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Chapter 19

Responses of forests in the eastern US to air pollution and climate change

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Abstract

The interactions of elevated atmospheric carbon dioxide (CO_2) with physical (i.e., precipitation, light, and temperature) and chemical (i.e., ozone (O_3), nitrogen and sulfur deposition, and nutrients) environmental factors that affect plant growth have been demonstrated in experiments that simulate managed and natural forest ecosystems in the eastern United States. Elevated atmospheric CO_2 has been shown to substantially enhance photosynthesis and carbon gain. The response of a southern tree species, loblolly pine (*Pinus taeda* L.), to a doubling of ambient CO_2 was a 50% increase (to 130%) in the rate of net photosynthesis and a 20% reduction in dark respiration, depending on the study and treatment conditions. Volume change showed similar trends with increases in stem wood volume growth of 52% to 152%. Carbon gain for northern tree species with similar experimental treatments showed a 37% increase in dry weight biomass for trembling aspen (*Populus tremuloides* Michx.) and a 73% increase in dry weight biomass for yellow poplar (*Lirodendron tulipifera* L.). The impact of a doubling of atmospheric CO_2 on forest net primary productivity at the regional scale indicates a potential increase of 49% in the southeastern United States and an increase of 30–37% in the northeastern United States.

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1. Introduction

Terrestrial vegetation initially evolved in a carbon dioxide (CO_2) atmosphere that saturated photosynthesis and enhanced the growth of C_3 plants. Estimated levels of atmospheric CO_2 for 420 MYA suggest that the first terrestrial plants grew in CO_2 concentrations 16 times greater than those of the present day (Yapp and Poths, 1992). In contrast, over the last 160 000 years, atmospheric CO_2 concentrations have been atypically low, ranging from 190 to 280 $\mu l\,l^{-1}$ (Barnola et al., 1994), until stabilizing at about 280 $\mu l\,l^{-1}$ CO_2 following the last glacial period. Beginning in the 19th century, CO_2 concentration began to rise in a logarithmic manner until it reached the 1999 annual mean value of 368 $\mu l\,l^{-1}$. Global CO_2 has been increasing annually by 1.43 $\mu l\,l^{-1}$ (Conway et al., 1994), but the 1997–1998 increase of 2.9 $\mu l\,l^{-1}$ represents the largest annual increase on record since measurements began in 1958. Trees from long-lived species in natural forest ecosystems will encounter a more than 100% increase in atmospheric CO_2 during their life span into the middle of this century, when atmospheric CO_2 is projected to be 530 to 600 $\mu l\,l^{-1}$ (Trabalka et al., 1986; Watson et al., 1990).

Terrestrial ecosystems are experiencing changes in their chemical and physical environments at unprecedented rates. One compilation of literature studying the effects of a doubling of atmospheric CO_2 found that the average growth stimulation among 156 plant species was 41% for C_3 plants, 22% for C_4 plants, and 15% for CAM species (Poorter, 1993). An analysis of the response of 39 tree species reported by Gunderson and Wullschleger (1994) found that trees grown at elevated atmospheric CO_2 had an average photosynthetic enhancement of 44%. Findings from these and additional forest ecosystem studies indicate the importance of rising atmospheric CO_2 concentrations and other environmental resources and ambient levels of pollutants in modifying the response of forests and associated plant communities.

The interaction of elevated CO_2 with other factors that affect plant growth has already been demonstrated to occur in agricultural crops and managed and natural forest ecosystems. Several forest research reviews by Eamus and Jarvis (1989), Bazzaz (1990), Musselman and Fox (1991), Strain and Thomas (1992), Rogers and Runion (1994), Gunderson and Wullschleger (1994), Ceulemans and Mousseau (1994), Idso and Idso (1994), Mickler and Fox (1998), and Mickler et al. (2000) have all shown that rising CO_2 will alter the competitive interaction that influences forest ecosystems by direct effects on plant growth and development.

Environmental stresses and limiting resources are frequently identified as potential factors that currently limit growth in forest ecosystems and that may reduce or eliminate any promotion of growth by elevated CO_2. Several studies have reported that the full potential of forest ecosystems to increase net primary productivity (NPP) in a rising CO_2 environment will not be achieved because of nutrient and water limitations (Kramer, 1981; Allen et al., 1990; Thomas et al., 1994; Joyce et al., 2000). However, the benefits of increased photosynthetic water-use and nutrient-use efficiency observed in research studies (Dougherty et al., 1998; Teskey, 1998; Hennessey and Harinath, 1998; Isebrands et al., 2000) with trees growing in a rising CO_2 environment, when other environmental parameters may be limiting, have important implications for long-term forest ecosystem productivity and sustainability.

