Rising atmospheric CO_2 and carbon sequestration in forests

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Rising CO_2 concentrations in the atmosphere could alter Earth's climate system, but it is thought that higher concentrations may improve plant growth through a process known as the "fertilization effect". Forests are an important part of the planet's carbon cycle, and sequester a substantial amount of the CO_2 released into the atmosphere by human activities. Many people believe that the amount of carbon sequestered by forests will increase as CO_2 concentrations rise. However, an increasing body of research suggests that the fertilization effect is limited by nutrients and air pollution, in addition to the well documented limitations posed by temperature and precipitation. This review suggests that existing forests are not likely to increase sequestration as atmospheric CO_2 increases. It is imperative, therefore, that we manage forests to maximize carbon retention in above- and belowground biomass and conserve soil carbon.

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Atmospheric CO_2 is an environmental paradox. It is an essential component in photosynthesis and thus essential for life, yet its increasing concentration in the atmosphere threatens to alter Earth's climate. Fossil fuel burning and changing land use since the onset of the Industrial Era have caused a steady rise in atmospheric CO_2 (Figure 1). While there is general agreement among scientists that the climate system is changing as a result of increasing atmospheric concentrations of CO_2 and other greenhouse gases, the degree to which temperature and precipitation patterns will change is uncertain. Nevertheless, strategies to remove CO_2 from the atmosphere are a focus of global change research and international treaty negotiations.

Terrestrial ecosystems are important in the Earth's carbon (C) balance and, potentially, in offsetting anthropogenic emissions of CO_2 (Figure 2). The biosphere (land and ocean) absorbs about half of the roughly 6 petagrams (Pg; 10^{15} grams) of C emitted annually from human activities (Schimel *et al.* 2001). On land, the largest C sink (1.3–2.9 Pg of C per year) is in the northern hemisphere (Houghton 2003), although substantial interannual variability exists (Schimel *et al.* 2001). As of the early 1990s, the temperate forests of the northern hemisphere have been thought to be a net sink of 0.6 to 0.7 Pg of C per year, based on forest inventories (Goodale *et al.* 2002). There is uncertainty, however, regarding the sources and sinks in the terrestrial biosphere (Houghton 2003). Moreover, it is not known whether present sequestration rates can be sustained, in view of the limits to forest regrowth and nutrient availability (Scholes and Noble 2001; Schimel *et al.* 2001).

Understanding the response of forest vegetation, associated soils, and soil organisms to elevated atmospheric CO_2 is central to determining the capacity of forested ecosystems to sequester anthropogenic CO_2. While reforestation and afforestation can clearly increase C sequestration (Prentice *et al.* 2001), it is not certain that rising atmospheric CO_2 will increase sequestration in existing forests. Here, we address how nitrogen (N) availability, air pollution, and C processing in forest ecosystems may limit sequestration in existing forests and associated soils with rising levels of atmospheric CO_2.

In a nutshell:

- An increase in carbon (C) sequestration by forests due to the fertilization effect is not likely to happen, because of limiting factors, including soil nitrogen and air pollution
- Long-term C sequestration in forest soils is dependent on soil type and characteristics, and is therfore unlikely to increase as a result of rising atmospheric CO_2
- Maximum C retention and conservation should be goals of forest management, in order to increase and retain long-term C pools
- Soil types that sequester substantial amounts of carbon should be identified and protected

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Where does the C go?

CO_2 enters the plant through stomata, the small pores in leaves through which CO_2, water vapor, and other gases are exchanged with the atmosphere. Within the leaf, CO_2 reacts with the rubisco enzyme complex, forming carbohydrates that are used to make various plant tissues and form storage pools (Figure 3). Some of the C assimilated in plants is released as CO_2 to the atmosphere through respiration. C is transferred to the soil by root exudates, root death, litter fall (leaves, twigs, and branches), and coarse woody debris (larger branches and trunks). Over time, litter and coarse woody debris on the forest floor and dead roots within the soil decompose via the soil food

