18.   Modern and Future Forests
in a Changing Atmosphere

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18.1 Introduction

Through direct observation and clever use of proxy signals, we can reconstruct the atmospheric conditions of past years, and that allows us to analyze the interactions between plants and the atmosphere in the near and distant past. Although predicting future conditions will always be fraught with uncertainty, we can state with a very high degree of confidence that trees grew in a lower CO_2 concentration in past decades and will experience a higher concentration of atmospheric CO_2 in the future. The inexorable increase in atmospheric CO_2 since the onset of industrialization in the eighteenth century is a global phenomenon that has been altering the environment of forests worldwide.

Since all C_3 plants, including trees, respond to atmospheric CO_2 concentration, forests also should respond to this altered environment. The primary response is straightforward: CO_2 is the substrate of photosynthesis, and as the substrate concentration increases so does the reaction rate. This analysis, however, is highly simplistic. Plants can adjust to changing $[CO_2]$ such that the relationship between photosynthesis and $[CO_2]$ changes (Stitt 1991). These adjustments are themselves responses to CO_2 that can alter the water or nutrient cycles of the forest or its vulnerability to biotic or climatic stresses (Fig.18.1).

In addition, myriad secondary and tertiary adjustments, feedbacks, and interactions affect how trees respond to CO_2, and thereby the response of a forest (Bazzaz 1990; Field et al. 1992). The net result can be nearly impossible to
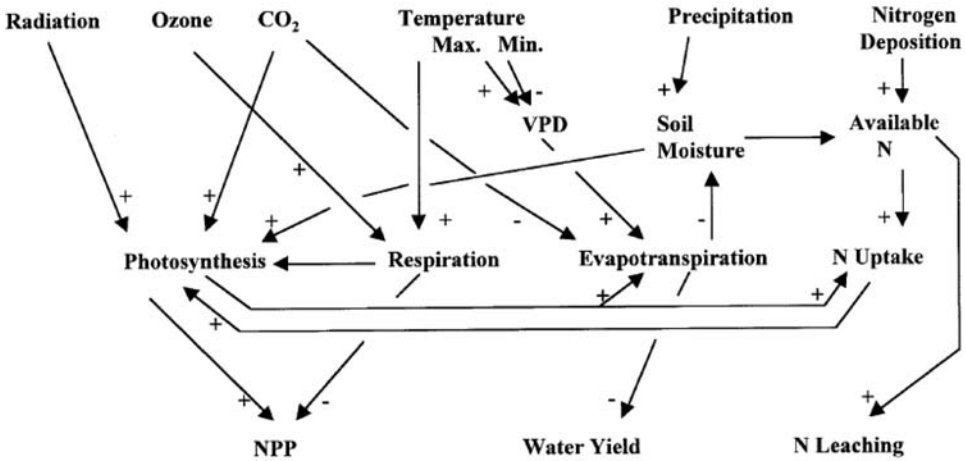
Figure 18.1. The primary response of plants to increased CO_2 concentration starts with an increase in photosynthesis, and this can lead to increased plant production. The outcome of this primary effect, however, is moderated by numerous secondary effects and the influences of other environmental variables. Figure is from Aber et al. 2001; copyright, American Institute of Biological Sciences.

predict or detect. As the primary responses to CO_2 become obscured, so too does our understanding and confidence in predicting how forest structure or function will change as the atmospheric [CO_2] continues to rise. These adjustments and feedbacks are perhaps the most important aspect of forest response to CO_2, and it is critical that analyses of forest response take a whole-system approach that considers CO_2 in relation to multiple interacting environmental variables and biotic factors. The greatest challenge is to account for issues of scale imposed by the inescapable constraints of the large size and long life span of trees. It is no easy matter to relate the responses of a leaf in a cuvette over a matter of minutes to those of a forest over decades, but it also is impossible to maintain a forest for decades in a cuvette to observe it. In this chapter we will consider how these seemingly incompatible needs and overwhelming complications are considered as we analyze how rising atmospheric [CO_2] has been influencing modern forests, and how forests will respond in the near future as humans continue to cause [CO_2] to increase.

18.2 CO_2 Influences on Modern Forests

When a 100-year-old tree in the forest today started out its life, the global average atmospheric [CO_2] was 295 ppm. The 25% increase in [CO_2] since then should have brought about an increased rate of photosynthesis and growth. Our modern forests may look substantially different today and be holding signifi-

cantly more C because of the human-caused increase in $[CO_2]$ during the twentieth century. Finding clear evidence of a past effect of rising $[CO_2]$ is difficult and indirect. Analyses of the global C cycle (Schimel 1995), including anthropogenic sources of CO_2 (e.g., fossil fuel burning, cement manufacturing, and land clearing), the modeled sink of CO_2 into the ocean, and the record of atmospheric $[CO_2]$ leave an unaccounted fraction (missing sink) that is presumed to have been sequestered by the terrestrial biosphere, of which forests are a major component. Some of this terrestrial sink is ascribed to the regrowth of forests after earlier land clearing; some may be a response to perturbation of the nitrogen cycle; and the rest, as much as 1.0 ± 0.5 Gt yr^{-1}, is attributed to increased growth in response to rising $[CO_2]$, or, CO_2 fertilization (Schimel 1995). Controlled experiments in which plants are grown in subambient concentrations of CO_2 support the premise that plant growth is stimulated over the range of 200 to 360 ppm CO_2 (Mielnick et al. 2001), but there have been few such experiments with woody plants and none with forests. Hence, we must rely on indirect evidence, such as tree-ring chronologies and forest inventory analysis, in which any effect of CO_2 is confounded by many other uncontrolled variables.

