Contrasting responses of forest ecosystems to rising atmospheric CO_2: Implications for the global C cycle

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[1] In two parallel but independent experiments, Free Air CO_2 Enrichment (FACE) technology was used to expose plots within contrasting evergreen loblolly pine (*Pinus taeda* L.) and deciduous sweetgum (*Liquidambar styraciflua* L.) forests to the level of CO_2 anticipated in 2050. Net primary production (NPP) and net ecosystem production (NEP) increased in both forests. In the year 2000, after exposing pine and sweetgum to elevated CO_2 for approximately 5 and 3 years, a complete budget calculation revealed increases in net ecosystem production (NEP) of 41% and 44% in the pine forest and sweetgum forest, respectively, representing the storage of an additional 174 gC m^{-2} and 128 gC m^{-2} in these forests. The stimulation of NPP without corresponding increases in leaf area index or light absorption in either forest resulted in 23–27% stimulation in radiation-use efficiency, defined as NPP per unit absorbed photosynthetically active radiation. Greater plant respiration contributed to lower NPP in the loblolly pine forest than in the sweetgum forest, and these forests responded differently to CO_2 enrichment. Where the pine forest added C primarily to long-lived woody tissues, exposure to elevated CO_2 caused a large increase in the production of labile fine roots in the sweetgum forest. Greater allocation to more labile tissues may cause more rapid cycling of C back to the atmosphere in the sweetgum forest compared to the pine forest. Imbalances in the N cycle may reduce the response of these forests to experimental exposure to elevated CO_2 in the future, but even at the current stimulation observed for these forests, the effect of changes in land use on C sequestration are likely to be larger than the effect of CO_2-induced growth stimulation.

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1. Introduction

[2] Worldwide, forests have an enormous impact on the global C cycle. Of the 760 Gt C in the atmosphere, photosynthesis by terrestrial vegetation removes approximately 120 Gt, almost 16% of the atmospheric pool each year. About half of this amount (56 Gt) is returned to the atmosphere annually by plant respiration, and the other half is returned by microbial respiration [*Field*, 2001; *Prentice et al.*, 2001; *Schimel et al.*, 2001]. Net primary production (NPP), the difference between gross canopy photosynthesis and plant respiration, represents the annual production of organic matter that is available to consumers. Though estimates vary considerably, forests, including woodlands and savannas, make up almost half of global NPP and approximately 80% of terrestrial NPP [*Whittaker*, 1975; *Field et al.*, 1998]. 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 reservoirs.

[3] Because trees use the C_3 pathway of photosynthesis, they are very responsive to increases in atmospheric CO_2 [*Long and Drake*, 1992; *Curtis*, 1996]; insofar as a stimulation of photosynthesis contributes to greater net primary production and ultimately greater net ecosystem production, this stimulation may slow the 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 yr^{-1} that is unaccounted for when all known C sinks in the terrestrial-ocean-atmo-

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sphere system are subtracted from known sources, 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 versus growth enhancement of trees by elevated CO_2, nitrogen deposition, and changes in climate remains uncertain.

[4] 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 $\mu L\ L^{-1}$, and it was at this level for at least the previous 1000 years [*Intergovernmental Panel on Climate Change* (*IPCC*), 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 atmosphere each year [*Field*, 2001; *Prentice et al.*, 2001; *Schimel et al.*, 2001]. Deforestation also adds considerable C to the atmosphere, but the amount is controversial, with estimates of less than 1 Gt per year to greater than 2 Gt per year [*Defries et al.*, 2002; *Houghton*, 2003; *Achard et al.*, 2005; *Sabine et al.*, 2004]. About half of the anthropogenic CO_2 from all sources remains in the atmosphere. Currently, the CO_2 concentration in the atmosphere is $\sim$376 $\mu L\ L^{-1}$, and it is expected to double from its pre-Industrial level to $\sim$560 $\mu L\ L^{-1}$ during the twenty-first century.

[5] There is a rich understanding of the response of potted plants and small trees to elevated CO_2 [*Sionit and Kramer*, 1986; *Curtis and Wang*, 1998; *Ceulemans et al.*, 1999; *Norby et al.*, 1999], but until recently, experiments had not been conducted at an appropriate spatial or temporal scale to examine the effect of elevated CO_2 on ecosystem processes regulating the C cycle. With the development of FACE (Free-Air CO_2 Enrichment) technology [*Hendrey et al.*, 1999; *McLeod and Long*, 1999; *Miglietta et al.*, 2001; *Okada et al.*, 2001], it is now possible to elevate atmospheric CO_2 in large plots in intact ecosystems without altering other microclimatic and biotic variables. Initially employed in agricultural systems [*Hendrey and Kimball*, 1994; *Kimball et al.*, 2002], approximately 24 FACE experiments currently are underway in non-agricultural 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 CO_2.

