
The Changing Role of Forests in the Global Carbon Cycle: Responding to Elevated Carbon Dioxide in the Atmosphere

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8.1 INTRODUCTION

Worldwide, forests have an enormous impact on the global C cycle. Of the 760 gigatons (10^{15} g, Gt) of C in the atmosphere, photosynthesis by terrestrial vegetation removes approximately 120 Gt, almost 16% of the atmospheric pool each year, and about half of this amount (56 Gt) is returned annually by plant respiration (Figure 8.1). The difference between gross canopy photosynthesis and plant respiration (see below) is defined as net primary production (NPP), and represents the annual production of organic matter that is available to consumers. Although estimates vary considerably, forests make up almost half of the global NPP, and approximately 80% of the terrestrial NPP (Figure 8.2). Thus, small changes in the capacity of forests to remove C from the atmosphere by photosynthesis, or return it to the atmosphere by respiration, or store it in wood and soils greatly affect the distribution of C between the terrestrial and atmospheric pool. Because trees use the C_3 pathway of photosynthesis, they are very responsive to increases in atmospheric CO_2 , and it has been hypothesized that a stimulation of photosynthesis and growth of trees may reduce the rate of accumulation of C in the atmosphere derived from fossil fuels. Mounting evidence suggests that a significant portion of the imbalance in the global C cycle, the 2.8 Gt year^{-1} that is unaccounted for when all known sinks are subtracted from known sources (Figure 8.1), may be explained by additional C uptake in temperate forests (Fan et al., 1998; Pacala et al., 2001; Janssens et al., 2003). How much of this sink is derived from land use change vs. growth enhancement of trees by elevated CO_2 , nitrogen deposition, and changes in climate remains uncertain.

The combustion of fossil fuels and other human activities, including deforestation and other changes in land use, is driving an imbalance in the global C cycle. Prior to the Industrial Revolution, the concentration of CO_2 in the atmosphere was approximately $280 \mu\text{l l}^{-1}$, and it was at this level for at least the previous 1000 years (Houghton et al., 1996). The injection of CO_2 into the atmosphere by the widespread combustion of fossil fuels currently adds approximately 6.4 Gt C to the

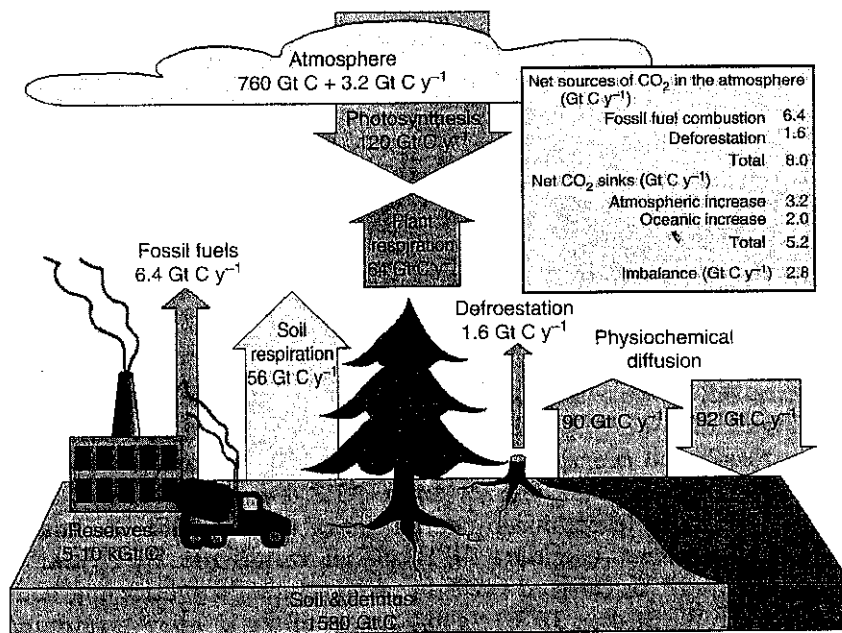


Figure 8.1 The global carbon cycle. Anthropogenic emissions are causing the amount of C in the atmosphere to increase by approximately 3.2 Gt year⁻¹. The cement plant and truck represent anthropogenic fluxes of C to the atmosphere caused by the combustion of fossil fuels during cement production, and the tree stump represents the contribution of changes in land use, primarily deforestation. The mass balance indicates a missing C sink of approximately 2.8 Gt. (Values compiled by K.L. Griffin from Field [2001], Prentice et al. [2001], and Schimel et al. [2001]. Drawing courtesy of K.L. Griffin, Lamont-Doherty Earth Observatory of Columbia University. With permission.)

atmosphere each year, and deforestation contributes another 1.6 Gt (Figure 8.1). About half of this anthropogenic CO₂ remains in the atmosphere. Carbon dioxide is a potent greenhouse gas; along with water vapor, methane and other gases, it maintains the habitable temperatures on Earth, but its further accumulation in the atmosphere is the primary driver of global warming. During 2002, the CO₂ concentration in the atmosphere was ~373 μl l⁻¹, and it is expected to double from

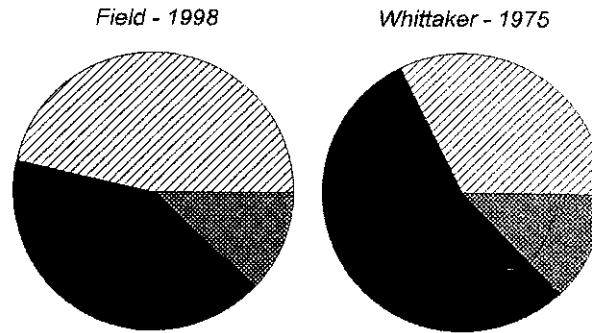


Figure 8.2 Two estimates of the contribution of forest ecosystems to global net primary production (NPP); black represents forest NPP, fine cross-hatch represents NPP from other terrestrial ecosystems and diagonal hatch represents ocean NPP. Field et al. (1998) combined estimates of radiation-use efficiency with satellite estimates of foliage cover to calculate NPP (global value: 105 Pg C year⁻¹). Whittaker (1975) derived NPP by census and biometric methods (Lieth and Whittaker, 1975) (global value: 85 Pg C year⁻¹, assuming C = 0.5 dry biomass). Tropical savannas were included as forest in both estimates.

its pre-Industrial level to ~560 $\mu\text{l l}^{-1}$ during the 21st century. Recent estimates suggest that a doubling of atmospheric CO₂ will force a 1.4°C to 5.8°C increase in global mean temperature (Houghton et al., 2001); this magnitude of warming is similar to the increase that occurred from the peak of the last ice age, approximately 15,000 years ago. But current climate change is happening over a much shorter time scale, a mere 50 to 100 years, and is far too rapid for many biological and ecological systems to adapt to the change.