Although experimental manipulations are the best way to conclusively establish cause-and-effect relationships, extrapolating from relatively simple experiments to effects on complex ecosystems should be done cautiously. Typical experiments on tree responses to environmental stresses address one or a few factors, for a short period of time, using seedlings or small trees in artificial growth chambers. Only recently have experimental methods evolved to allow treatment of forest stands in natural conditions and, because of the expense, such experiments are few. Nevertheless, through judicious analysis of experimental evidence coupled with increasingly sophisticated model representations of complex systems, the scientific community is achieving a measure of capability to assess consequences of environmental change on large spatial and temporal scales. On a regional, national, and worldwide scale, estimates of the direction and magnitude of changes to NPP and the possible enhancement of temperate forest ecosystem carbon accumulation are being made with increasing confidence.

The studies described in this paper represent some of the research conducted in the first 10 years of the USDA Forest Service Global Change Research Program throughout the eastern United States, and are designed to provide a sound scientific basis for making regional and national management and policy decisions regarding forest ecosystems in the context of global change challenges. Scientific findings from related published studies are discussed as part of the general effects of global change on eastern US forest growth and physiology.

2. Physiological and growth responses of trees to environmental change

2.1. Effects of elevated CO_2

The enhancement of net photosynthesis due to elevated CO_2 concentrations is one consistent finding among studies in the southern, northeast, and north-central regions of the United States. In experiments conducted in the southern United States, when the ambient CO_2 concentration was doubled, rates of net photosynthesis in loblolly pine (*Pinus taeda* L.) increased by 50% to 130%, depending on the study and the treatment conditions. This increase was consistent for all age classes (i.e., seedlings, saplings, and trees). The average increase in net photosynthesis under twice-ambient CO_2 concentration, relative to the rates in the current ambient concentration, was about 90–100%, irrespective of growing conditions or age of the trees. There was a positive linear relationship between net photosynthesis and atmospheric CO_2 concentration for the CO_2 range of 350 to 700 $\mu l\, l^{-1}$ (Teskey, 1995). In this range, a change in CO_2 concentration of 10 $\mu l\, l^{-1}$ produces a positive change in the rate of net photosynthesis in loblolly pine of about 3% and, more importantly, indicates that the process is more limited by the availability of the substrate, i.e., CO_2, than by nutrients or other environmental factors.

Studies on other pine species generally have reported similar responses to elevated CO_2. Large increases in rates of net photosynthesis have been reported in Scots pine (*Pinus sylvestris* L.) (Wang et al., 1995) and Monterey pine (*Pinus radiata* D. Don) (Conroy et al., 1990). Exceptions to this have occurred in studies where photosynthetic compensation, or down regulation, has been reported in pot studies using ponderosa pine seedlings (*Pinus ponderosa* P. Laws. ex C. Laws) (Callaway et al., 1994; Grulke et al., 1993).

In the northeast and north central United States, tree responses to elevated CO_2 were evaluated for trembling aspen (*Populus tremuloides* Michx.), yellow poplar (*Liriodendron tulipifera* L.) and eastern white pine (*Pinus strobus* L.). In general, increasing atmospheric CO_2 concentrations increased photosynthetic rates, leaf production, height growth, and dry weight for these species. For example, rates of net photosynthesis in yellow poplar increased from 12% to 144% across studies with potted seedlings and field-grown saplings given various fertilization and irrigation treatments. Most of the enriched CO_2 responses observed for yellow poplar in Ohio (Isebrands et al., 2000) were similar to those reported in the southeastern US (Norby et al., 1992; Wullschleger et al., 1992; Gunderson et al., 1993). These findings suggest that field-planted yellow poplar, when exposed to enriched CO_2 and grown with limited nutrients, limited soil moisture, and ambient or elevated O_3, will display enhanced growth and photosynthetic assimilation.

For other tree species, the effect of elevated CO_2 concentrations on net photosynthesis is almost always positive, but the magnitude of the response appears to be quite variable, depending on species and growth conditions. Photosynthetic responses in the range found for loblolly pine and yellow poplar have been reported in deciduous hardwood species, such as European beech (*Fagus sylvatica* L.) (El Kohen et al., 1993), white oak (*Quercus alba* L.) (Gunderson et al., 1993), *Populus* hybrids (Ceulemans et al. cited in Ceulemans and Mousseau, 1994), chestnut oak (*Quercus montana* Willd.) (Bunce, 1992), as well as other conifers, e.g., Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Townend, 1993).