18.2.1 Tree-Ring Evidence

In 1984 LaMarche and colleagues reported that they had detected possible evidence of a CO_2 fertilization effect in the annual rings of subalpine conifers growing at high altitude sites in the southwestern United States (LaMarche et al. 1984). By that time, growth rates of the trees had increased significantly since the mid-nineteenth century. The positive growth trend was attributed to rising warm-season temperatures until about 1960, but there were no apparent climatic trends that could explain the more recent growth increases. The recent growth increases were thought to be consistent in magnitude with the increase in atmospheric $[CO_2]$, leading to speculation that increased CO_2 uptake and storage could be occurring in the high-altitude habitats and that growth enhancement from elevated CO_2 should be included in global C balance models (LaMarche et al. 1984).

The LaMarche evidence was difficult to interpret, in part because their trees were highly stressed and slow growing, but primarily because of the absence of quantitative analysis of climatic records from nearby weather stations. In contrast, quantitative correlation of tree-ring chronologies with climatic records was conducted for conifers in the Cascade Mountains of western Washington (Graumlich, Brubaker, and Grier 1989) and in the Sierra Nevada Mountains of California (Graumlich 1991). In Washington, annual production was significantly correlated with long-term variation in summer temperature and short-term variation in annual precipitation, and it was uncorrelated with atmospheric $[CO_2]$. In three of the five Sierra Nevada sites, twentieth-century growth variation could be modeled as a function of climatic variation. Elevated $[CO_2]$ was a possible explanation for unexplained growth increases at two sites, but other

possible explanations also were offered. Regardless of whether the growth increases at the sites studied by LaMarche were indeed a response to CO_2 fertilization, there is no evidence for a general effect of rising [CO_2] on the forests of the western United States.

While tree-ring chronologies collected elsewhere seemed to show an unexplained trend of increasing growth that was consistent with (but certainly not diagnostic of) a CO_2 fertilization effect (West et al. 1993; Graybill and Idso 1993), other tree-ring investigations have concluded that tree growth patterns were not related to increasing [CO_2] (Kienast and Luxmoore 1988; D'Arrigo and Jacoby 1993). Jacoby and D'Arrigo (1997) concluded that the evidence for CO_2 fertilization was inconclusive for trees growing in natural settings, where there can be many other limiting and interacting factors. The absence of clear evidence in tree-ring chronologies of a CO_2 fertilization effect should not be taken to mean that rising [CO_2] has had no effect on modern forests, or by extension that an effect in the future is unlikely; rather, the ambiguous record is probably a reflection of the aforementioned problem of detection in the face of multiple feedbacks and interacting environmental and biological factors.

18.2.2 Forest Inventory Analysis

On a global scale, forests account for a large fraction of C absorbed annually by the terrestrial biosphere. About half of the C absorbed in photosynthesis (gross primary production, GPP) is lost in plant respiration in the process of synthesizing organic matter (net primary production, NPP), and much of the rest is equaled by soil microbial (heterotrophic) respiration. The small excess in assimilation over total ecosystem respiration (net ecosystem production, NEP), however, represents C sequestration, which is an important factor in the relationship between fossil fuel emissions and the increase in atmospheric [CO_2]. Sequestration in forests can be due to CO_2 fertilization or a result of land use history (Houghton, Hackler, and Lawrence 1999). The current forests of the northeastern United States, for example, mostly began after the land was abandoned from agriculture in the late 1800s. Since the stands are young, they are sequestering C, but as the stands get older, the amount of C sequestered annually will decline. Estimation of the size of the terrestrial C sink in the future based on observations of twentieth-century forests requires that CO_2 fertilization and land use change be accounted for separately, because their relative contributions to the C sink will change in the future.

Caspersen et al. (2000) used forest inventory analysis to estimate the relative contributions of growth enhancement and historical changes in land use to the C accumulation in forests in the eastern United States. Two successive inventories between the late 1970s and mid-1990s provided data on aboveground biomass, changes in biomass due to growth and mortality, and the age structure of the plot. Since the biomass of a stand is the cumulative result of growth and mortality rates over the age of the stand, Caspersen et al. (2000) could construct stand growth curves based on current rates of growth. The predicted standing

biomass was then compared to the actual standing biomass; and discrepancies were ascribed to changes in growth rates. The researchers concluded that C accumulation since 1930 was overwhelmingly due to forest regrowth rather than growth enhancement. The fraction of regional-scale aboveground net ecosystem production (dry matter accumulation) that could be attributed to growth enhancement was 2.0 $\pm$ 4.4%, with an upper limit of 7.0%. (The upper limit is not inconsistent with experimental data on tree responses to CO_2 enrichment, given the change in atmospheric [CO_2] that occurred between 1930 and 1995.) Growth enhancement might include CO_2 fertilization, nitrogen deposition, and offsetting factors such as ozone pollution or calcium depletion. The Caspersen et al. (2000) analysis has been challenged because their analytical approach was not sufficiently robust to estimate small changes in growth (Joos, Prentice, and House 2002). The problem again is one of detecting a response to CO_2 that is independent of other environmental influences, stand developmental history, and regional-scale land-use patterns.

18.3 Forests in a Future Atmosphere

Understanding the influence of CO_2 on modern forests is of interest in part because of our general desire to understand how our planet works. More importantly, however, responses of forests today may provide insight into the responses of future forests. Our perspective is a time frame of about 30 to 100 years, during which [CO_2] is expected to rise from the current (2001) level of 372 ppm to about 450 ppm in 2030 and 700 in 2100, based on a middle-range scenario of fossil fuel emissions (IPCC 1992). Individual trees and forests living today, and the people who enjoy them, will experience this important environmental change. Hence, this time frame is relevant to public policy decisions about energy use and the environment.