The objectives of this chapter are to describe the major components of the terrestrial C cycle with an emphasis on current uncertainties in estimating these components, particularly for forest ecosystems; and, to compare the responses of two contrasting forest ecosystems to an experimental increase in atmospheric CO₂.

8.2 CARBON FLOW IN FOREST ECOSYSTEMS: POOLS AND FLUXES

Carbon is transferred through and stored in ecosystems by a myriad of physiological, ecological, and geochemical processes (Schlesinger, 1997; Clark et al., 2001) that may respond independently to the different facets of global change. Microbial respiration in the soil, for example, is extraordinarily sensitive to temperature, whereas photosynthesis responds strongly to changes in both atmospheric CO₂ and temperature. Predicting the effects of changing climatic conditions and atmospheric chemistry on the C cycle requires a clear understanding of these different processes. Broadly defined, C cycles comprise pools and fluxes, where a pool is a C reservoir lasting 1 year or longer (Hamilton et al., 2002), and fluxes represent the rates of C transfer from one pool to another. C pools typically are expressed per unit land area; fluxes are expressed per unit land area per annum. Although the major processes (fluxes) and pools in ecosystem C cycles were identified over 30 years ago (Whittaker, 1975), quantification of many of these processes remains clouded with uncertainty, and few studies have attempted to “close” the C budget for individual forest stands. The following discussion presents the currently held definitions for the major process regulating the flow of C through forest ecosystems and highlights a few of the most important uncertainties in their quantification.

Carbon enters ecosystems from the atmosphere by net photosynthesis, and is expressed as gross primary production (GPP) (Figure 8.1). Here photosynthesis is defined as the net reduction of CO₂ by plant canopies to sugars and structural materials. This net value represents C fixed by the primary carboxylating enzyme in chloroplasts, rubisco (rubisco: ribulose biphosphate carboxylase-oxygenase [EC 4.1.1.39]), minus the amount immediately returned to the atmosphere by photorespiration, but does not include oxidative respiration in mitochondria. GPP cannot be directly measured because of the need to separate C uptake by photosynthesis and losses by mitochondrial respiration. At the stand or ecosystem level,

GPP typically is estimated by scaling appropriate leaf-specific measurements in space and time (Wofsy et al., 1993), by process-based models (Aber et al., 1996; Luo et al., 2001), or calculated from stand-level estimates of transpiration (Schäfer et al., 2003). Alternatively, the sum of all subordinate C increments and losses can be used to calculate the rate of GPP necessary to meet these demands (Ryan et al., 1996; Hamilton et al., 2002).

Particularly in monospecific stands where obtaining representative physiological parameters and a physical description of the canopy are relatively straightforward, process-based models provide an effective means of calculating GPP. In many models, the strength of this approach stems from the rigorous and mature theory relating the biochemistry of carbon fixation to leaf biochemical properties and environmental conditions (von Caemmerer, 2000).

Once CO₂ becomes chemically reduced by photosynthesis, carbohydrates are expended to meet metabolic needs of plants and the corresponding rates of autotrophic respiration (R_a) result in a substantial return of C back to the atmosphere, globally amounting to ~64 Gt yr⁻¹ (Figure 8.1). Carbohydrates consumed in oxidative respiration by mitochondria are used to support the maintenance and construction of plant tissues in roots, stems, and foliage. Assumed to be 50% of GPP (Waring et al., 1998), R_a can exceed 70% of GPP in some forests (Hamilton et al., 2002) and varies with forest age (Makela and Valentine, 2001). Because of the sheer magnitude of R_a and its strong sensitivity to temperature, it is an important process defining the capacity of forests to store atmospheric C (Valentini et al., 2000).

The calculations of respiratory fluxes at the ecosystem level are made by scaling tissue specific rates, usually as a function of tissue nitrogen content and temperature (Ryan, 1995; Ryan et al., 1996; Hamilton et al., 2002; Meir and Grace, 2002), or measured directly at the stand level by micrometeorological methods (Baldocchi et al., 1988; Baldocchi, 2003). Unfortunately, the current understanding of environmental and physiological regulation of R_a is far from complete.

In contrast to photosynthesis, there is no theory for predicting variation in respiration rates for individual tissues. Respiration used to maintain cellular integrity, build ion gradients, and transport materials is highly sensitive to temperature, and this sensitivity results in a strong relationship between short-term variation in temperature and the rates of CO₂ evolution by plant tissues (Atkin and Tjoelker, 2003). The temperature dependence of R_a provides a convenient tool for extrapolating tissue-specific rates to the stand level. However, the rate of oxidative respiration also varies with the supply of carbohydrates, resulting in a linkage to the rate of photosynthesis and to the utilization of carbohydrates by sink tissues (Dewar et al., 1999; Atkin and Tjoelker, 2003). Under this form of control, respiration rates should vary with photosynthesis, as is implied by the observed correlation between R_a and GPP (Waring et al., 1998). The absence of a clear understanding of when seasonally and when during ecosystem development that R_a is under temperature or substrate control is a major impediment to estimating its response to current and future conditions.

The origin of respired CO₂ is not always clear, which contributes additional uncertainty to our estimates of ecosystem R_a. The fraction of soil respiration derived from plant roots vs. soil microbes (Andrews et al., 1999), the capacity of C to move in solution in the transpiration stream through trees (Teskey and McGuire, 2002), and “contaminate” estimates of bole respiration, and the activity of mitochondrial respiration during photosynthesis (Loreto et al., 2001; Wang et al., 2001) are just a few of the uncertainties that undermine quantitative estimates of R_a. An improved understanding of the origins and regulation of plant respiration under field conditions will greatly enhance the accuracy of forest carbon budgets.