In addition to the direct effect of CO_2 concentration on net photosynthesis, elevated CO_2 concentrations directly affected dark respiration. Rates of dark respiration reported in two studies found reductions in the rate of respiration when foliage was exposed to higher concentrations of CO_2 (Teskey, 1995, 1998). The observed 20% reduction is significant, but the cause of this effect remains unknown. The apparent reduction in dark respiration appears to be further evidence that carbon gain will be enhanced in elevated CO_2 conditions. However, the relative contribution of increasing atmospheric CO_2 to overall carbon balance will be less than the stimulatory effect of CO_2 on rates of net photosynthesis.

2.2. Effects of elevated temperature

The effect of elevated air temperature reported in studies that manipulated air and soil temperature, provides some indication of the magnitude of the effect we can expect from air temperature on carbon gain. In the southern United States, a 2 °C increase in air temperature resulted in a less than 10% decrease in net photosynthesis in loblolly pine (Teskey, 1998). In comparison, the effect of elevated CO_2 on net carbon assimilation at twice ambient CO_2 concentrations was more than 100% greater than that at ambient CO_2 concentrations. Branch growth and leaf area development were slightly lower in the higher air temperature treatment, but again the effect was much smaller than the effect of elevated CO_2 concentration. There was no apparent effect of the 2 °C elevation in air temperature on the timing of budburst or the duration of the growing season. However, elevated air temperature in another study caused earlier pollen release and the initiation of female strobili development in loblolly pine trees (Connor et al., 1998).

Air temperature is expected to increase as the concentration of greenhouse gases increases in the atmosphere. A future $+2$ °C increase in air temperature in the southeastern US will have little negative impact on carbon gain or phenological growth patterns in loblolly pine, particularly as it will occur under conditions of much higher CO_2 concentrations (Burkett et al., 2000).

Increases in air temperature in the eastern United States have the potential to affect the belowground portions of forest ecosystems. These effects may be observed through at least three major pathways: (1) decreases in soil moisture resulting from increased evapotranspiration, (2) increased rates of root respiration and perhaps of root growth, and (3) increased rates of soil organic matter decomposition and accompanying impacts upon nutrient availability, especially nitrogen (Joslin and Johnson, 1998). Reductions in soil moisture will undoubtedly result if precipitation, solar radiation, humidity, and cloud cover remain constant while average temperature increases.

Lockaby et al. (1998) noted that small increases in soil temperature (1–3 °C) increased soil decomposition rates and nitrogen immobilization at two sites in the southeastern US. The study demonstrates the sensitivity of loblolly pine litter early in the decomposition processes, especially nitrogen immobilization, to small shifts in the temperature of the forest floor. Differences in litter decomposition among sites suggest that the positive effect of temperature on early litter decomposition may not be manifested on forest sites with poor litter quality or reduced precipitation. Litter, senescent roots, decaying macrofauna, and the organic component in the A horizon of southern forest soils account for up to 90% of the soils' cation exchange capacity and nearly all the mineralizable nitrogen and phosphorus. In the northeastern United States, the responses of red maple (*Acer rubrum* L.), red spruce (*Picea rubens* Sarg.), and American beech (*Fagus grandifolia* Ehrh.) litter to a 5 °C increase in soil temperature showed significant losses of foliage mass and nutrients (Rustad et al., 2000). Red maple litter lost 27% more mass and 33% more carbon than control plots during the first 6 months of decay. After 30 months, red spruce lost 19% more mass and carbon than control plots. American beech lost 19% more mass and 16% more carbon after 1 year of decay than did litter on control plots.

Experimental evidence supports the hypothesis that an increase in soil temperature of 1.0–5.0 °C may have significant effects on belowground C and N cycling in eastern United States forests (Lockaby et al., 1998; Rustad et al., 2000). Soil C and N cycling are important to eastern forest ecosystems because of potential feedbacks to the atmosphere that could affect climate change, the relationship of these cycles to forest productivity and health, and the potential for nutrient export from watersheds to sensitive downstream wetlands and coastal water bodies. Oxidation of methane (CH_4), nitrogen oxides NO_x flux, and litter decomposition showed variable responses that depended on litter quality, nitrogen availability, and soil moisture. Because of this complexity, it is not possible to definitively state whether eastern United States forest soils will be a net source or sink of carbon as a consequence of atmospheric warming. However, the balance of experimental evidence and observations suggests that increased soil respiration and litter decomposition, together with decreasing soil organic matter with increasing air temperature, will result in a net efflux of C from the soil to the atmosphere. Increases in air temperature and the subsequent release of nutrients and organic constituents in the soil solution may strongly affect the cycling of C and N within forest ecosystems.