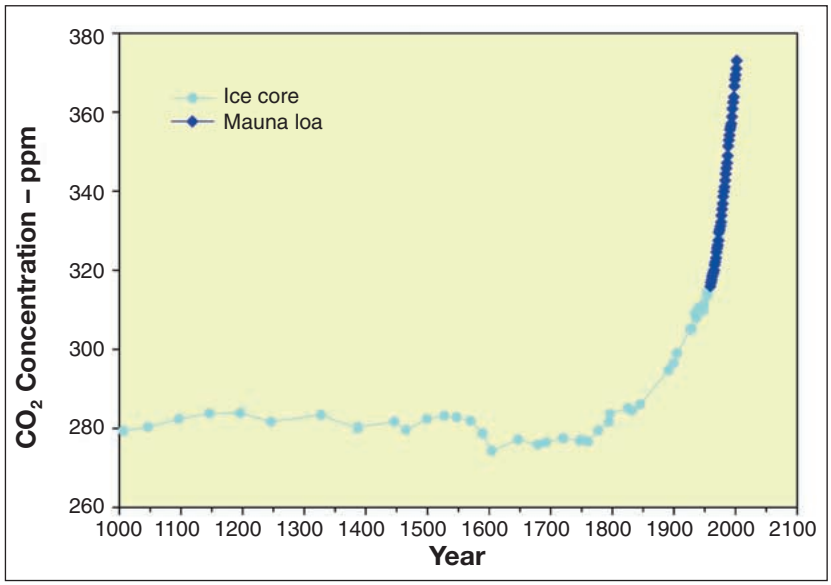


Figure 1. *Atmospheric CO_2 concentrations over the past millennium. From a pre-industrial level of approximately 280 ppm in the atmosphere, CO_2 concentrations have risen to over 370 ppm in the year 2000. By the end of the 21st century – depending on future industrial trends – concentrations are projected to reach 540 to 970 ppm (Prentice* et al. *2001). (Data sources: Etheridge* et al. *1998; Keeling* et al. *2004.)*

chain and are converted into soil organic matter. Decomposition releases most of the C to the atmosphere as CO_2, but a small portion is sequestered.

Not all tree growth is equally suited for long-term C sequestration in biomass (Figure 3). Deciduous trees hold their leaves for 1 year while conifers can hold needles for as long as 8 or more years. Fine roots live for days or years, depending on the species (Matamala *et al.* 2003). In contrast, tree trunks, large branches, and large roots, which remain on the tree for several decades or centuries, are the primary sites of C sequestration. As branches fall and trees die, decomposition releases CO_2 to the atmosphere (Harmon *et al.* 1990). When trees are harvested, some of the biomass is left to decompose; a portion is converted into manufactured forest products such as buildings, furniture, and paper items. Forest products have a carbon-storage half-life ranging from only 4 years for items made of paper to 65 years for building materials and furniture (Pussinen *et al.* 1997), times similar to those found in leaf litter and branch decomposition. To increase C sequestration in trees the amount of C allocated to trunks and large branches must be increased or the trees must live longer; C that is allocated to leaves and fine roots is recycled to the atmosphere too quickly to be an effective C sink.

Most of the annual C accumulation in growing forested ecosystems is found in trees and forest-floor litter; only a small portion enters the underlying mineral soil (Hooker and Compton 2003). Soil C compounds can be classified based on turnover time (Trumbore 1997): the "active" (or "fast") pool turns over in days to a year, the "intermediate" pool turns over in years to decades, and turnover in the "passive" (or "slow") pool takes more than a century. The active pool consists of easily decomposed litter and fine roots. The intermediate pool is a mixture of compounds with varying turnover times, but in many soils this pool contains the most C (Trumbore 1997). The passive pool – most important to long-term C sequestration – is composed of persistent organic compounds, such as humus, and accumulates very slowly.

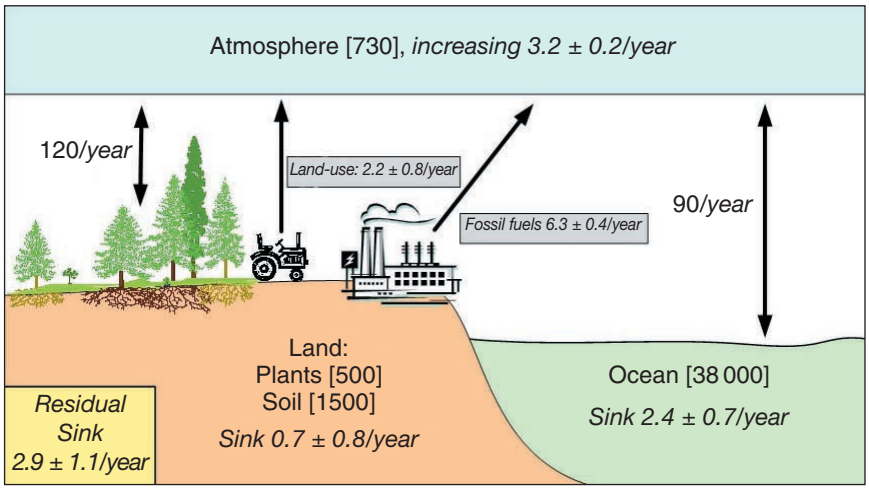


Figure 2. *The global C cycle. The global C cycle is represented showing the C pools (in brackets), atmospheric exchanges (double-headed arrows), anthropogenic emissions (arrows), and sinks (in italics). All units are in Pg C (1 Pg = 10^{15} grams = one billion metric tons) and fluxes in Pg C per year. The indicated C pools are annual averages over the 1980s. Atmospheric C is increasing by approximately 0.44% per year. To balance the global budget a residual sink for 2.9 Pg of C is needed; this represents C that is not accounted for – missing C (Houghton 2003). In contrast to the static view conveyed here, the C system is dynamic and coupled to the climate system on seasonal, interannual, and decadal timescales. (Data sources: pools and exchanges from Prentice* et al. *2001; anthropogenic emissions and sinks from Houghton 2003.)*

Will elevated CO_2 increase forest C sequestration?