Surprisingly, perhaps, there is much better evidence describing the responses of trees to future CO_2 levels than to past levels. It is much easier to add CO_2 to the air in an experimental system than it is to remove CO_2, and therefore, there is a wealth of data from controlled, replicated experiments investigating various responses to elevated [CO_2] (Eamus and Jarvis 1989; Ceulemans and Mousseau 1994; Curtis and Wang 1998). We can also make use of observational data from stands of trees near natural springs that have been creating a high [CO_2] environment for many decades. Dendrochronological studies of the drought-impacted trees at the CO_2 springs in Tuscany, Italy, however, have yielded conflicting results (Hättenschwiler et al. 1997; Tognetti, Cherubini and Innes 2000) depending on which trees were measured and how the data were analyzed (Norby et al. 1999). These conflicts illustrate both the difficulty of finding unambiguous expressions of growth response and the overriding importance of confounding environmental factors. Experimental approaches to investigating tree and forest responses to future CO_2 concentrations circumvent many of the problems associated with observations of natural systems. The CO_2 concentra-

tion can be precisely controlled and monitored, and responses can be compared to those of comparable plants under ambient conditions. Other environmental variables can be controlled or at least equalized across treatments so that problems of confounding factors are minimized. Interactions between $[CO_2]$ and temperature, N availability, soil moisture, or ozone can be explored. Over the past two decades of research there has been a gradual increase in scale and complexity of the experiments: from potted seedlings in growth chambers, to saplings grown in field chambers for several growing seasons, to forest stands exposed in the open air.

18.3.1 Experimental Studies with Young Trees

Our questions of interest concern the responses of forests in future decades, yet it is impossible to devise a reasonable experiment that exposes an entire forest for a significant fraction of its life cycle. Instead, researchers interested in forest responses must investigate individual components and specific mechanisms of forests with the hope that their answers will be valid and relevant at the larger scale of interest. Early experiments were of short duration (weeks) with young tree seedlings in pots in growth cabinets, but as the need to address the role of forests in the global C cycle became clearer (Kramer 1981), experiments were directed toward defining mechanisms of responses that would be relevant to unmanaged forests, such as nutrient interactions (Norby, O'Neill, and Luxmoore 1986) and competition (Tolley and Strain 1984). Experiments in field chambers allowed investigations over several growing seasons with the influence of multiple, interacting, and fluctuating resources and provided a context for investigating potential important ecological feedbacks such as litter decomposition (Cotrufo, Ineson, and Rowland 1994), herbivory (Lindroth et al. 1997) and nitrogen mineralization (Zak et al. 2000).

While we continue to struggle to understand how the primary responses to $[CO_2]$ are altered by various adjustments, feedbacks, and interactions in the forest environment, we can be confident that we have a good understanding of the primary responses themselves. Norby et al. (1999) reviewed the responses of freely rooted trees exposed to elevated $[CO_2]$ in field experiments and concluded that for the most part the earlier experiments with seedlings were correct. The responses are as follows:

- Photosynthesis is increased approx 60% with an increase of 300 ppm CO_2, and there is little evidence of the long-term loss of sensitivity to CO_2 that was suggested by earlier experiments with potted seedlings.
- The relative effect of $[CO_2]$ on aboveground biomass is highly variable in experiments, but this static measure of response is inappropriate for characterizing a dynamic process that is confounded by the developmental pattern of the plant. When aboveground growth is normalized to constant leaf area, as is appropriate for addressing responses in a closed-canopy forest, annual wood increment per unit leaf area increased 26%, with a fairly consistent response across different tree species and experimental systems (Fig. 18.2).
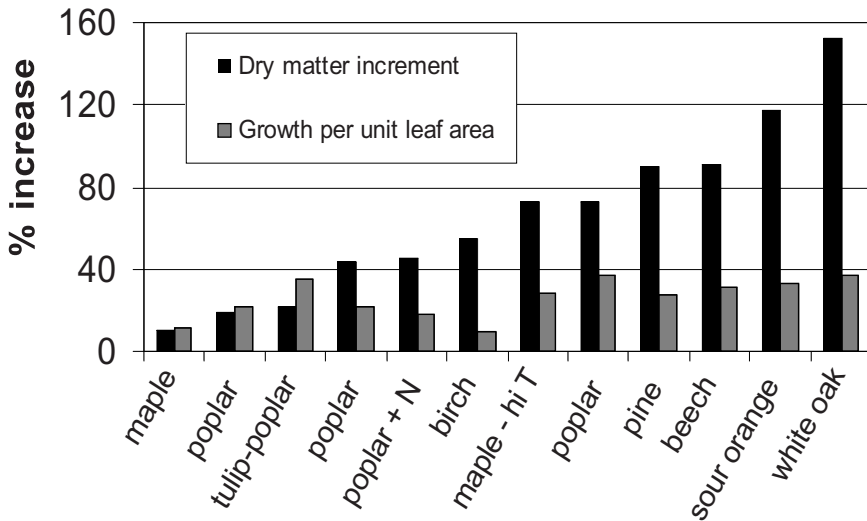
Figure 18.2. The relative effect of elevated [CO_2] (600–700 ppm) on the aboveground dry matter increment of tree seedlings and saplings grown in field chambers. The wide range in response does not represent inherent differences between species but rather the confounding effect of increasing leaf area and exponential growth. Expressing annual stem growth per unit leaf area adjusts for exponential growth pattern and may be more relevant to growth responses that may occur in a closed-canopy forest. The experiments represented in this graph and the conceptual basis for the analysis are in Norby (1996) and Norby et al. (1999).