Net primary production (NPP) is the difference between GPP and R_a; in addition to providing energy in the form of reduced C compounds for nonphotosynthetic organisms, NPP contributes to the accumulation of C in ecosystems. In contrast to GPP and R_a, the annual increment of woody tissue, a major component of NPP in forest ecosystems, can be estimated

directly from measurements of diameter growth and allometric relationships. However, a number of processes, some small and some large, often are not included and their absence may contribute to substantial underestimates of NPP (Clark et al., 2001). NPP includes the annual production of foliage as well as coarse and fine roots. Estimating fine root production and turnover is inherently difficult (Nadelhoffer and Raich, 1992; Publicover and Vogt, 1993; Hertel and Leuschner, 2002), which is compounded by high spatial variability within forests. The contribution of fine root production to NPP range from 33% to 67% (Jackson et al., 1997; Grier et al., 1981; Santantonio and Grace, 1987), and recent evidence that root longevities may have been substantially underestimated (Matamala et al., 2003) will likely alter these previous estimates. The production of short-lived materials (less than 1 year), including losses of dissolved organic carbon, and herbivory and volatilized organic compounds should be included (Clark et al., 2001), although with the exception of leaf litter, these other elements tend to be relatively small proportion of NPP. Herbivory, fine root mortality, and losses of volatile and nonvolatile organic compounds contributed to less than 10% of NPP in a rapidly growing loblolly pine plantation (Hamilton et al., 2002).

Globally, heterotrophic respiration (R_h) returns approximately 56 Gt C to the atmosphere each year; similar to the amount from R_a and almost ten times more than the amount of C injected into the atmosphere annually from the combustion of fossil fuels (Figure 8.1). Most of this flux is derived from rhizosphere and soil organisms including bacteria, fungi, and soil invertebrates. Estimates of R_h suffer from many of the same scaling issues as R_a , and present an additional formidable challenge — separating R_h from root-derived R_a . Carbon dioxide evolved from soils is derived from a combination of autotrophic respiration from plant roots and soil microorganisms, and assigning this C to the proper source is critical for determining NPP and NEP. Mycorrhizal fungi and bacteria living in the sphere of influence of fine roots, the rhizosphere, raise an additional problem. Should they be considered part of the root or part of the soil C budget? Wiant (1967) argued that root respiration should include all

processes oxidizing plant-derived organic compounds in and on the surface of fine roots, including mycorrhizal fungi and microorganisms oxidizing root exudates.

Hanson et al. (2000) identified three general approaches to quantify the contribution of R_a and R_h to soil CO_2 efflux. The first approach, "component integration," involves physically isolating and measuring the individual fluxes of different components of the plant-soil system and then adding them up. Hamilton et al. (2002) and George et al. (2003) used a variation of this approach to quantify the belowground C budget for a pine forest and a sweetgum forest exposed to elevated CO_2 ; R_h was calculated as the difference between total soil CO_2 efflux and the respiration rate of unearthened fine roots. The potential effects of disturbing the plant-soil system are the primary limitations of this approach. The second category includes various methods of "excluding roots," by inserting barriers or digging trenches in the soil, physically removing roots, or measuring soil CO_2 fluxes from soil under large canopy gaps where the influence of plant roots presumably is minimal. Disturbance effects and large increases in CO_2 efflux derived from rapid decomposition of newly severed roots are potential limitations of these methods. The third approach includes various methods of "isotope labeling," where intrinsic variation in soil and root C isotopic composition or the introduction of a label is used to identify the source of respired CO_2 . Andrews et al. (1999) used the sudden exposure of an intact pine forest to ^{13}C -depleted air to determine that roots contributed 55% of total soil respiration at the surface late in the growing season.

Estimates of the contribution of R_a derived from roots to total soil CO_2 efflux vary considerably. In a literature survey, Hanson et al. (2000) reported that the median value for the contribution of R_a to total soil CO_2 efflux was 50% to 60%. However, ~31% of the studies in this survey reported a percent contribution of fine roots to soil CO_2 efflux of at least 60%, and ~20% of the studies reported a proportional root contribution of at least 40%. A recent study of a rapidly growing pine plantation indicated that R_h was ~22% of total soil CO_2

efflux, but increased sharply in plots exposed to elevated levels of atmospheric CO₂ (Hamilton et al., 2002).

Net ecosystem production (NEP) is of great importance to our understanding of the transfers of C between the atmosphere and terrestrial ecosystems as it represents the net accumulation of C in ecosystems, and thus provides a measure of C sequestration. As defined by Woodwell and Whittaker (1968), NEP is the difference between NPP and heterotrophic respiration (R_h). This definition is incomplete in that it does not include a number of nonrespiratory fluxes, such as C losses as volatile organic carbon and methane (Randerson et al., 2002). While the absolute magnitude of these nonrespiratory losses often is small (e.g., Hamilton et al., 2002), the impact of these molecules can be quite large. For example, the volatile organic compound isoprene is a precursor to tropospheric ozone, a potent oxidant with enormous potential to reduce ecosystem productivity. A more inclusive definition of NEP, therefore, is simply the change in total C stocks in a given ecosystem over time (Randerson et al., 2002). Net biome production (NBP) (Schulze and Heimann, 1998) is functionally equivalent to NEP, but applies to regional C increments and losses from fire, harvest, and other episodic disturbances. Although mathematically simple, quantifying NEP represents a formidable challenge.

Setting aside modeling approaches (Aber et al., 1996; Kicklighter et al., 1999; Waring and McDowell, 2002) and inversion methods based on static gas sampling of the atmosphere (Pacala et al., 2001), estimation of net C storage in ecosystems takes one of three approaches: (1) direct measurement of C fluxes, either by chamber or micrometeorological methods; (2) physiological scaling in combination with biometric measurements; or (3) direct measurement of C stocks over time, either within a site or along a chronosequence. The chamber and micrometeorological methods require a continuous record of C fluxes for a given ecosystem over an entire year that is either measured or backfilled with a model. The annual integral of net ecosystem exchange by these methods is equivalent to NEP.

Chamber-based measurements are restricted to low-stature communities (e.g., Drake et al., 1996; Shaver et al., 1998; Dore et al., 2003; Obrist et al., 2003) and require intermittent sampling, while the eddy flux method provides a continuous record of CO₂ fluxes over relatively large land areas (Baldocchi et al., 1988; Curtis et al., 2002; Baldocchi, 2003). For forest ecosystems, this latter micrometeorological approach is not amenable to comparative studies involving relatively small plots. In free-air CO₂ enrichment (FACE) experiments, for example, where the plot size exposed to ambient or elevated levels of atmospheric CO₂ is less than 1/10 ha (DeLucia et al., 1999; Norby et al., 2002), the scaling of physiological fluxes combined with biometric estimates of standing biomass (O'Connell et al., 2003) or direct measurement of changes in C stocks (Boone et al., 1988; Lichter, 1998) are more appropriate for estimating NEP. In accounting for changes in C stocks through time, particular attention is paid to changes in live and dead vegetation, the major components of NEP, with smaller changes in forest floor and soil C (Boone et al., 1988; Hamilton et al., 2002). Approaches to estimating NEP from physiological scaling suffer from the same uncertainties employed in estimating R_a and R_h discussed above. Changes in most C stocks can readily be measured on annual or greater time steps, but often it is difficult to detect change in soil C pools over relatively short periods.