The most obvious way to increase C sequestration is to increase forest growth. Elevated atmospheric CO_2 concentrations increase photosyn-

thetic type that includes most forest tree species – by increasing CO_2 uptake (Norby *et al.* 1999). This increase is a result of molecular competition within leaves for binding sites on the rubisco molecule shifting to increase carboxylation and decrease oxygenation. Tree productivity should therefore increase if other growth factors such as nutrients, water, or temperature are not limiting. Theoretically, elevated CO_2 will enhance photosynthesis and decrease the need for plants to open their stomates as widely as they do at lower CO_2 concentrations, allowing them to conserve water (Schäfer *et al.* 2002). This CO_2-induced increase in primary productivity and water use efficiency is commonly known as the "fertilization effect". It is often assumed that forested ecosystems will increase C sequestration rates with rising concentrations of atmospheric CO_2. Indeed, this assumption is the basis for projecting future C fluxes with most state-of-the-art global vegetation models (Cramer *et al.* 2001).

Evidence is now emerging that this fertilization effect is variable and often limited by environmental factors. In most experiments, elevated CO_2 increases photosynthesis (at least initially), but the long-term effect on ecosystem productivity is unclear. Early results from an open-air CO_2 enrichment experiment in a young North Carolina forest showed increased ecosystem net primary productivity during the first 2 years of exposure (DeLucia *et al.* 1999), but later findings indicate that this productivity declined with time (Finzi *et al.* 2002). Trees in Italy that are near springs emitting high CO_2 concentrations grow no faster than their counterparts away from the springs (Tognetti *et al.* 2000). Although elevated CO_2 may increase the C assimilation rate, it does not necessarily mean that growth will be increased, as other limiting factors come into play, particularly in natural ecosystems (Norby *et al.* 1999; Hungate *et al.* 2003).

There are a number of factors that could diminish the effect of CO_2 fertilization on forest growth. Clearly, increasing temperature and drought can reduce growth, but perhaps more importantly, changing climatic patterns can affect net ecosystem productivity (Knapp *et al.* 2002). There is a mounting body of evidence, however, for limitations beyond temperature and precipitation. These involve: (1) the potential for N availability to restrict the ability of forests to sustain CO_2-induced increases in growth; (2) the effects of regional air pollution – N deposition and tropospheric ozone – on C sequestration; and (3) the reallocation of C in forests as a result of rising atmospheric CO_2 with potential effects on C sequestration.