- Root-to-shoot mass ratio does not typically change (after correcting for developmental effects), but the production of physiologically active fine roots may be enhanced.
- Foliar nitrogen concentrations generally are lower in CO_2-enriched trees.

  Additional analyses have indicated the following conclusions:

- Stomatal conductance is lower in field-grown trees exposed to elevated [CO_2] for more than 1 year (Medlyn et al. 2001).
- There probably are no direct effects of CO_2 on leaf respiration (Amthor 2000).
- Litter nitrogen is only slightly lower and this does not result in demonstrable effects on decomposition (Norby et al. 2001a).

These conclusions all derive from experiments with small trees grown individually or in small groups for one to several years. It is encouraging that there is a general concurrence between these field studies and older studies with seedlings, but there are still many differences between young trees in open-top chambers and mature forest trees (Lee and Jarvis 1995). It is important to recognize the limitations of the data before using the results to predict the future state of

forests. In particular, we must account for the overriding influence of tree and stand development, ecological feedbacks that could not be replicated in a small group of saplings, and nonlinearity in the physiological responses to [CO_2].

18.3.2 Stand-Level Responses

The application of free-air CO_2 enrichment (FACE) methodology to forest systems (Hendrey et al. 1999) has permitted a new series of experiments in which new hypotheses and critical uncertainties can be explored at the forest stand scale (Karnosky et al. 2001). Important scale-related questions identified in previous open-top chamber experiments that can be addressed in these FACE experiments include the following:

- Does maximum stand leaf area index (LAI) increase in elevated [CO_2]?
- Does growth per unit leaf area remain enhanced after canopy closure?
- Is fine root turnover increased by CO_2 enrichment after a soil is fully exploited by root systems?
- Do feedbacks through the nitrogen cycle lead to down regulation of the tree growth response?
- Do effects of CO_2 on stomatal conductance translate to lower stand water use?
- Do differential effects of CO_2 on competing species alter stand structure?

Many of these questions are components of a more general one posed by Strain and Bazzaz (1983): "The initial effect of elevated CO_2 will be to increase NPP [net primary productivity] in most plant communities. . . . A critical question is the extent to which the increase in NPP will lead to a substantial increase in plant biomass. Alternatively, increased NPP could simply increase the rate of turnover of leaves or roots without changing plant biomass" (Strain and Bazzaz 1983). The fate of increased C absorbed by a future forest in a CO_2-enriched atmosphere is one of the defining questions that must be answered if we are to understand how future forest metabolism will be different from that of today and what the implications are for forest management strategies to reduce the rate of increase in [CO_2] in the atmosphere through enhanced C sequestration.

18.3.3 Oak Ridge Experiment on CO_2 Enrichment of Sweetgum

Four FACE experiments have been initiated in forest ecosystems: two in young, expanding stands and two in established plantations of evergreen or deciduous trees (Karnosky et al. 2001). The objective of the FACE experiment in Oak Ridge, Tennessee, has been to understand how the eastern deciduous forest will be affected by CO_2 enrichment of the atmosphere, and what the feedbacks are from the forest to the atmosphere. The forest stand under study is a sweetgum (*Liquidambar styraciflua*) plantation that was established in 1988. Beginning in 1998, the forest canopy was exposed to an elevated concentration of atmospheric CO_2 ($\sim$ 550 ppm) by emitting CO_2-enriched air from vent pipes that surround the 25 m diameter experimental plots (Norby et al. 2001b).

The responses of this simple forest stand to three years of CO_2 enrichment

should inform us about the metabolism of forest stands in 50 to 100 years or should at least reveal the range of responses that might occur. Measurements of a wide range of processes clearly show that the trees responded to the higher CO_2 in predictable ways. Photosynthesis was stimulated, the stimulation was consistent throughout the canopy and with varying weather conditions, and it has not declined through time (Gunderson et al. 2002). Leaf area index was not altered by CO_2 enrichment (Norby et al. 2001b), so it can be presumed that gross primary productivity, or the total amount of C absorbed by the stand, increased. Net primary productivity (NPP) increased 21% during the first four years of CO_2 enrichment (Fig. 18.3), a response that represents a fundamental change in the metabolism of this forest stand that could have ramifications throughout the C cycle (Norby et al. 2002). In many respects the responses to CO_2 enrichment in a stand of loblolly pine (*Pinus taeda*) in North Carolina, of similar age and stature, were similar: increased photosynthesis, no change in leaf area index, higher GPP, and a 27% increase in NPP (Luo et al. 2001; DeLucia, George, and Hamilton. 2002; Hamilton et al. 2002). Although N limitations might eventually impose a constraint on response (Oren et al. 2001) and the stimulation of photosynthesis declines in older needles (Rogers and Ellsworth 2002), the increase in NPP has been sustained for at least 4 years (Hamilton et al. 2002).