8.3 ECOSYSTEM RESPONSES OF PINE AND SWEETGUM FORESTS TO ELEVATED CO₂

Although there is a rich understanding of the response of potted plants and small trees to elevated CO₂, until recently experiments had not been conducted at an appropriate spatial and temporal scale to examine the effect of elevated CO₂ on ecosystem processes regulating the C cycle. With the development of FACE technology (Hendrey et al., 1999; McLeod and Long, 1999; Miglietta et al., 2001; Okada et al., 2001), it became possible to elevate atmospheric CO₂ in large plots in intact ecosystems without altering other microclimatic variables and without restricting the movement of animals,

including important herbivores. Initially employed in agricultural systems (Hendrey and Kimball, 1994; Kimball et al., 2002), approximately 24 FACE experiments currently are underway in nonagricultural ecosystems, ranging from deserts and grasslands to large-stature forests (Nowak et al., 2004). Two of the longest running forest experiments, a loblolly pine (*Pinus taeda* L.) plantation (DeLucia et al., 1999; Naidu and DeLucia, 1999) and a sweetgum (*Liquidambar styraciflua* L.) plantation (Norby et al., 2001), provide a unique opportunity to examine the responses of contrasting evergreen and deciduous forest ecosystems, respectively, to elevated atmospheric CO₂.

Loblolly pine and sweetgum trees are both early successional species of southeastern forests in North America and often compete with one another following agricultural abandonment, with sweetgum favoring moister soils (Keever, 1950). Although these species share similar life history characteristics, the difference in leaf and fine root longevity may directly alter the retention and cycling of C in these different forests, and may further affect the C cycle indirectly by altering the rate of ecosystem nitrogen transformations. Foliage of loblolly pine, an evergreen species, lives for approximately 18 months, whereas sweetgum is a deciduous species, and the leaves live for 6 months or less. Similarly, longevity of loblolly pine fine roots is about 3.4 times longer than that of sweetgum fine roots (Matamala et al., 2003).

In the Duke Forest FACE experiment, 30-m diameter plots in a loblolly pine forest have been exposed to ambient plus 200 $\mu\text{l l}^{-1}$ CO₂ almost continuously since late 1996. This forest, located near Chapel Hill, North Carolina (35° 58' N, 79° 05' W), is on heavily weathered clay-rich Alfisol soils with relatively low nitrogen and phosphorus availability (Schlesinger and Lichter, 2001; Hamilton et al., 2002). Trees were 13 years old when fumigation was initiated. The experimental sweetgum plantation located on the Oak Ridge National Environmental Research Park in Roane County, Tennessee (35° 54' N, 84° 20' W) was established on moderately well-drained, silty-clay-loam soils classified as an Aquatic Hapludult; these soils are somewhat richer in nutrients than the

pine forest in North Carolina (Norby et al., 2001; George et al., 2003). The sweetgum trees were 10 years old at the initiation of fumigation, slightly younger than the pine forest, and daytime CO_2 concentration in the experimental plots has averaged approximately $550 \mu\text{l l}^{-1}$ during the growing season since April 1998. These CO_2 treatments were chosen for the two experiments because, based on current projections, this CO_2 level is anticipated by 2050 (Houghton et al., 2001). Both experiments use the same FACE technology (Hendrey et al., 1999) and include fully instrumented control plots.

Although these experiments employed similar technology to comparably sized forest stands at similar developmental stages, there are important differences between them, and direct comparisons of the results, particularly of the absolute values of various C pools and fluxes, must be treated cautiously. In addition to having a less diverse community of plants in the understory, the sweetgum experiment experiences cooler temperatures and is established on more nutrient rich soils than the pine experiment (Zak et al., 2003). Moreover, estimates of the major ecosystem pools and fluxes of C were made by different investigators who used, in some cases, different scaling approaches and measurements. With these caveats in mind, these contrasting forests provide the most direct and comprehensive comparison of the response of different forest types (evergreen and deciduous) to elevated CO_2 currently available.

Exposure to elevated CO_2 substantially increased C storage and cycling in these forests (Table 8.1), but the magnitude of stimulation for different components of the carbon budget varied considerably. Gross primary production was stimulated by elevated CO_2 to a similar amount (18% to 23%) in the pine and sweetgum plantations. Neither experiment included direct measurement of GPP. In the pine experiment, GPP was estimated as NEP plus ecosystem respiration, which included the sum of the major respiratory C losses from plants and microbes ($R_e = R_{\text{soil}} + R_{\text{wood}} + R_{\text{canopy}} + \text{herbivory}_{\text{aboveground}} + \text{dissolved inorganic carbon [DIC]}$); for sweetgum, it was calculated as NPP plus plant respiration ($R_a = R_{\text{wood}} + R_{\text{canopy}} + R_{\text{fine root}}$). Carbon losses by $\text{herbivory}_{\text{aboveground}}$ and DIC in the

Table 8.1 Carbon Budgets ($\text{g C m}^{-2} \text{ year}^{-1}$) for Loblolly Pine and Sweetgum Forests Under Ambient and Elevated Atmospheric CO_2

	Pine			Sweetgum		
	Ambient	Elevated	% Δ	Ambient	Elevated	% Δ
GPP	2371	2805	18	1952	2377	23
R_a	1704	1604	-6	970	1240	32
NPP	705	897	27	972	1137	17
R_h	216	574	166	622	680	9
NEP	428	602	41	401	512	28

Note: GPP = gross primary production, R_a = plant respiration, NPP = net primary production, R_h = heterotroph respiration and NEP = net ecosystem production. Each value represents an average of three (pine) or two (sweetgum) experimental plots. The percent difference between ambient and elevated CO_2 plots is indicated by % Δ . The budget was calculated for plots exposed to elevated CO_2 for 2 years for pine and 3 years for sweetgum.

pine plantation were small and can be ignored (Hamilton et al., 2002). Although a quantitative analysis of the sources of error in these estimates for either forest is not available, it is important to note that a number of simplifying and perhaps imprecise assumptions were employed in scaling the respiratory fluxes measured for individual tissues at a given instant in time to annual values for the entire ecosystem.