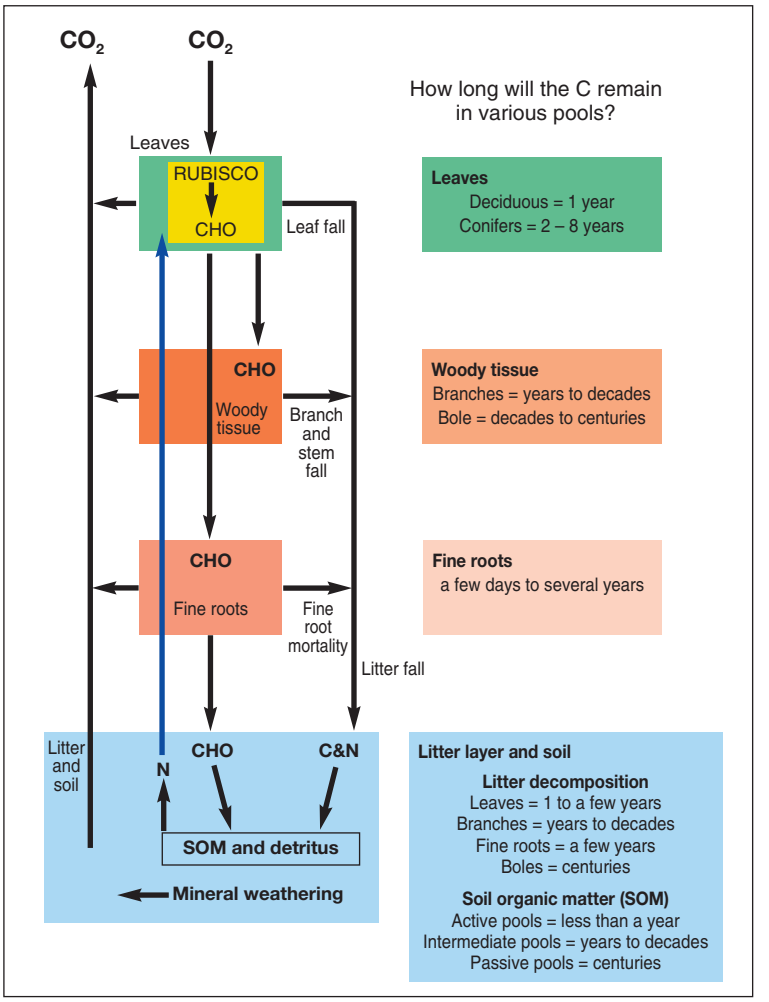


Figure 3. *Diagrammatic representation of C uptake, release, and retention time in forested ecosystems. CHO represents the movement of photosynthates between plants, soils, and the atmosphere.*

Nitrogen availability

At the cellular level, enzymes are required to convert atmospheric CO_2 into carbohydrates. They are also required for plant growth and maintenance. To produce enzymes, plants must have adequate N. In fact, most of the N in leaves is found in enzymes, especially rubisco, which facilitate uptake of CO_2 during photosynthesis.

Mineral weathering, along with mineralizing litter and soil organic matter, form the soil pools of N and other essential nutrients which are taken up by fine roots and associated mycorrhizae and moved throughout the plant (Figure 3). Although the amount of N in different tissues may vary, it is essential for sustained plant growth (Finzi *et al.* 2002). If the soil N is deficient, growth is limited. Consequently, plants will increase growth in response to increasing levels of atmospheric CO_2 only if there is a sustained increase in nutrient use efficiency or there is continuing supply of N (Finzi *et al.* 2002). The increased N supply can be met by: (1) N reallocated from within the plant; (2) increased mineralization in the litter and soil; (3) fertilizers; and (4) air pollution (N deposition).