What was (or will be) the fate of the additional C that was removed from the atmosphere by these stands each year? As Strain and Bazzaz (1983) asked, Does the increased production result in a greater accumulation of tree biomass, or does the additional fixed C turn over faster with no net accumulation in the plant? In the first year of the sweetgum study, increased NPP resulted in a
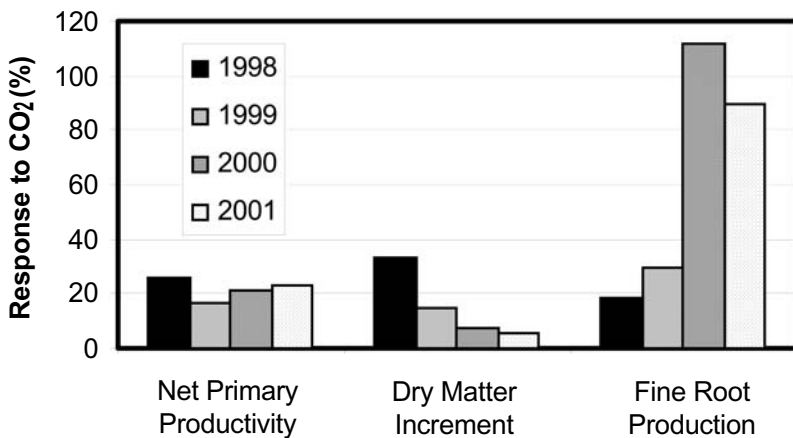

Figure 18.3. The relative response to elevated CO_2 (550 ppm) of NPP, dry matter increment (wood production), and fine root production in a sweetgum forest stand in a FACE experiment in Oak Ridge, Tennessee. (Norby et al. 2002.)

substantial (33%) increase in aboveground dry matter production (Norby et al. 2001b), similar to the 25% increase in relative basal area increment in the first full year of the loblolly pine experiment (DeLucia et al. 1999). Caution is needed, however, in the interpretation of these data: the first-year response of a tree to a sudden increase in $[CO_2]$ from 360 to 550 ppm is not analogous to a tree growing 50 years in the future with a relatively constant (or gradually increasing) CO_2 concentration. As the sweetgum experiment progressed, the response of aboveground dry matter increment rapidly diminished to only a 6% increase, whereas the aboveground growth response was sustained in the pine stand (Hamilton et al. 2002). Instead of accumulating in wood, the extra C in the sweetgum stand was allocated to fine-root production, which was significantly stimulated (see Fig. 18.3). The allocation to short-turnover pools (fine roots and leaves) instead of longer-lived pools (wood) has significant implications for the C sequestration potential of this stand (Norby et al. 2002). The C that is allocated to fine roots enters the soil as organic C and therefore creates the potential for sequestration in long-lived soil organic matter pools. Analyses of the pine stand, however, discount the potential for significantly increased C sequestration in the soil (Schlesinger and Lichter 2001).

The vision of the future forest that the sweetgum experiment presents is one in which C cycles through faster but does not accumulate in the trees to a significant extent. This is not the same vision that emerged from previous experiments in field chambers; the difference may be attributable to the shift in allocation that occurs in association with the transition from exponential to linear growth. What are the consequences of faster C cycling? The evidence is likely to be much more subtle compared to changes in tree growth. Increased fine root production or turnover could alter soil microbial populations and processes, which in turn could alter nutrient cycling through the ecosystem. Faster C cycling could alter the interactions between plants, insects, and disease. The many interactions and feedbacks shown in Fig. 18.1 have not been resolved and probably never will be, but it is clear that the effect of atmospheric $[CO_2]$ on future forests cannot be considered only in terms of tree growth.

18.3.4 Water Use

The focus of most of the research on forest responses to $[CO_2]$ concerns the C budget: that is, the global C cycle, stand-level C budgets, or the prospect for additional C sequestration. Global change encompasses other values besides carbon, and there is increasing recognition (e.g., the Third Assessment Report of the Intergovernmental Panel on Climate Change) of the importance of considering other issues of consequence to ecological or human systems, including interactions with insects and disease, invasive species, resource economics, aesthetics, and so forth (Gitay et al. 2001). Water is an especially critical consideration. Forests are important mediators of water quality and supply, and water availability is a critical regulator of ecological processes.

There is a strong expectation that elevated atmospheric $[CO_2]$ will have im-

portant consequences for forest water use and, in turn, for ecosystem-scale processes that depend on soil water availability (Wullschleger, Tschaplinski, and Norby 2002). The basis of this expectation is the response of stomatal conductance to elevated CO_2, which has been shown to decrease in numerous studies (Morison 1985; Field, Jackson, and Mooney 1995; Medlyn et al. 2001). Although the leaf-level responses of stomatal conductance to $[CO_2]$ are important, they are by themselves insufficient to draw conclusions about processes operating at longer temporal and larger spatial scales. It is the canopy-scale integration of these effects that will ultimately address higher-order questions about forest water use and impacts of potential water conservation on ecosystem-scale processes.

FACE experiments in forest stands present a unique opportunity to explore feedbacks and interactions associated with stomatal and canopy conductance and their role in dictating the response of whole-plant water use to elevated $[CO_2]$. Measurements made on upper-canopy leaves from sweetgum trees exposed to ambient and elevated $[CO_2]$ showed that stomatal conductance is almost always lower in leaves measured at elevated $[CO_2]$ (Fig. 18.4A). Treatment-induced reductions ranged from 14% to 40% and, for the data set presented here, significant effects of elevated $[CO_2]$ on stomatal conductance were observed on 7 out of 11 days (Wullschleger et al. 2002). Although these CO_2-mediated effects were strong for leaves of the upper canopy, there were no significant effects of CO_2 enrichment on stomatal conductance for leaves in the middle- to lower-canopy positions. As a result, there were only modest reductions in canopy-averaged conductance due to elevated $[CO_2]$ as calculated from sap-flow data (Wullschleger et al. 2002). Reductions in canopy conductance due to elevated $[CO_2]$ averaged 14% over the season, and only minor effects of elevated $[CO_2]$ were observed on whole-stand transpiration (Fig. 18.4B). Stand transpiration tended to be less for trees in the elevated compared to the ambient $[CO_2]$ treatment and across the entire growing season averaged 2.8 and 3.1 mm d^{-1} in the two treatments, respectively (Wullschleger and Norby 2001). Stand transpiration on a monthly basis indicated few differences in water use between treatments, although a few significant differences were observed early in the season (Fig. 18.4C). Seasonal estimates of canopy transpiration were 540 mm and 484 mm for stands measured at ambient and elevated CO_2 concentrations, respectively: a difference of just 10% (Wullschleger and Norby 2001). There were no effects of elevated CO_2 on stand transpiration in the loblolly pine FACE experiment, where stomatal conductance of the dominant pines declined with CO_2 enrichment only during severe drought (Schäfer et al. 2002). Indirect effects of litter production on soil moisture were more important to the water budget than were direct effects of $[CO_2]$ on transpiration.