Plant respiration (R_a) includes C losses from wood (R_{wood} ; stems, branches, and coarse roots); foliage (R_{canopy}), and fine roots ($R_{\text{fine root}}$). The proportion of GPP lost by R_a appeared greater in the pine (57% to 72%) than in the sweetgum forest (34% to 52%; Table 8.1), but was stimulated by elevated CO_2 only in the sweetgum stand. With the exception of foliage, annual respiratory losses were greater from pine wood and fine roots than for sweetgum. Greater tissue specific rates of leaf respiration for sweetgum (Tissue et al., 2002) than for pine (Hamilton et al., 2001) contributed to slightly higher R_{canopy} in the former (560 to 570 $\text{g C m}^{-2} \text{ year}^{-1}$) than in the latter (463 to 492 $\text{g C m}^{-2} \text{ year}^{-1}$), even though peak canopy mass was approximately twice as large in the pine (1054 to 1105 $\text{g dry matter [DM] m}^{-2}$) (DeLucia et al., 2002) than in

the sweetgum (486 to 553 g DM m⁻²) (Norby et al., 2003) forest. Respiration from pine stems, branches, and coarse roots (ambient plots: 488 g C m⁻² year⁻¹; elevated plots: 519 g C m⁻² year⁻¹) (Hamilton et al., 2002), although unaffected by CO₂ was considerably greater than for sweetgum (ambient plots: 150 g C m⁻² year⁻¹; elevated plots: 230 g C m⁻² y⁻¹) (R.J. Norby, 2004, unpublished results, based on Edwards et al., 2002). As with stems, C losses by R_{fine root} were higher in the pine forest than the sweetgum forest. Although maintenance respiration per unit root mass was slightly greater in sweetgum than for pine, the average annual standing biomass of fine roots was two- to three-fold greater in the pine forest (George et al., 2003).

Although it is becoming increasingly evident that short-duration changes in atmospheric CO₂ do not affect tissue-specific respiration rates (Hamilton et al., 2001; Davey et al., 2003), substantial increases in R_{wood} and R_{fine root} for trees grown under elevated CO₂ contributed to an increase in R_a in the sweetgum forest (Table 8.1). Increased biomass increment and substrate levels under elevated CO₂ caused a 23% increase in growth respiration and a 48% increase in maintenance respiration, respectively, for sweetgum stems (Edwards et al., 2002). This stimulation was driven in part by greater wood production under elevated CO₂. Given that wood production in the pine forest also was stimulated, it is curious that this forest did not exhibit an increase in R_{wood}. The answer may be found in the different assumptions about the relative respiration rates of branches vs. boles in these two forests.

Although absolute respiratory losses by fine roots appear lower in the sweetgum forest than the pine forest, elevated CO₂ caused a substantial increase in R_{fine root} only in the former (ambient plots: 245 g C m⁻² year⁻¹; elevated plots: 455 g C m⁻² year⁻¹) (George et al., 2003). Tissue-specific rates of respiration for sweetgum were unaffected, but a 73% increase in the standing mass of fine roots contributed to the large stimulation of R_{fine root} for this species exposed to elevated CO₂.

Greater respiratory losses may have contributed to lower NPP in the pine forest relative to sweetgum, but NPP was

substantially increased by elevated CO_2 in both forests (Table 8.1). Values of NPP have been calculated somewhat differently at both sites, but these differences have relatively little effect on the absolute values and the magnitude of the treatment effect. For the pine forest, NPP was calculated as the sum of biomass increments ($I_{\text{wood}} + I_{\text{leaf}} + I_{\text{coarse root}} + I_{\text{fine root}}$), plus the major inputs to detritus, litterfall, and fine root turnover ($D_{\text{litterfall}} + D_{\text{fine root}}$), plus losses as dissolved organic carbon (DOC) in the soil (Hamilton et al., 2002). For the deciduous sweetgum trees, I_{leaf} is 0, and root production was calculated directly from minirhizotron analysis rather than from $I_{\text{fine root}}$ plus $D_{\text{fine root}}$. DOC was not measured. Given these differences and that these forests experience different edaphic factors and climatic regimes, it is not possible to conclude that elevated CO_2 caused a greater stimulation of NPP for the pine forest (27%) than for the sweetgum forest (17%). In 2000, when the C budget for sweetgum was calculated, R_a was stimulated by elevated CO_2 , which provides a plausible explanation for why this forest may have experienced a lesser stimulation of NPP for that year. However, the percent stimulation for sweetgum varied between 16% and 38% depending on the year (Figure 8.3). Calculating long-term averages of the behavior of the more labile C pools will strengthen the direct comparisons of the response of these forests to elevated CO_2 .

Perhaps more important than the potential differences in the magnitude of the response between these contrasting forest types is the observation that the distribution of the response to elevated CO_2 among various C stocks was quite different. Enhanced wood production was the primary factor increasing NPP for the pine forest exposed to elevated CO_2 (DeLucia et al., 1999; Hamilton et al., 2002), while the treatment caused a substantial shift in C allocation in sweetgum (Norby et al., 2002). After the first year of exposure to elevated CO_2 , the stimulation of wood production in sweetgum abated and was replaced by an equivalent increase in fine root production. If these differences are sustained they have important implications for the forest products industry as well as the future role of forests in the global C cycle. A stimulation of

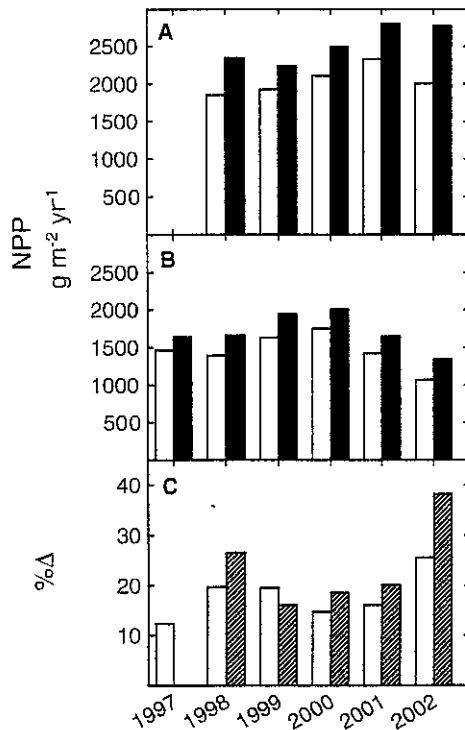


Figure 8.3 Net primary production (NPP; g DM m⁻² y⁻¹) for experimental plots in a loblolly pine forest (A) and sweetgum forest (B) exposed to ambient (~370 μl l⁻¹, open bars) and elevated (~570 μl l⁻¹, closed bars) levels of atmospheric CO₂. The percent stimulation of NPP (pine, open bars; sweetgum, hatched bars) is illustrated in (C). NPP was calculated as the sum of woody biomass increment and annual litterfall. In the pine forest, the treatment was initiated in August 1996, and some of the 1997 litter was formed before the initiation of the treatment. (Data from D. Moore, E. DeLucia, and R. Norby, unpublished, 2004.)

harvestable wood production, particularly in young pine stands, will be beneficial to the forestry industry (Groninger et al., 1999), and provided that this wood is used in durable products, will contribute to a net removal of C from the atmosphere. Allocation of extra C to highly labile fine roots in sweetgum, however, may contribute far less to C sequestration in biomass,

as the mean residence time of C in sweetgum fine roots is just 1.2 years (Matamala et al., 2003). Although the potential for C sequestration in biomass is less, more C is cycled into the soil in the sweetgum forest, where there is a potential for some of it to be sequestered in soil organic matter.