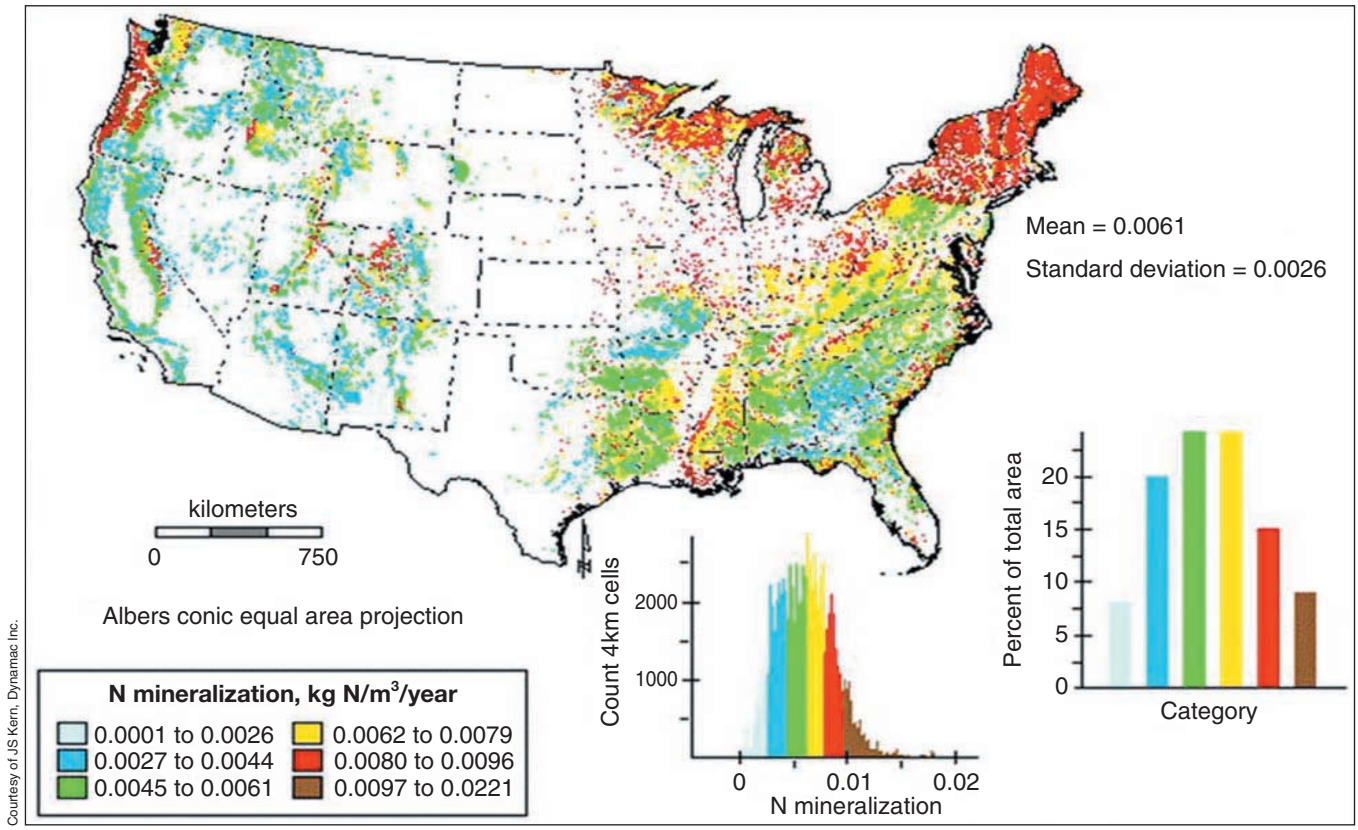


Figure 4. *The distribution of mineralizable N in forested lands of the US. Mineralizable N represents the N in soils that is available to plants. Notice that forest soils containing the highest levels of N occupy less than 10% of the total, and that soils relatively rich in N are found in the northern regions.*

At the ecosystem level, soil N availability can limit the CO_2 fertilization effect and rising atmospheric CO_2 can alter decomposition and N mineralization and fixation, thus changing N availability in the soil (McGuire *et al.* 1995). A long-term study in a North Carolina pine forest failed to find increased N mineralization with elevated CO_2 exposure (Finzi *et al.* 2002). Increased C storage, if it occurs with rising atmospheric CO_2, places an additional demand on available N. As organic matter contains N, storing more C requires removing some N from the actively cycling pool and sequestering it, along with the C, in wood, leaves, litter, and soil. Litter and soil are both rather high in N, creating a continuing demand for it and other nutrients.

Modeling studies support the concept of N limitation and show that the observed increase and subsequent slowing of plant growth in response to elevated CO_2 is a consequence of nutrient limitation (Pan *et al.*1998). Applying a biogeochemical model to forest stands in the western Cascade Mountains of the Pacific Northwest, McKane *et al.* (1997) suggest that soil N is a primary constraint on the ability of those forests to sequester C. In 100-year model runs, elevated atmospheric CO_2 and temperature raised total ecosystem C storage by less than 10% for a N-poor site versus 25% for a N-rich site. Vegetation models that account for N limitation also predict much less C sequestration under future climate scenarios than do models that assume N is always sufficient (Pan *et al.*1998; Hungate *et al.* 2003).

The availability of N varies between and within forested regions. Consequently, the CO_2 fertilization potential for particular forest stands will also vary. For example, in forested lands of the US (Figure 4), the distribution of N not only varies from region to region, but the land area with the most N that can be mineralized (ie the most available N) is less than 10% of the total. In areas where N is deficient, C sequestration is not likely to increase with rising levels of CO_2.

Regional air pollution

Fossil fuel combustion and intensive agriculture have increased atmospheric inputs of nitrate (NO_3^-) and ammonium (NH_4^+) to forests, grasslands, and cultivated lands (Figure 5). Such anthropogenic deposition of N on N-poor soils could relieve limitations on forested land, which would allow CO_2-induced growth stimulation. Model simulations suggest that N deposition in temperate forests of eastern North America and Europe allows for up to 25% of the C sequestration in these forests (Townsend *et al.* 1996). However, results from tracer studies using N isotopes in temperate forests in the US and Europe show the C sequestration resulting from growth stimulation by N deposition to be less than 10%, if only woody tissues, which have longer turnover times, are considered (Nadelhoffer *et al.* 1999).

While soil N is important for forest growth, N deposition appears to play only a minimal role in increasing C sequestration when compared to the negative effects of air pollution. In fact, N deposition could lead to forest decline if available N exceeds the capacity of plants to use it; N compounds can bond with calcium and magnesium ions in soil, which can then be leached from the ecosystem, thereby limiting plant growth (Nosengo 2003). Although rising CO_2 and N deposition may have increased forest growth over the past several decades, the magnitude of these increases has been considerably reduced by concurrent increases in air pollution – primarily tropospheric ozone (Ollinger *et al.* 2002).

In the US, vast areas of forests are potentially impacted to varying degrees by tropospheric, or ground-level ozone pollution (Hogsett *et al.* 1997; Figure 6). On a global scale, damaging ozone concentrations (defined as >60 ppb) occur over 29% of the world's temperate and sub-polar forests and are predicted to affect 60% of these forests by 2100 (Fowler *et al.* 1999).