2.3. Effects of water availability

In addition to changes in atmospheric CO_2 and temperature, precipitation may also change, but the magnitude and direction of change across the eastern United States is uncertain. Water availability and water-use efficiency will remain important factors contributing to the actual level of productivity of eastern United States forests. Several studies have reported that drought can significantly decrease the stimulatory effect of CO_2 enrichment in tree species (Guehl et al., 1994; Tschaplinski et al., 1995), yet it has also been shown that CO_2 enrichment can decrease whole-plant water use by increasing water-use efficiency (Overdieck and Forstreuter, 1994). Dougherty et al. (1998) used irrigated and non-irrigated treatments under elevated CO_2 concentrations to study stomatal conductance and leaf area development. Irrigation increased annual volume growth by 30% in drought years, and had less effect in years with average or above-average precipitation. Although a 30% increase in growth is appreciable, it was far less than the 108% average yearly increase over 4 years in fertilized plots, compared with growth in the unfertilized plots. These results illustrate the relative importance of nutrients in determining productivity in the southern United States.

The effect of elevated CO_2 on stomatal conductance was not consistent among studies involving loblolly pine. Most of the studies found no significant changes in stomatal conductance to water vapor for foliage measured in both ambient and elevated CO_2 concentrations, including all the studies using mature forest trees and saplings (Groninger et al., 1998; Sword, 1998; Teskey, 1998). However, the studies in open-top chambers reported a reduction in stomatal conductance in the range of 15% due to elevated CO_2 (Alemayehu et al., 1998). The differences in the results among the studies suggest that stomatal conductance in loblolly pine trees may be relatively insensitive to changes in CO_2 concentrations, at least in the 350 to 700 $\mu\text{mol}\,\text{mol}^{-1}$ range, but also indicate that the stage of development and the growth conditions may alter the sensitivity of the stomata to CO_2 concentration.

2.4. *Effects of ozone and interactions*

Ozone is considered one of the most significant pollutants affecting forest growth and health in the eastern United States. The effects of O_3 on eastern forest-tree species growth and physiological processes have been studied in the eastern United States for more than 20 years. The response of trembling aspen to seasonal O_3 doses comparable to O_3 concentrations found across the lower Great Lakes region was 43, 21 and 33% decrease in leaf, stem, and root biomass, respectively (Isebrands et al., 2000). Work by Karnosky (1981) suggests that ambient concentrations of O_3 in Wisconsin have contributed to mortality of sensitive genotypes of eastern white pine and that in the northeast and north central US, natural selection has already contributed to the alteration of genetic diversity of forest stands in high O_3 areas.

In the southern United States, loblolly pine (McLaughlin and Downing, 1998) and shortleaf pine (Flagler et al., 1998) experienced significant physiological effects from ambient O_3 concentrations. Flagler et al. (1998) found that ambient O_3 concentrations reduced foliage biomass and leaf area compared with a charcoal-filtered control treatment. Additionally, there was no interaction between O_3 and soil water availability so ozone uptake continued even when the plants were under moderate and severe water stress. McLaughlin and Downing (1998) also reported that the current O_3 concentrations in the region were correlated with reductions in tree growth.

Atmospheric CO_2 and O_3 have substantial impacts on forest growth and are increasing in the atmosphere as a consequence of human activity. Tree responses to CO_2 and O_3 are complex, and become even more difficult to interpret in the presence of other known stressors (i.e., nitrogen limitation or saturation, increasing temperature, precipitation extremes, and insects and diseases). In general, increasing atmospheric CO_2 increases photosynthetic rates, height growth, and biomass production. Increasing atmospheric O_3 decreases photosynthetic rates and biomass production, and increases leaf senescence. The amount and sometimes the direction of growth and physiological parameter changes are dependent on plant factors, such as tree age and genotype. Higher CO_2 concentrations may compensate for some other environmental stresses (see reviews by Mickler and Fox, 1998; Mickler et al., 2000). For example, most studies show that CO_2 enrichment increases growth even though light and/or nutrients are limiting. It is becoming evident that increasing CO_2, O_3, temperature, and drought impact fundamental plant processes, which then affect susceptibility to plant-feeding insects, such as southern pine beetle (McNulty, 1998; Wilkens, 1998) and gypsy moth (Williams et al., 2000).