[6] Our objective in this paper was to synthesize for the first time current data that contrast the responses of the major elements of the carbon cycle to elevated atmospheric CO_2 in two experimental forests with different leaf longevities. Carbon is transferred through and stored in ecosystems by a myriad of physiological, ecological, and geochemical processes [*Schlesinger*, 1997; *Clark et al.*, 2001], leading to the hypothesis that intrinsic differences in the turnover rate of the forest canopy and other reservoirs may ultimately alter the capacity of different forest types to store atmospheric C.

2. Experimental Exposure of Contrasting Forests to Elevated Atmospheric CO_2

[7] 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]. Though 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].

[8] In the Duke Forest FACE experiment, 30-m diameter plots in a continuous loblolly pine forest have been exposed to ambient plus 200 $\mu L\ L^{-1}$ CO_2 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. Similar plots (25-m diameter) were established in an experimental sweetgum plantation located on the Oak Ridge National Environmental Research Park in Roane County, Tennessee (35°54′N, 84°20′W), on moderately well drained silty-clay-loam soils classified as an Aquic Hapludult; these soils have greater total nitrogen and phosphorus concentration and are thus somewhat more fertile 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 in April 1998, slightly younger than the pine forest, and the daytime CO_2 concentration in the experimental plots has averaged approximately 550 $\mu L\ L^{-1}$ during the growing season. On the basis of current projections of the use of fossil fuels [*IPCC*, 2001], the CO_2 levels chosen for these experiments will be achieved by 2050. Both experiments use the same FACE technology [*Hendrey et al.*, 1999] and include fully instrumented control plots.

[9] Though these experiments employed similar technology to comparably sized forest stands at similar developmental stages, there are important differences between these independent experiments, and direct comparisons of the results, particularly of the absolute values of various C pools and fluxes, should be treated cautiously. In addition to having a less diverse community of plants in the understory, the sweetgum stand experiences cooler temperatures and is established on more fertile soils than the pine stand [*Zak et al.*, 2003]. Moreover, estimates of the major ecosystem pools and fluxes of C were made by different investigators using in some cases different scaling approaches and measurements. With these caveats in mind, these contrast-