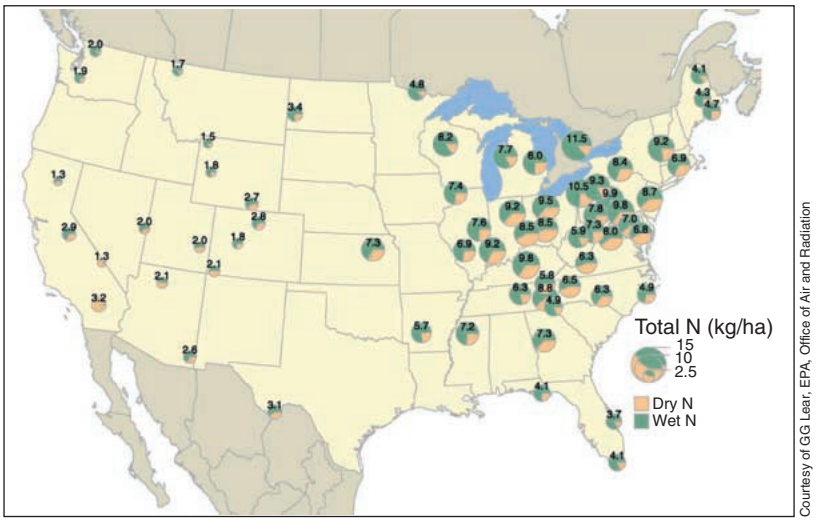


Figure 5. *Annual N deposition for the US. Map of wet and dry deposition, which illustrates the extent and magnitude of deposition. The size of the circles corresponds to the relative magnitude of deposition and the color represents the form (wet versus dry), with the total amount shown as kilograms per hectare. The eastern part of the US has deposition values 2–3 times greater than the western section.*

Ozone is formed in sunlight by the reactions of volatile organic compounds and nitrogen oxide air pollutants. Global warming could exacerbate risks to forests from ozone, because hot weather and high atmospheric pressure promote its formation. Moreover, increased fossil fuel use will probably increase the production of ozone-forming air pollutants.

In trees, ozone reduces CO_2 assimilation and alters C allocation (Andersen 2003). It causes foliage to die and drop prematurely, which reduces the amount of C available for growth and sequestration. In some cases, the stimulatory effect of CO_2 on forest productivity is reduced by more than 20% by ozone pollution (Tingey *et al.* 2001; Ollinger *et al.* 2002; Karnosky *et al.* 2003). In addition, the interacting effects of CO_2 and ozone can alter the susceptibility of plants to pest damage and diseases (Percy *et al.* 2002).

Ozone not only reduces C sequestration in trees; it also inhibits sequestration in soils. In a field experiment, the passive soil C pool was decreased by 5% when exposed to CO_2 and ozone combined compared to elevated CO_2 over 4 years of exposure (Loya *et al.* 2003).

