman *et al.* (2004) note that riverine transport of DOC has increased markedly in many places throughout the world over the past few decades (Schindler *et al.*, 1997; Freeman *et al.*, 2001; Worrall *et al.*, 2003); they suggest this phenomenon may be related to the historical increase in the air's  $\text{CO}_2$  content.

The researchers' first piece of evidence for this conclusion came from a three-year study of monoliths (11-cm diameter x 20-cm deep cores) taken from three Welsh peatlands—a bog that received nutrients solely from rainfall, a *fen* that gained more nutrients from surrounding soils and groundwater, and a riparian peatland that gained even more nutrients from nutrient-laden water transported from other terrestrial ecosystems via drainage streams—which they exposed to either ambient air or air enriched with an extra 235 ppm of  $\text{CO}_2$  within a solardome facility. This study revealed that the DOC released by monoliths from the three peatlands was significantly enhanced—by 14 percent in the bog, 49 percent in the fen, and 61 percent in the riparian peatland—by the additional  $\text{CO}_2$  to which they were exposed, which is the order of response one would expect from what we know about the stimulation of net primary productivity due to atmospheric  $\text{CO}_2$  enrichment, i.e., it is low in the face of low soil nutrients, intermediate when soil nutrient concentrations are intermediate, and high when soil nutrients are present in abundance. Consequently, Freeman *et al.* concluded that the DOC increases they observed “were induced by increased primary production and DOC exudation from plants,”

which conclusion logically follows from their findings.

Nevertheless, and to further test their hypothesis, they followed the translocation of labeled  $^{13}\text{C}$  through the plant-soil systems of the different peat monoliths for about two weeks after exposing them to ~99 percent-pure  $^{13}\text{CO}_2$  for a period of five hours. This exercise revealed that (1) the plants in the ambient-air and  $\text{CO}_2$ -enriched treatments assimilated 22.9 and 35.8 mg of  $^{13}\text{C}$  from the air, respectively, (2) the amount of DOC that was recovered from the leachate of the  $\text{CO}_2$ -enriched monoliths was 0.6 percent of that assimilated, or 0.215 mg ( $35.8 \text{ mg} \times 0.006 = 0.215 \text{ mg}$ ), and (3) the proportion of DOC in the soil solution of the  $\text{CO}_2$ -enriched monoliths that was derived from recently assimilated  $\text{CO}_2$  (the  $^{13}\text{C}$  labeled  $\text{CO}_2$ ) was 10 times higher than that of the control.

This latter observation suggests that the amount of DOC recovered from the leachate of the ambient-air monoliths was only about a tenth as much as that recovered from the leachate of the  $\text{CO}_2$ -enriched monoliths, which puts the former amount at about 0.022 mg. Hence, what really counts, i.e., the net sequestration of  $^{13}\text{C}$  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  $\text{CO}_2$ -enriched monoliths. In the end, therefore, even though the  $\text{CO}_2$ -enriched monoliths lost 10 times more  $^{13}\text{C}$  via root exudation than did the ambient-air monoliths, they still sequestered about 55 percent more  $^{13}\text{C}$  overall, primarily in living-plant tissues.

In light of this impressive array of pertinent findings, it would appear that continued increases in the air's  $\text{CO}_2$  concentration and temperature would not result in losses of carbon from earth's peatlands. Quite to the contrary, these environmental changes—if they persist—would likely work together to enhance carbon capture by these particular ecosystems.

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

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## 7.8. Other Benefits

Other benefits to plants of CO<sub>2</sub> enhancement documented in this section include superior nitrogen-use efficiency, increased nutrient acquisition, greater resistance to pathogens and parasitic plants, greater root development, greater seed and tannin production, and improved performance of transgenic plants. In addition to these benefits to plants, CO<sub>2</sub> enrichment benefits all life on earth by reducing plant emissions of isoprene, a chemical responsible for the production of tropospheric ozone.

### 7.8.1. Nitrogen-Use Efficiency

Long-term exposure to elevated atmospheric CO<sub>2</sub> concentrations often, but not always, elicits photosynthetic acclimation or down regulation in plants, which is typically accompanied by reduced amounts of rubisco and/or other photosynthetic proteins that are typically present in excess amounts in plants grown in ambient air. As a consequence, foliar nitrogen concentrations often decrease with atmospheric CO<sub>2</sub> enrichment, as nitrogen is mobilized out of leaves and into other areas of the plant to increase its availability for enhancing sink development or stimulating other nutrient-limited processes.

In reviewing the literature in this area, one quickly notices that in spite of the fact that photosynthetic acclimation has occurred, CO<sub>2</sub>-enriched plants nearly always display rates of photosynthesis that are greater than those of control plants exposed to ambient air. Consequently, photosynthetic nitrogen-use efficiency, i.e., the amount of carbon converted into sugars during the photosynthetic process per unit of leaf nitrogen, often increases dramatically in CO<sub>2</sub>-enriched plants.

In the study of Davey *et al.* (1999), for example, CO<sub>2</sub>-induced reductions in foliar nitrogen contents and concomitant increases in photosynthetic rates led to photosynthetic nitrogen-use efficiencies in the CO<sub>2</sub>-enriched (to 700 ppm CO<sub>2</sub>) grass *Agrostis capillaris* that were 27 and 62 percent greater than those observed in control plants grown at 360 ppm CO<sub>2</sub> under moderate and low soil nutrient conditions,