In both forests, the increases in NPP with elevated CO₂ were driven by greater rates of biomass accumulation associated with a stimulation of photosynthesis rather than increases in the capacity of the forest canopy to capture light energy. The canopies of both forests at the time these C budgets were calculated were at their maxima, with leaf area indices (LAI) of ~4 and ~6 for the pine and sweetgum forest, respectively (DeLucia et al., 2002; Norby et al., 2003). The stimulation of biomass increment without corresponding increases in LAI and light absorption resulted in 23% to 27% stimulation in radiation-use efficiency (ϵ), defined as biomass increment per unit absorbed photosynthetically active radiation. Values of ϵ for the sweetgum forest (2001 ambient plot: 2.01 g MJ⁻¹ and elevated plot: 2.48 g MJ⁻¹) (Norby et al., 2003) were considerably greater than for the pine forest (ambient plot: 0.49 g MJ⁻¹; elevated plot: 0.62 g MJ⁻¹) (DeLucia et al., 2002). Most of the difference in the absolute magnitude of ϵ between these forests is likely to stem from the year-round light absorption in pine without corresponding growth during the winter. In fact, the ratio of NPP/LAI, a proxy for ϵ , is remarkably similar between forests (pine: 176; sweetgum: 170). Current evidence suggests that LAI and light absorption of forests is not likely to be affected by increasing CO₂.

Calculation of microbial respiration from the soil (R_h) continues to be problematic, as it requires differentiating C derived from plant roots from C derived from soil microorganisms (Keltling et al., 1998; Edwards and Norby, 1999), yet quantifying this variable is important for estimating NEP from NPP. The pine and sweetgum experiments used different approaches to solve this problem. In the pine experiment R_h was estimated as the difference between R_{soil} and $R_{\text{fine root}}$; where R_{soil} was measured as CO₂ efflux from the soil surface (Andrews and Schlesinger, 2001), and $R_{\text{fine root}}$ was calculated as the product of standing root biomass and temperature-adjusted respiration rates

measured on unearthed but attached roots (Hamilton et al., 2002; George et al., 2003). For the sweetgum forest, R_h was calculated as the product of R_{soil} and the ratio of fine root-to-microbial respiration ($R_{fine\ root}/R_h$), where the ratio $R_{fine\ root}/R_h$ was based on an analysis of the isotopic composition of C evolved from the soil, as in Andrews et al. (1999). In sharp contrast to R_a , estimates of R_h revealed a strong stimulation by elevated CO_2 in the pine forest (166%) compared to the sweetgum forest (9%) (Table 8.1).

A number of factors may have contributed to the differential responsiveness of R_h to elevated CO_2 in these forests, including broad differences in the composition of the soil microbial communities. Pine roots, for example, are associated with ectomycorrhizal fungi, while sweetgum roots are associated with vesicular-arbuscular mycorrhizal fungi. In addition, elevated CO_2 disproportionately stimulated litter inputs of C to the soil in the pine relative to the sweetgum forest, thereby providing more substrate for soil microbial populations. Leaf litter represents a highly labile C source, and the amount of litter was ~19% greater in the elevated CO_2 plots in the pine forest (Finzi et al., 2001), but only ~10% greater in the elevated CO_2 plots in the sweetgum forest (Norby et al., 2003). The nutrient contents of pine and hardwood leaf litter in the pine forest were unaffected by growth under elevated CO_2 (Finzi et al., 2001); microbial populations in this forest should therefore respond solely to the increased input of litter C. Nitrogen concentration is significantly lower in the CO_2 -enriched sweetgum litter, but since the litter decomposes so quickly, potential effects of litter quality on decomposition are minimal (Johnson et al., 2004).

NEP was stimulated by elevated CO_2 and the absolute values were comparable between these forests (Table 8.1). For the pine experiment, NEP was calculated as the sum of biomass increments plus the increase in forest floor biomass ($I_{wood} + I_{leaf} + I_{coarse\ root} + I_{fine\ root} + I_{forest\ floor}$); in the sweetgum forest, NEP was calculated as $NPP - R_h$. That NEP was calculated independently from the respiratory fluxes in the pine forests revealed an interesting and potentially important inconsistency. While this estimate of NEP is consistent with the value

calculated as $NPP - R_h$ for the ambient plots, there is a large discrepancy for the elevated CO_2 plots, where NEP calculated by subtraction is only ~54% of the value presented in Table 8.1. This discrepancy suggests that the estimate of $R_{\text{fine root}}$ for this forest is too small, or the value of R_h is too large or some combination of the both. Andrews et al. (1999) estimated that the root contribution to R_{soil} was 55% under elevated CO_2 , similar to the 48% in this analysis, suggesting that many small errors may have contributed to this discrepancy. A similar inability to close the C budget for this pine forest under elevated CO_2 was recently reported by Schäfer et al. (2003).

Ignoring human-induced changes in land cover, NEP represents C sequestration in ecosystems (International Geosphere-Biosphere Programme, 1998). There is great uncertainty about the potential for forest ecosystems to abate the accumulation of anthropogenic C in the atmosphere and the contribution of the CO_2 -fertilization effect to the observed residual terrestrial C "sink" of $\sim 2.8 \text{ Gt year}^{-1}$. Recent evidence suggests that reforestation and afforestation in eastern North America and Western Europe contribute substantially to this sink (Fan et al., 1998; Pacala et al., 2001; Janssens et al., 2003). How much of this sink is derived from changes in land use relative to stimulations in tree growth caused by elevated CO_2 , nitrogen deposition and climate remains controversial. Schimel et al. (2000) estimate that as much as one third of additional C stored in forest ecosystems in North America is derived from a combined stimulation of tree growth by CO_2 and climate, whereas Caspersen et al. (2000) estimate that approximately 2% but with an upper limit of 7% of the observed increase in aboveground net ecosystem production was caused by a CO_2 -stimulation of growth. Although their approach has been criticized for not being sufficiently robust to estimate small changes in growth (Joos et al., 2002), this upper limit is consistent with experimental data.