The results of the sweetgum FACE experiment show that large reductions in stomatal conductance at elevated $[CO_2]$ do not necessarily translate to equivalent reductions in rates of canopy transpiration; that is, the response is dampened as the scale increases (Sellers et al. 1996; Raupach 1998; Wilson, Carlson, and Bunce 1999). While FACE experiments can demonstrate some of these scale
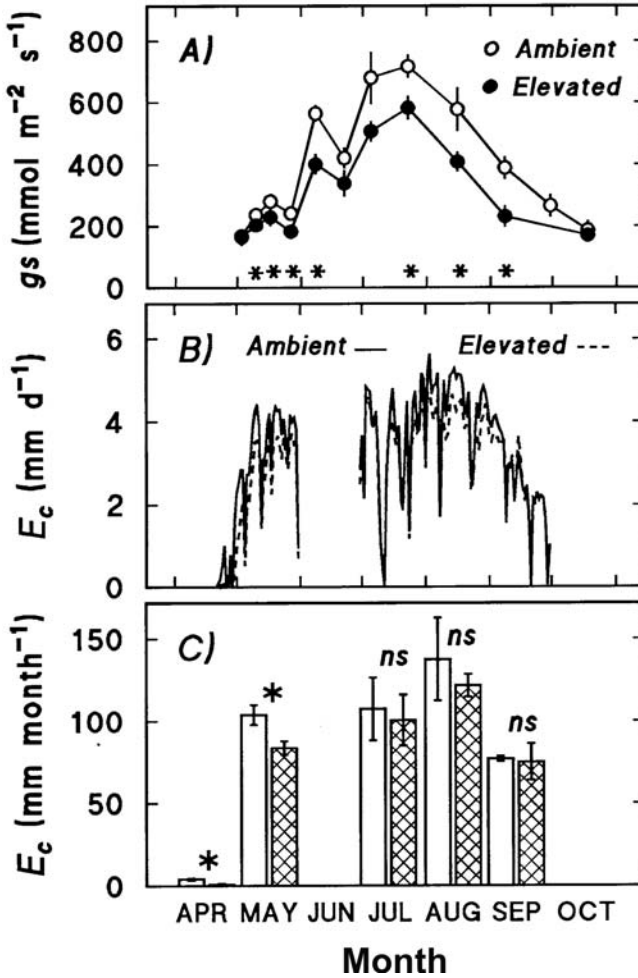
Figure 18.4. Seasonal patterns of: **(A)** stomatal conductance, **(B)** daily stand transpiration, and **(C)** monthly rates of stand transpiration for sweetgum trees measured in both ambient and elevated CO_2 concentration. The open bars in **(C)** are for the ambient [CO_2] treatments, whereas the crosshatched bars are for the elevated [CO_2] treatments. Asterisks indicate significant differences between [CO_2] treatments. ns designates no significant differences. Figures are from Wullschleger and Norby (2001) and Wullschleger et al. (2002); copyright, New Phytologist Trust.

dependencies, other important feedbacks operate at much larger scales. Atmospheric transport processes exert increasingly more control on water vapor exchange as the scale increases from leaf to canopy. The degree to which the canopy is decoupled from the atmosphere (Jarvis and McNaughton 1986) can be expected to increase in canopies that are more extensive than a 25 m diameter FACE plot, and this will further diminish the CO_2 effect on evapotranspiration (Wilson, Carlson, and Bunce 1999). Significant effects of elevated [CO_2] on stand transpiration were difficult to detect from one day to the next because of the dependence of the CO_2 responses on climate and soil resources (Wullschleger et al. 2002). Day-to-day variability in radiation, vapor pressure deficit, and longer-term variation in soil water availability masked what otherwise might have been a much larger CO_2-induced response given more favorable conditions (Gunderson et al. 2002; Wullschleger et al. 2002). Similarly, changes in litter production confounded direct effects of [CO_2] on soil moisture in the loblolly pine FACE experiment (Schäfer et al. 2002). Such conclusions are not usually intuitively obvious, and they complicate, confound, and compromise our ability to measure important biological impacts in CO_2-enrichment studies (see also Ellsworth et al. 1995; Senock et al. 1996; Kellomäki and Wang 1998). Hence, it is not yet at all clear how water balance will be affected by the higher [CO_2] in the forests of the future.