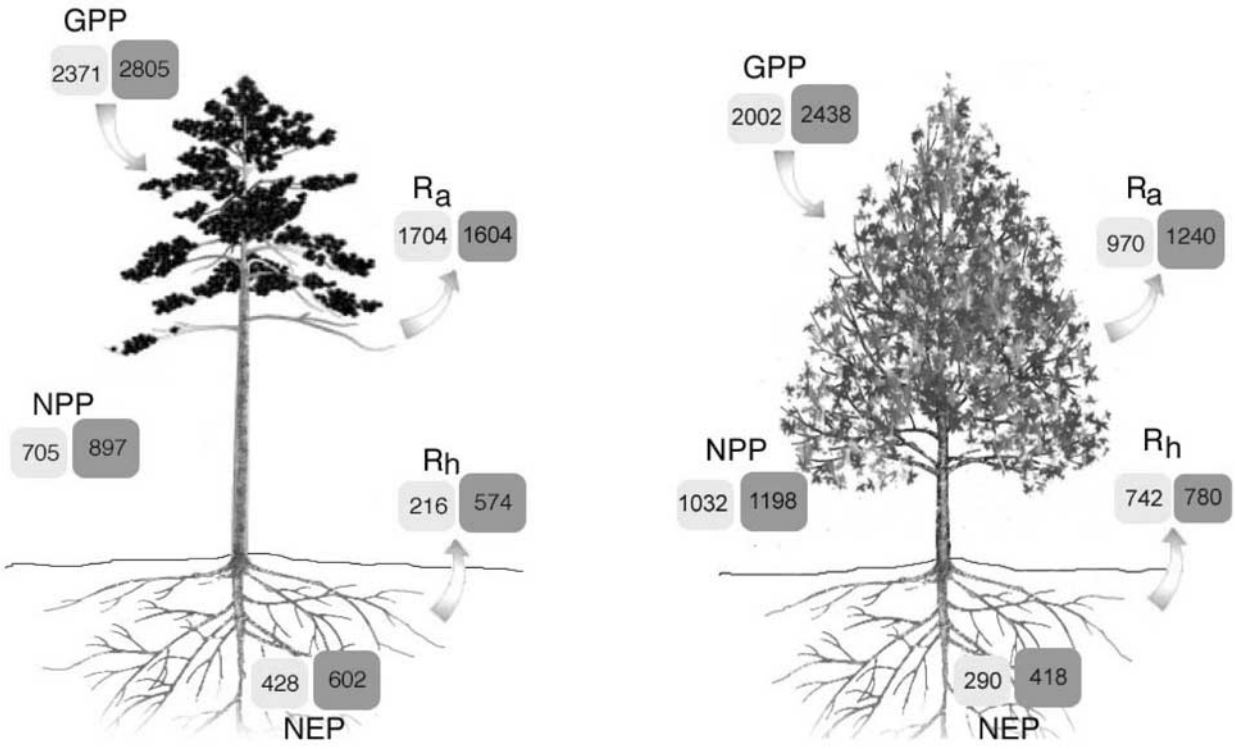

Figure 1. Carbon budget for the year 2000 expressed per mass of carbon (g C m^{-2} yr^{-1}) for (left) a pine forest and (right) a sweetgum forest exposed to ambient (~370 μL L^{-1}; light bubbles) and elevated (~570 μL L^{-1}; dark bubbles) atmospheric CO_2. Gross primary production (GPP) represents annual net photosynthesis; respiration from plants (R_a) and soil microbes (R_h) return large quantities of C to the atmosphere; net primary production (NPP) represents the annual increment of C in the ecosystem, and net ecosystem production (NEP) represents the accumulation of C following losses by R_h. The range in values for the different plots in pine NPP under ambient and elevated CO_2 was 653–766 g m^{-2} yr^{-1} and 876–928 g m^{-2} yr^{-1}, respectively, and the range in values for pine NEP under ambient and elevated CO_2 was 392–477 g m^{-2} yr^{-1} and 578–635 g m^{-2} yr^{-1}, respectively. The range in values for sweetgum NPP under ambient and elevated CO_2 were 957–1154 g m^{-2} yr^{-1} and 1146–1249 g m^{-2} yr^{-1}, respectively. The calculation of NEP for the sweetgum forest was derived from treatment means, so plot-to-plot variation was not estimated. *Hamilton et al.* [2002] provide a discussion of the variation in these estimates for the pine forest. A. Singsaas prepared the illustration.

ing forests provide the most direct and comprehensive comparison currently available of the response of different forests types (evergreen and deciduous) to elevated CO_2. The C cycle of the two sites was compared for the year 2000, which was the fourth full year of CO_2 enrichment of the pine stand and the third year for the sweetgum stand. The major assumptions and calculations used to estimate aspects of the C cycle in the pine forest are presented by *Hamilton et al.* [2002] and for the sweetgum forest by *Norby et al.* [2002]. Additional methods are provided in the text.

3. Ecosystem Responses of Pine and Sweetgum Forests to Elevated CO_2

[10] Exposure to elevated CO_2 substantially increased the rate of tree growth and C cycling in these forests, but the magnitude of stimulation for different components of the carbon budget varied considerably (Figure 1). Gross primary production (GPP) was stimulated by elevated CO_2 to a similar amount (18–22%) in the pine and sweetgum plantations. It should be noted that neither experiment included direct measurement of GPP. In the pine experiment, GPP was estimated as the amount of C necessary to meet the demand of net ecosystem production (NEP) plus ecosystem respiration (R_e), which included the sum of the major respiratory C losses from plants and microbes ($R_e = R_{soil} + R_{wood} + R_{canopy} + \text{Herbivory}_{aboveground} + \text{DIC}$); for sweetgum it was calculated as NPP plus plant respiration ($R_a = R_{wood} + R_{canopy} + R_{fine\ root}$).

[11] In the sweetgum forest, annual respiration from foliage was estimated by multiplying tissue-specific rates from *Tissue et al.* [2002] by leaf area duration from *Norby et al.* [2003]. Stem maintenance respiration was estimated by multiplying the volume-specific annual rates for wood (partitioned into lower bole, upper bole and branches) from *Edwards et al.* [2002] by stand biomass/wood specific gravity. Growth respiration was calculated by *Edwards et*

al. [2002], and fine root respiration is from *George et al.* [2003]. Carbon losses by $\text{Herbivory}_{\text{aboveground}}$ and dissolved inorganic carbon (DIC) in the pine plantation were small and were ignored [*Hamilton et al.*, 2002; *Knepp et al.*, 2005]. 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. Thus it is encouraging that using independent methods, *Schäfer et al.* [2003] derived similar values for GPP to those for the pine forest (Figure 1).