Studies on trembling aspen show that O_3 usually decreases growth although the effect varies significantly with genotype (Isebrands et al., 2000). Similar results have been reported by Flagler et al. (1998) in shortleaf pine (*Pinus echinata* Mill.) and in other southern pine species. Root growth appears particularly sensitive to O_3. In contrast, substantial increases in relative belowground C allocation were found in response to elevated CO_2. Trembling aspen experiments with both elevated CO_2 and O_3 suggest that elevated CO_2 does not compensate for reduced growth caused by elevated O_3. When N limits growth, there appears to be no response to elevated CO_2. Because CO_2 and O_3 change the chemical composition of the foliage, resistance to insect attack and nutritional value of foliage are altered. Elevated O_3 appears to increase insect growth and elevated CO_2 decreases insect growth. Under field conditions, changes in insect physiology may offset increases or decreases in biomass production that are associated with a changing atmosphere.

Consistent growth responses of yellow poplar to O_3 have not been reported, even though the species shows visual foliar symptoms of exposure. After 2 years of exposure to 2 × CO_2 and 2 × O_3 treatment in an open-top chamber experiment, yellow poplar had 6% increased leaf biomass, 14% increased stem biomass, and 20% increased root biomass compared with other treatments (Rebbeck, 1996). Elevated CO_2 appears to increase yellow poplar growth regardless of level of exposure to O_3 (Isebrands et al., 2000). In general, research on yellow poplar suggests that, under field conditions, this species will increase biomass production in elevated atmospheric CO_2 even when nutrients and moisture are limited and in the presence of O_3.

After 4 years of CO_2 and O_3 treatments on white pine, no significant growth effects were detected despite some annual stimulatory effects in height growth, increased stem dry weight and total plant dry weight, and increased needle retention (Rebbeck, 1996).

Although the findings from these studies are not conclusive, they add to the existing body of information (Eagar and Adams, 1992; Fox and Mickler, 1996; Olson et al., 1992) that has clearly demonstrated that concentrations of O_3 that are higher than the current ambient concentration are detrimental to the growth and physiological activity of forest throughout the US. However, the balance between O_3 and CO_2 concentrations, as well as other regional pollutants (e.g., nitrogen deposition), will be important in determining the absolute growth response of pine and hardwood forests in the eastern US.

3. Discussion

A positive response of carbon gain to elevated CO_2 concentrations lasting up to 3 years has been demonstrated for some eastern forest species. A key question still remaining is whether the effect will last for extensive periods of time, and whether it will result in a dramatic long-term stimulation of growth for forest species in the eastern United States. The answer to whether long-term increases in productivity are possible in an enriched CO_2 environment appears to be determined by whether or not the plant growth is constrained by important physiological or growth parameters. A species such as loblolly pine has a greater potential for utilizing elevated CO_2. Loblolly pine has a long growing season, including multiple flushes of foliage growth and it is not a high nutrient-demanding species. Loblolly pine growth characteristics allow it to incorporate carbohydrates into growing sinks for long periods during the year when photosynthetic rates are highest and the potential for accumulating carbohydrates is greatest. But the growth potential may be constrained by the availability of nutrients for growth. In the northeast and north central US, 61% of the timberland is dominated by maple–beech–birch and oak–hickory forest type groups. The shorter growing season, single flush of foliar growth, and higher nutrient demands of these mixed deciduous forest species may present a lesser opportunity for increased growth in the short term. Additionally, the effect of nitrogen saturation and calcium depletion on some forest soils may constrain future long-term potential productivity in the region (Fenn et al., 1998). These issues still remain unresolved but are critical to determining the long-term growth potential that could result from increased atmospheric CO_2 concentrations.

4. Conclusions

Predicting the current and future impacts of global change on eastern United States forests is predicated on experimental manipulations of individual tree species or a small number of naturally co-occurring tree species. The experimental methods employed with forest trees have a major impact on how results from these studies should be interpreted at the stand and regional scales. Significant greenhouse, open-top chamber, and pollutant-delivery system effects are common in tree experiments, limiting extrapolation of many experimental results to natural field conditions. Tree-level experiments are typically short lived (1–5 years) yet trees are long-lived perennial species, so there is no direct evidence showing how changing atmospheric chemistry and environmental conditions would affect plant processes over the tree's life span or the longer term. Extrapolations of experimental results to natural ecosystems using process models have concluded that the long-term effects of increasing atmospheric CO_2 are likely to decline in magnitude over time (Luo et al., 1999). However, field exposures of loblolly pine seedlings (Alemayehu et al., 1998), saplings (Dougherty et al., 1998; Hennessey and Harinath, 1998), mature loblolly pine (Teskey, 1998), and yellow poplar (Isebrands et al., 2000) to elevated CO_2 have not demonstrated any acclimation. Open-air exposure experiments and field physiological studies conducted over long time periods will eventually increase our understanding of individual species and forest community responses to elevated CO_2 and global change stressors, as will improvements to physiological process models.

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