18.4 Modeling the Responses of Future Forests

Experiments have revealed a great deal of information and insight about how trees and forests will respond to the increases in [CO_2] and, to a lesser extent, to the warmer climate that will attend the rising [CO_2]. The experiments, however, cannot create a future reality, even if we knew the exact combination of atmospheric and climatic variables to try to reproduce. Only a small fraction of the tree species and forest environments on Earth have been studied. More experiments with different species, in different environments, and with different combinations of interacting variables will certainly expand our understanding. Larger-scale experiments in intact forests will provide new insights about important forest processes that have not been incorporated in smaller-scale experiments. Nevertheless, predictions of the state of the future forest in a higher-CO_2 world must come from models. A wide variety of models have been employed: biochemical and biophysical, whole-tree, gap-phase dynamics, forest biogeochemistry, and global vegetation models. All of these are informed to some extent by experimental results, and continued model improvement will come with a closer communication between experiments and model building. Here we will discuss how observations and experimental data were used with models to address the important social, economic, and political need for an assessment of the future state of ecosystems in response to rising atmospheric [CO_2] and the climatic change that is expected to accompany it.

18.4.1 National Assessment: Objectives and Approach

The National Assessment of the Potential Consequences of Climate Variability and Change synthesized, evaluated, and reported on what was known about the potential consequences of climatic variability and change for the United States in the twenty-first century (National Assessment Synthesis Team 2001). This first National Assessment brought together both stakeholders and scientific experts to begin a national process of research, analysis, and dialogue about the potential changes in climate, their impacts, and what could be done to adapt to an uncertain and changing climate. Because of limitations on present knowledge, the assessment sought to identify the highest priority uncertainties about which more must be known to understand climate impacts, vulnerabilities, and society's ability to adapt. Regional teams sought to identify key climatic vulnerabilities in the context of other global changes. Similarly, sector teams examined these vulnerabilities in national sectors of water, agriculture, human health, forests, and coastal areas and marine resources. The objectives of Forest Sector assessment were to synthesize what was presently known about the potential consequences of climate variability and change on U.S. forests in consideration of other environmental, social, and economic changes (Joyce et al. 2001).

Modeling analyses were an integral part of the Forest Sector analyses of productivity, natural disturbances, biodiversity, and timber markets. Two climate scenarios were used to provide a quantitative description of plausible future climates for the next 100 years (National Assessment Synthesis Team 2001). Both scenarios suggest that the U.S. climate is going to get warmer. The Canadian model scenario suggests a drier Southeast in the twenty-first century while the Hadley scenario suggests a wetter one. Forest productivity was examined using the biogeochemical models within the VEMAP study (Pan et al. 1998; Aber et al. 2001). These models include the effect of elevated [CO_2] as it interacts with nutrients and water on ecosystem dynamics. Biodiversity responses to climatic change were modeled at the level of the species, communities, and biomes (Hansen et al. 2001). These analyses assumed that the environment-organism relationship remained unaltered in the future, and that natural disturbances regimes were unchanged. Two statistical models describe the potential distribution of individual tree species based on present-day environmental factors, without a CO_2 effect. The biome-level model describes changes in vegetation structure based on light, energy, and water limitations, including the effect of CO_2. Land-use changes or other global changes, such as air quality, were not included in these ecological analyses. The socioeconomic analysis was based on a dynamic optimization model that incorporated changes in forest productivity, shifts between forest and agriculture land, and timber prices to examine climate change impacts on the forestry sector.

18.4.2 National Assessment: Conclusions

Aber et al. (2001) concluded that, under climatic change, forest productivity would likely increase with the fertilizing effect of atmospheric CO_2, but that

those increases will be strongly tempered by local conditions, such as moisture stress and nutrient availability. Across a wide range of climate scenarios in several biogeochemical models, modest warming resulted in increased C storage (often greater than 10%) in most forest ecosystems in the conterminous United States (Fig. 18.5). However, under some warmer scenarios, forests, notably in the Southeast and the Northwest, experienced drought-induced losses of C, often greater than 10%. Elevated [CO_2] in the models compensated for negative effects
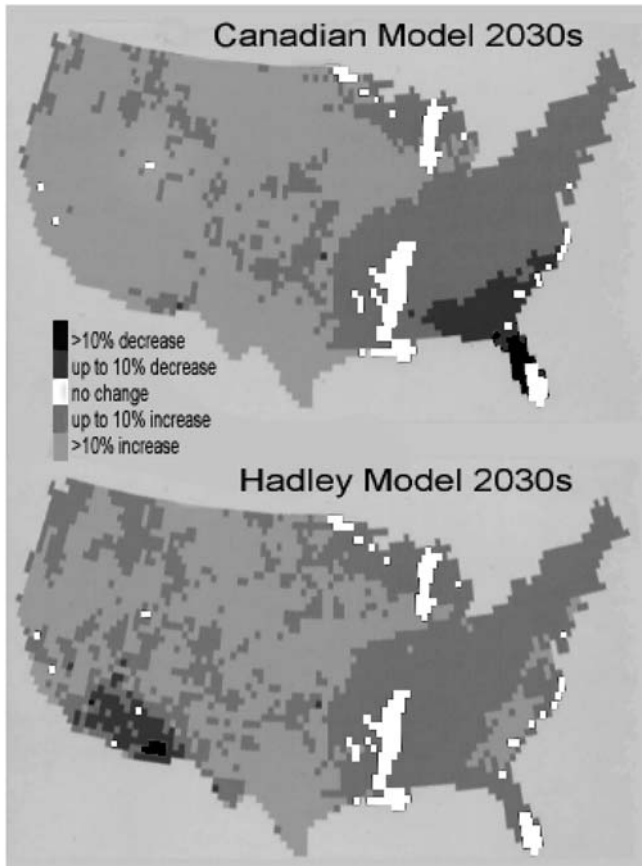