Based on the observed stimulation of NEP in these forests and assuming that the response of NEP to CO_2 is linear, the $\sim 55 \mu\text{l l}^{-1}$ increase in CO_2 between 1930 and 1995, the approximate interval examined by Caspersen et al. (2000),

should have contributed to an 8% to 12% stimulation in C sequestration. Although young forests have considerable capacity to respond to increases in atmospheric CO₂, the magnitude of the responses observed for these forests suggests that the effect of changes in land use on C sequestration are greater than the effect of a CO₂-induced growth stimulation. Detecting a response to CO₂ that is independent of other environmental influences, stand developmental history, and regional-scale land-use patterns remains a problem.

The Duke and the Oak Ridge FACE experiments provide novel insights into the response of forest ecosystems to an increase in atmospheric CO₂, but the picture they paint is incomplete. Both experiments exposed trees to a step change in CO₂ — one day the experimental plots experienced ambient CO₂ and the next day and from then on it was elevated to the level expected in the year 2050. Extrapolations from perturbation experiments such as these are difficult because ecosystem C sequestration rates are projected to respond differently to gradual vs. step increases in atmospheric CO₂ (Luo et al., 2003). Respiration is generally proportional to the sizes of various C pools, and increases in pool sizes are cumulative. The difference between a step increase in GPP and a gradual increase in respiration translates to a transient response in C sequestration rate (Luo et al., 2003). Hence, we cannot assume that the effect of CO₂ enrichment on stimulation of NEP in these experiments will persist. By compiling several data sets including growth measurements of trees growing next to natural CO₂ springs, Idso (1999) concluded that the growth stimulation caused by elevated CO₂ attenuates strongly with time. A second but no less important limitation of these experiments is that trees are exposed to elevated CO₂, but without the intimately related increase in air temperature that is expected, leaving the question unresolved of how elevated CO₂ and temperature interact to affect C cycling. The recent construction of a forest nitrogen budget for the Duke loblolly pine experiment and an analysis of interannual variation in the growth response to elevated CO₂ for this forest provide tentative answers to these questions.

8.4 INTERANNUAL VARIATION IN THE GROWTH RESPONSE OF A PINE FOREST TO ELEVATED CO₂

One might expect that on nutrient deficient soils, the stimulation of tree growth should abate as forests outpace the capacity of soils to provide N and other nutrients. Oren et al. (2001) and Finzi et al. (2002) have demonstrated that at least early in the loblolly pine FACE experiment, the growth of pine trees is co-limited by CO₂ and N. The N and C cycles are tightly coupled, and it has been hypothesized that elevated CO₂, by increasing carbon and decreasing the N concentration of foliage, will reduce N mineralization rates from decomposing litter, thereby retarding the growth stimulation by elevated CO₂ (Zak et al., 1993; Finzi et al., 2002). Evidence to date tacitly supports this hypothesis, but it is far from conclusive.

The annual N requirement for pine grown under elevated CO₂ increased by 16% (Finzi et al., 2002), but there is no evidence yet that elevated CO₂ has altered microbial N cycling in this forest or in the sweetgum forest (Zak et al., 2003). Greater litter production in these forests when exposed to elevated CO₂ has not yet altered the supply of microbial N for tree growth. Thus, it appears that the N demand under elevated CO₂ is outpacing supply, but this potential imbalance has not yet reduced the growth stimulation. Johnson et al. (2004) concluded that in the sweetgum experiment, increased demand for N is small relative to its availability, and an N limitation is not likely to constrain the growth response to elevated CO₂ in the foreseeable future. It is reasonable to anticipate that the stimulation in growth without a corresponding increase in the supply of N will lead to a reduction in the response to elevated CO₂, but given the potentially large storage of N in tree stems and soils, the relatively high spatial variation of N in various components of these ecosystems and low experimental replication, it may take several years for an N limitation to become evident.

At just over 6 years of exposure to elevated CO₂, the Duke experiments provide a unique opportunity to examine the strength of the growth stimulation with time as well as its

interaction with changing environmental conditions. The reduction in stomatal conductance often observed for plants grown under elevated CO_2 (Curtis, 1996; Medlyn et al., 2001) leads to the hypothesis that the growth enhancement should be disproportionately greater in drought years (Strain and Bazzaz, 1983). And, because photorespiration becomes a larger drain on carbon assimilation as temperature increases, it also has been suggested that the stimulation of photosynthesis, and perhaps growth, will be greatest at high temperatures (Long, 1991; Drake et al., 1997). Although manipulative experiments to directly test these hypotheses at the scale of an intact forest ecosystem are not yet possible, an examination of the interannual variation in the response of NPP to CO_2 may provide an indirect test.

From the first year of the treatment in 1997 for the pine forest and in 1998 for the sweetgum forest, elevated CO_2 caused a substantial and sustained increase in NPP (~12% to ~38%) (Figure 8.3). In addition to being responsive to CO_2 and soil N availability, regression analyses revealed that NPP in this pine forest was highly responsive to precipitation during the growing season. Precipitation during the growing season varied from approximately 500 to 800 mm over the 6 years of this experiment, and this variation caused a ~27% increase in NPP. In contrast to one of the hypotheses posed above, the pine forest plots exposed to ambient and elevated CO_2 responded similarly to increasing precipitation (e.g., there was no trend in the percent stimulation of NPP with rainfall, Figure 8.4). The absence of an interaction between NPP and rainfall stems from the observation that unlike many angiosperms, the stomata of loblolly pine needles are relatively insensitive to growth under elevated CO_2 (Ellsworth, 1999). Because more litter accumulated on the forest floor, thereby retarding soil evaporation, soil moisture was somewhat greater in plots exposed to elevated CO_2 (Schäfer et al., 2002), but this had a negligible effect on NPP. The proportional response to elevated CO_2 was, however, greatest in warm years, as predicted by the kinetic properties of the primary carboxylating enzyme in C_3 photosynthesis (Drake et al., 1997).