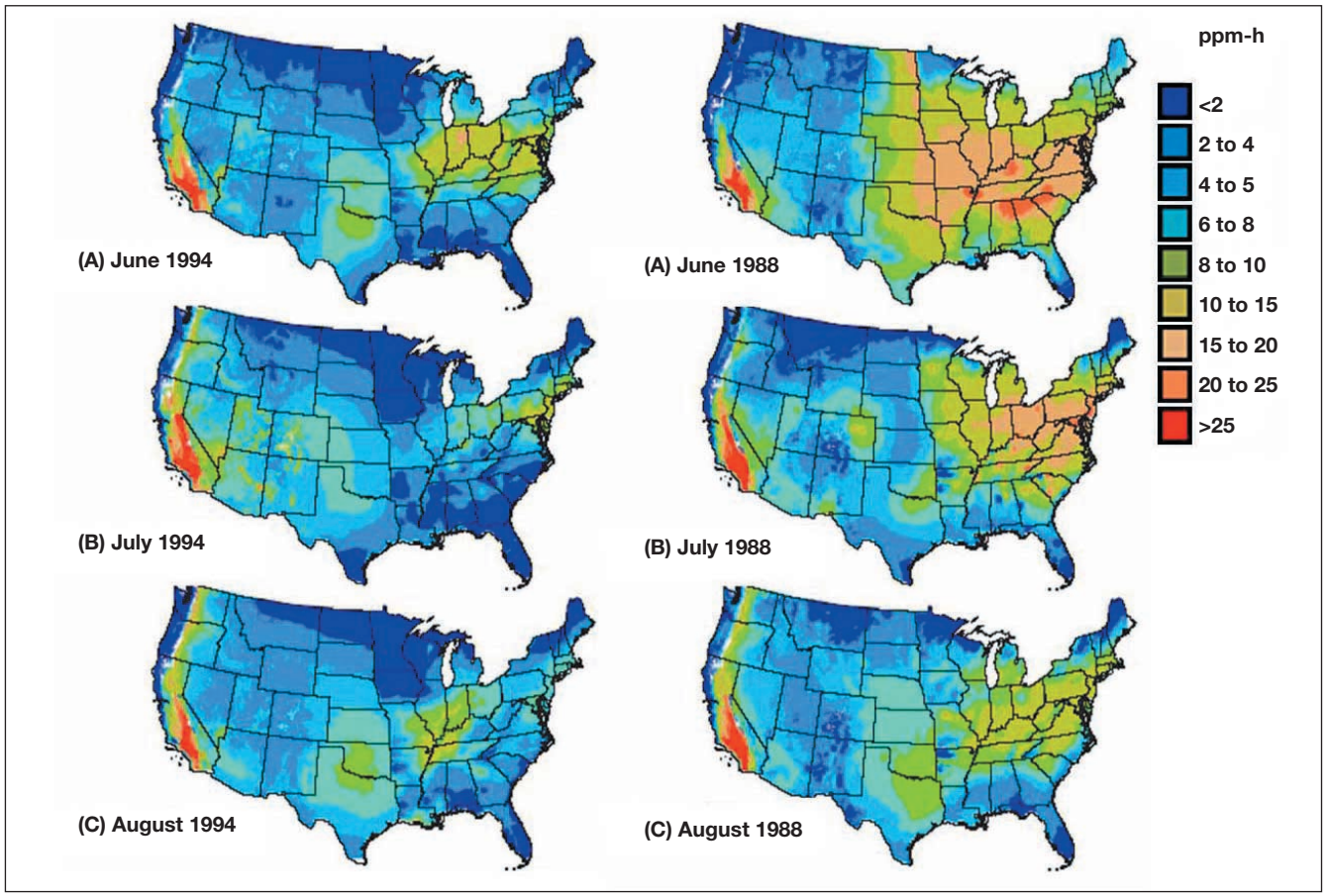
Carbon reallocation

It appears unlikely that rising CO_2 will cause a sustained increase in C sequestration, because of limitations such as N availability and ozone. However, if rising CO_2 could increase the allocation of C into long-term storage pools in wood or mineral soil, it would increase sequestration even without a sustained increase in plant growth. If C is reallocated, in order to have much influence on sequestration it must result in trees that live substantially longer or are substantially larger than they would have been without being exposed to elevated CO_2.

If rising CO_2 increased wood density or tissue C content, sequestration would increase. Yet, observed effects of elevated CO_2 on wood density range from no effect (Calfapietra *et al.* 2003) to a small increase that diminished with exposure time (Telewski *et al.* 1999), suggesting that increases in wood density will not create a major C sink.

If rising CO_2 increases plant size, more C would be sequestered. Experimental studies show that if water and nutrients are adequate, elevated CO_2 does initially increase plant growth, but the CO_2 benefit decreases with time. Nevertheless, the initial advantage of increased growth may be maintained even though increased net ecosystem productivity tapers off, if larger trees could gain a competitive advantage that would prevail throughout their lifetime (Calfapietra *et al.* 2003). The unanswered question is whether tree stands will ultimately have more volume of wood than stands growing at that same site without the benefit of elevated CO_2, or if the stand volume will be unchanged but concentrated in fewer, larger trees. It is not clear that rising CO_2 will permit plants at specific sites to grow larger than they would otherwise, given the availability of other resources.

Increasing the duration of leaves and roots, or tree life spans could also increase C sequestration. However, elevated CO_2 has been shown to decrease needle longevity (Schäfer *et al.* 2002) and to increase C allocation to foliar nonstructural carbohydrates, leaves, and fine roots, which are rapidly respired without adding to sequestration (Norby *et al.* 2003; Olszyk *et al.* 2003). In loblolly pine (*Pinus taeda*), elevated CO_2 reduced the age of maturity while cone and seed production increased (LaDeau and Clark 2001); accelerated maturation may shorten life span, resulting in faster C turnover, but not necessarily



Courtesy of EH Lee, EPA, Office of Research and Development

Figure 6. *Monthly ozone exposures expressed as SUMO6 across the US, illustrating the monthly and year-to-year variability depending on temperature and emissions. Ozone concentrations peaked during the record high temperatures and drought of 1988 throughout the eastern half of the US. More typical conditions prevailed during 1994. SUMO6 is the sum of all hourly ozone concentrations between 7 am and 7 pm that are equal to, or exceed, 60 ppb over a 3-month growing season. Exposures were spatially interpolated to relate ozone concentrations to elevation, temperature, and geographical coordinates following the procedure of Hogsett* et al. *(1997).*

more biomass. Accelerated maturation is compounded by the fact that the ability of forests to sequester C decreases with time (Finzi *et al.* 2002).

Climate, topography, soil parent material, time, and organisms determine the amount of C in soils (Johnson 1995). Elevated CO_2 only directly affects the organisms in this relationship. To increase C sequestration in soil, elevated CO_2 must increase C pools with turnover times of decades and centuries. C in the active pool is lost too quickly. The passive soil C pool, which contains persistent organic material such as humus, is obviously important to sequestration, but intermediate pools – those that turn over on decadal time periods – can also be important. Alternatively, sequestered C can be maintained by reducing the loss of passive C through management practices that minimize erosion and oxidation of C compounds in soils (Johnson 1995).