Figure 18.5. Projections of relative changes in vegetation carbon between 1990 and the 2030s for two climate scenarios. Under the Canadian model scenario, vegetation carbon losses of up to 20% are projected in some forested areas of the Southeast in response to warming and drying of the region by the 2030s. A carbon loss by forests is treated as an indication that they are in decline. Under the same scenario, vegetation carbon increases of up to 20% are projected in the forested areas in the West that receive substantial increases in precipitation. Output is from the TEM (Terrestrial Ecosystems Model) as part of the VEMAP II (Vegetation Ecosystem Modeling and Analysis Project) study.

of climatic change and enhanced the positive effects, but the impact of the changed climate (temperature and precipitation) on vegetation C was greater than that of elevated [CO_2]. When the natural disturbance of fire was included, changes in climate alone increased fire frequency (Dale et al. 2001). But, the occasional years of favorable growth conditions (elevated CO_2 and favorable climate) resulted in increased fuel loadings in the western United States and further increased fire frequency and intensity. An important lesson here is that the net effect of multiple factors at the ecosystem scale can be quite different from that implied by an analysis of CO_2 or fire effects alone.

The changes in C storage result from assumptions within the models that describe the influence of favorable growth conditions, including elevated [CO_2], on C accumulation. The biogeochemical models (Biome-BGC, CENTURY, TEM) variously assume that with increased [CO_2], production (or potential production) increases, transpiration or canopy conductance decrease resulting in increased soil moisture, and leaf [N] decreases resulting in decreased litter decomposition (Pan et al. 1998, Aber et al. 2001). There is some experimental evidence to support all of these assumptions, yet as we have discussed above, many of the responses have not proven to be robust or are moderated as the scale of observation or length of exposure increases (e.g., lower transpiration, lower foliar [N], reduced litter quality and decomposition). Just as the results differed across these biogeochemical models because of the differing assumptions within each model, changing the assumptions within each model about the internal dynamics of CO_2 could also result in different C dynamics.

Additionally, these model analyses did not include the effects of other components of global change, such as nitrogen deposition and ground-level ozone concentrations. Interactions between nitrogen, ozone, and elevated CO_2 concentrations can result in increases or decreases in forest productivity depending upon the relative atmospheric concentrations (e.g., Percy et al. 2002). These issues lead to the recognition that model results cannot be taken as an exact representation of future forests, but rather should be seen as providing guidance on the range of possible responses and future vulnerabilities, as well as highlighting the importance of continual dialogue between experimentalists and modelers to ensure the best representation of field experimental results into models.

As discussed above, carbon is not the only endpoint of interest. The effects of climatic change and elevated [CO_2] on species dynamics and biodiversity were evaluated jointly with ecophysiological processes at the biome scale. Across the different modeling approaches used to examine biodiversity, common patterns in the response of forests occurred (Hansen et al. 2001). Oak-hickory and oak-pine in eastern North America and ponderosa pine and arid-tolerant hardwoods in the West expand in area. Suitable habitats projected to greatly decrease in area or disappear from the coterminous United States included: alpine ecosystems, subalpine spruce-fir forests, aspen, maple-beech-birch forests, sagebrush, and loblolly-shortleaf pine ecosystems. These models used only the current organism-environment relationship and did not include population factors, dispersal ability, or disturbance to their environment. In this analysis, most

species habitats were projected to move 100 to 530 km north in 100 years, nearly twice the estimated dispersal rates during the Holocene (10–45 km/century). The pace of land-use and climatic change is likely to be rapid relative to the adaptability of species, leading to rapid shifts in species, ranges, and extinctions (Hansen et al. 2001). Here, the influences of elevated [CO_2] may be small in comparison to other global changes.

The effects of climatic change on forest productivity will have socioeconomic implications, especially in the timber and recreation markets (Irland et al. 2001). Analyses using the results of the biogeochemical models described above generated forest productivity gains for North America that increased timber inventories over the next 100 years (Irland et al. 2001). The increased wood supply reverberates through the local economy but has minimal impact at the national scale. At a finer scale, climatic change results in product differences (hardwood vs. softwood), regional differences (increased timber output in the South more than in the North), and welfare differences (consumers benefit but timber producer profits decline). These analyses suggested that timber producers could possibly adjust and adapt to climatic change under the relatively benign scenarios used here if new technologies and markets are recognized in a timely manner.

18.5 Summary

The increase in the atmospheric CO_2 concentration over the past century has been an unprecedented change in the global environment. The increase will continue for decades to come, as there is no sign that the human activities causing the change will abate anytime soon. The National Assessment in the United States was based on the observations from experiments and models that increased atmospheric [CO_2], and the associated climatic variability and change, have potential consequences for future forests, including their productivity, carbon storage, composition, fire regimes, and timber markets. Forest response to atmospheric and climatic change must be analyzed in the context of multiple, interacting environmental variables, interactions, and feedbacks, as well as economic and social factors, such as national and international economic activity and markets, population growth, and societal perceptions about these changes in forests. There is a need to enhance the communication between experimental results and models and to develop a comprehensive system to make the enormous amounts of data and information more accessible and useful to public and private decision makers. Rapid changes in forests in response to [CO_2] and climatic change could challenge current management strategies, and these changes will co-occur with such human activities as multiple uses of forests, agricultural and urban encroachment, and the stresses of air pollution. Understanding how to minimize the vulnerability of ecosystems and human society to atmospheric and climatic change and climate variability will require a broader interpretation of those global change factors and novel approaches that integrate

the dynamics of environmental, economic, and social systems in response to change.

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