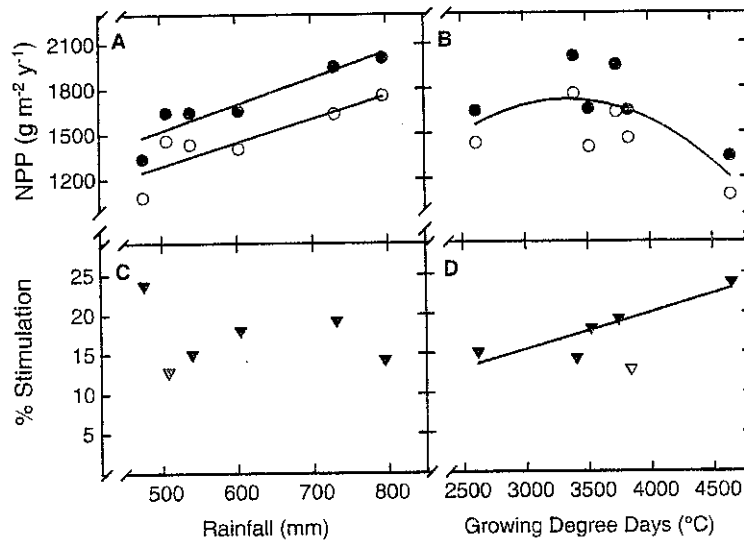


Figure 8.4 Net primary production (NPP; g DM m⁻² year⁻¹) for loblolly pine forest plots exposed to ambient (open symbols, ~370 μl l⁻¹) and elevated atmospheric CO₂ (~570 μl l⁻¹, closed symbols), and its percent stimulation, plotted as a function of total rainfall during the growing season and growing degree days. The shaded symbol represents data collected in 1997; foliage in this year developed before the treatment. Data are for the Duke free-air CO₂ enrichment experiment, and each point represents a mean value for a given year (1997–2002). The coefficients of determination and *p* values for all regressions were >0.5 and <0.05, respectively, and where a single line is shown, the regressions for the control and treatment plots did not differ. (Data are from D. Moore and E. DeLucia, unpublished, 2004.)

As inferred from interannual variation in the growth response, elevated temperature stimulated NPP in cool years but caused NPP to decrease in warm years (Figure 8.4). Respiration consumes a major portion of the carbon fixed by GPP (57% to 71%) (Table 8.1), and is profoundly temperature dependent (Atkin and Tjoelker, 2003), thus explaining the decline in NPP in warm years. Unlike the response to precipitation, pine forest plots exposed to elevated CO₂ responded

to temperature differently from those under ambient CO₂; the percent stimulation caused by elevated CO₂ increased with increasing temperature. Although this relationship must be interpreted with caution, as it was derived from a correlation, it is consistent with the theoretical prediction for photosynthesis and GPP.

Photosynthesis in C₃ plants is responsive to CO₂ because rubisco, the primary carboxylating enzyme, is not saturated at current concentrations, and because the reaction catalyzed by this enzyme is competitively inhibited by O₂ (Zelitch, 1973). Moreover, the specificity of rubisco, its relative affinity for CO₂ vs. O₂, is temperature dependent, decreasing strongly with rising temperature (Long and Drake, 1992). A consequence of this decline in specificity is that the stimulation of photosynthesis by elevated CO₂ progressively increases with increasing temperature (Long, 1991; Long and Drake, 1992). A greater percentage stimulation of photosynthesis by elevated CO₂ has been confirmed for loblolly pine (Myers et al., 1999), and it is therefore likely that this disproportionate increase in the stimulation of photosynthesis and GPP explain the observed increase in the percent stimulation of NPP in warm years. Further affirmation of this mechanism stems from the use of process-based models. Application of the PnET-II model (Aber et al., 1995, 1996) to this forest produced the same pattern of increasing percent stimulation of NPP by CO₂ in warm years, as observed in Figure 8.4 (C.J. Springer and R.B. Thomas, unpublished data, 2004).

8.5 CONCLUSIONS

At least early in stand development, loblolly pine and sweetgum forests on nutrient-deficient soils and experiencing the full suite of biological interactions and variation in the environment have considerable capacity to respond to changes in atmospheric CO₂ derived from the combustion of fossil fuels. The experimental simulation of plus 200 µl l⁻¹ CO₂ caused an additional 174 g C m⁻² to be stored in the pine forest, representing a 41% stimulation of NEP, and an additional 111 g C m⁻² to be stored in the sweetgum forest, representing a 28%

stimulation of NEP (Table 8.1). Although there is no evidence yet that the observed stimulation of forest productivity is systematically declining with time, there is considerable interannual variation in its absolute magnitude and enhancement. Net primary production in the pine forest was greater in years with more precipitation than in dry years, and this response to precipitation was not altered by elevated CO_2 . In contrast, elevated CO_2 lessened somewhat the reduction in NPP observed at elevated temperature (Figure 8.4). Forest productivity is likely to be stimulated by increasing atmospheric CO_2 , at least early in stand development, and for pine forests this increase will be greater in warm than in cool years.

Respiratory fluxes return large quantities of C to the atmosphere and are important determinants of the total C sequestration in ecosystems, yet the magnitude and regulation of these fluxes remains poorly understood. In the pine and sweetgum stands, R_a alone returned 50% to 72% of GPP to the atmosphere and greater R_a in the sweetgum forest than in the pine forest may explain its lower NPP (Table 8.1). Further research on the different components of respiration, with an emphasis on understanding seasonal variation in its temperature dependence and the interaction of temperature dependence with the rate of substrate supply, will greatly enhance our understanding the forest C cycles.

Differences in how forests respond to elevated CO_2 will alter their capacity to store additional C. In the pine forest exposed to elevated CO_2 additional C was allocated to boles and branches, whereas the sweetgum forest responded with a disproportional increase in fine root production. These tissues have profoundly different mean residence times potentially altering the duration of C storage. The residence time of C is longer in wood than in fine roots suggesting that the pine forest offers a longer-term storage of atmospheric C than the sweetgum forest. This statement must be tempered by our lack of understanding of the fate of C derived from decomposition of sweetgum roots. Insofar as this C becomes incorporated in recalcitrant soil organic matter, its residence time in the soil can be greatly extended.

The imbalance between the rate of N supply and utilization in the pine forest (Finzi et al., 2002) suggests that the stimulation of productivity by elevated CO₂ would be short-lived; 7 years or less, the duration of these experiments, admittedly is a small fraction of the “life” of these forests and an abatement in the growth response may appear in the future. The stimulation of productivity observed in these experiments may provide a short-term benefit to the forest products industry and slow the rate of increase of CO₂ in the atmosphere; however, faced with such an enormous injection of C into the atmosphere, even if sustained, these CO₂-induced stimulations in productivity are far from sufficient to reverse the accumulation of C in the atmosphere (DeLucia et al., 1999; Hamilton et al., 2002).

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