Evidence that rising CO_2 will increase C sequestration in soil is generally lacking. Although elevated CO_2 can increase net primary production, the additional C is either allocated to fine root production, which is rapidly turned over, or is respired directly by soil organisms. Elevated CO_2 has been shown to have little or no effect on passive soil organic matter (Schlesinger and Lichter 2001). In fact, the amount of passive soil organic matter is more dependent on soil characteristics, such as soil maturity and mineralogy, than on vegetation production (Trumbore 1997; Hagedorn *et al.* 2003).

Experimentally elevated CO_2 levels have not resulted in long-term increases in litter (Schäfer *et al.* 2002; Norby *et al.* 2003) or soil organic matter production (Schlesinger and Lichter 2001). Elevated CO_2 stimulated fine root production in deciduous forest species, which in turn increased soil respiration as the C was cycled through short-term pools without adding to the C present (King *et al.* 2001; Norby *et al.* 2002). Elevated CO_2 did not stimulate more fine root production or allocation of C to fine roots in Douglas fir (Olszyk *et al.* 2003), although C allocation was shifted belowground (Hobbie *et al.* 2004). Similar findings were reported for a loblolly pine forest exposed to elevated CO_2 (Schlesinger and Lichter 2001). Hobbie *et al.* (2004) hypothesize that the additional C assimilated by plants exposed to elevated CO_2 was used by the belowground biota with no movement of C into long-term stor-

age. This is supported by reported changes to belowground food chains due to elevated CO_2 (Fransson *et al.* 2001).

Model simulations suggest that higher N availability may increase litter quality and subsequent C sequestration (McMurtrie *et al.* 2000). There is no clear evidence of that happening in the field, however. Elevated CO_2 increased C to N and lignin to N ratios in tissues while decreasing decomposition rates in some C3 plants, but not in C4 plants (Ball 1997). In a survey of six species from alpine, temperate grassland, and tropical forest ecosystems, Hirschel *et al.* (1997) concluded that elevated CO_2 did not affect litter quality or decomposition rates. Similarly, elevated CO_2 experiments show no effect on mineralization or the availability of N for plant growth (Zak *et al.* 2003).

Conclusions

Changes in climatic conditions, growing season length, precipitation, cloud cover, and temperature have contributed to increases in global net primary production over the past two decades (Nemani *et al.* 2003), suggesting that terrestrial ecosystems are sequestering more C. Nevertheless, the fertilization effect of rising atmospheric CO_2 does not appear to be an important factor in the increased sequestration. Land-use changes, particularly the regrowth of forests on land previously used for agriculture, have played a major role (Schimel *et al.* 2001); in general, recovery from historic land use may be the dominant current terrestrial sink for C (Caspersen *et al.* 2000).

There is little experimental evidence to suggest that either rising atmospheric CO_2 or N deposition will contribute to sustained stimulation of C sequestration in forests or associated soils. Nutrient limitations in unmanaged forests are likely to constrain tree response to rising CO_2, while increased soil respiration seems to be balancing the increased input of C to soil (Schlesinger and Lichter 2001).

As rising CO_2 is not expected to stimulate C sequestration in forests, it is imperative that the C in these ecosystems be conserved. Forested landscapes should be managed to maximize C accumulation and retention in trunks and large branches. Soils accumulate C very slowly, and the passive C pool is largely a function of soil characteristics. Particularly important is protecting soil C, including the litter layer, during and following logging activities, especially in forest types that hold high levels of soil C, such as those in cool climates and bog and swamp woodlands (Johnson and Kern 2003).

Regionally, elevated tropospheric ozone is already reducing C sequestration in forests. Ozone not only reduces sequestration in natural forests, but also affects reforestation and afforestation projects. Consequently, it is important to reduce the extent and magnitude of exposures.

Managing forested ecosystems to maximize C sequestration and retention will require a detailed knowledge of past, present, and future land use, and how those practices affect carbon sources and sinks at regional scales. Social, political, and economic effects on C sequestration must be quantified and any ensuing conflicts with C conservation resolved before effective sequestration strategies for forests can be developed.

Promoting terrestrial sinks will certainly help lower atmospheric CO_2 concentrations, but some perspective is warranted. Even if all of the C that was lost from the land due to human activities over the last 250 years could be returned, it would only lower atmospheric C concentrations by about 70 parts per million (ppm) from projected concentrations of 500–950 ppm by 2100 (Scholes and Noble 2001). This amounts to only a 7–14% reduction. Avoiding additional loss of land C is therefore critical.

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