[12] 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 (57–72%) than the sweetgum forest (48–51%), but was stimulated by elevated CO_2 only in the sweetgum stand. Although respiration from foliage was greater in the sweetgum forest, the annual respiratory C losses from wood and roots were greater for pine 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 (560–570 gC m^{-2} yr^{-1}) than in the latter (463–492 gC m^{-2} yr^{-1}), even though peak canopy mass was approximately twice as large in the pine forest (1054–1105 gDM m^{-2} [*DeLucia et al.*, 2002]) than in the sweetgum forest (486–553 gDM m^{-2} [*Norby et al.*, 2003]). Respiration from pine stems, branches, and coarse roots (ambient plots: 488 gC m^{-2} yr^{-1}; elevated plots: 519 gC m^{-2} yr^{-1} [*Hamilton et al.*, 2002]), though unaffected by CO_2, was considerably greater than for sweetgum [ambient plots: 150 gC m^{-2} yr^{-1}; elevated plots: 230 gC m^{-2} yr^{-1}; R. J. Norby, unpublished results, 2004, based on *Edwards et al.* [2002]). As with stems, C losses by $R_{\text{fine root}}$ were higher in the pine forest than the sweetgum forest. Though 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].

[13] Though it is becoming increasingly evident that short-duration changes in atmospheric CO_2 do not affect tissue-specific respiration rates [*Hamilton et al.*, 2001; *Davey et al.*, 2003], substantial increases in R_{wood} and $R_{\text{fine root}}$ for trees grown under elevated CO_2 contributed to an increase in R_a in the sweetgum forest (Figure 1). Increased growth rates and substrate levels under elevated CO_2 caused a 23% increase in growth respiration per unit stem volume and a 48% increase in maintenance respiration per unit stem volume in sweetgum [*Edwards et al.*, 2002], resulting in an increase of 50% in total whole-stand stem respiration. Given that wood production in the pine forest was stimulated, it is curious that this forest did not exhibit an increase in R_{wood}. In another FACE experiment with relatively large trees, *Gielen et al.* [2003a] observed that during a period of no stimulation of stem growth, elevated CO_2 had no effect on stem respiration for three *Populus* species. Differences in when during the year respiration was measured therefore may have contributed to different responses observed for the sweetgum and pine forests.

[14] Absolute respiratory losses by fine roots appeared lower in the sweetgum forest than the pine forest, but elevated CO_2 caused a substantial increase in $R_{\text{fine root}}$ only in the former (ambient plots: 245 gC m^{-2} yr^{-1}; elevated plots: 455 gC m^{-2} yr^{-1} [*George et al.*, 2003]). Tissue specific rates of respiration for sweetgum were unaffected, but a 73% increase in the annual average standing mass of fine roots contributed to the large stimulation of $R_{\text{fine root}}$ for this species exposed to elevated CO_2.

[15] Greater respiratory losses may have contributed to lower NPP in the pine forest relative to the sweetgum forest, but NPP was substantially increased by elevated CO_2 in both. Values of NPP were calculated somewhat differently at both sites, but these differences had 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 ($I_{wood} + I_{leaf} + I_{\text{coarse root}} + I_{\text{fine root}}$), 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 forest, I_{leaf} is 0, and root production was calculated directly from minirhizotron analysis [*Norby et al.*, 2004] rather than from $I_{\text{fine root}}$ plus $D_{\text{fine root}}$. DOC was not measured in the sweetgum forest. Given these differences and that these forests experience different edaphic factors and climatic regimes, it is not possible to conclude based on the analysis of this 1 year that elevated CO_2 caused a different stimulation of NPP for the pine forest than for the sweetgum forest (Figure 1).

[16] The response of NPP to CO_2 enrichment averaged over 5 years for the sweetgum forest was 24%, and the response of the pine forest averaged over 6 years was 18% (Figure 2) [*Norby et al.*, 2004]. The discrepancy between these average values and those illustrated in Figure 1 stems in part from interannual variation in the response to elevated CO_2. In addition, a recent reanalysis by D. J. Moore et al. (Inter-annual variation in the response of tree growth and productivity of a *Pinus taeda* forest exposed to elevated CO_2, submitted to *New Phytologist*, 2005) (hereinafter referred to as Moore et al., submitted manuscript, 2005) of two major components of NPP for the pine forest (biomass increment and litterfall) indicates that the average enhancement caused by elevated CO_2 was lower than reported in previous studies [*DeLucia et al.*, 1999; *Hamilton et al.*, 2002; *Schäfer et al.*, 2003]. The correction applied by Moore et al. (submitted manuscript, 2005) compensated for pretreatment differences in tree growth that were not included in the statistical treatment of the data by previous investigators.

[17] Perhaps more important than the potential differences in the magnitude of the response between these contrasting forests types is that they allocated additional C differently. The capacity of ecosystems to sequester C is defined by its rate of uptake, GPP, and its residence times in various pools [*Luo et al.*, 2003]; even with similar responses of GPP to elevated CO_2, allocation of C to pools with different residence times would greatly affect the duration of storage.

[18] In most years, 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], though at times litterfall contributed as much as 55% of

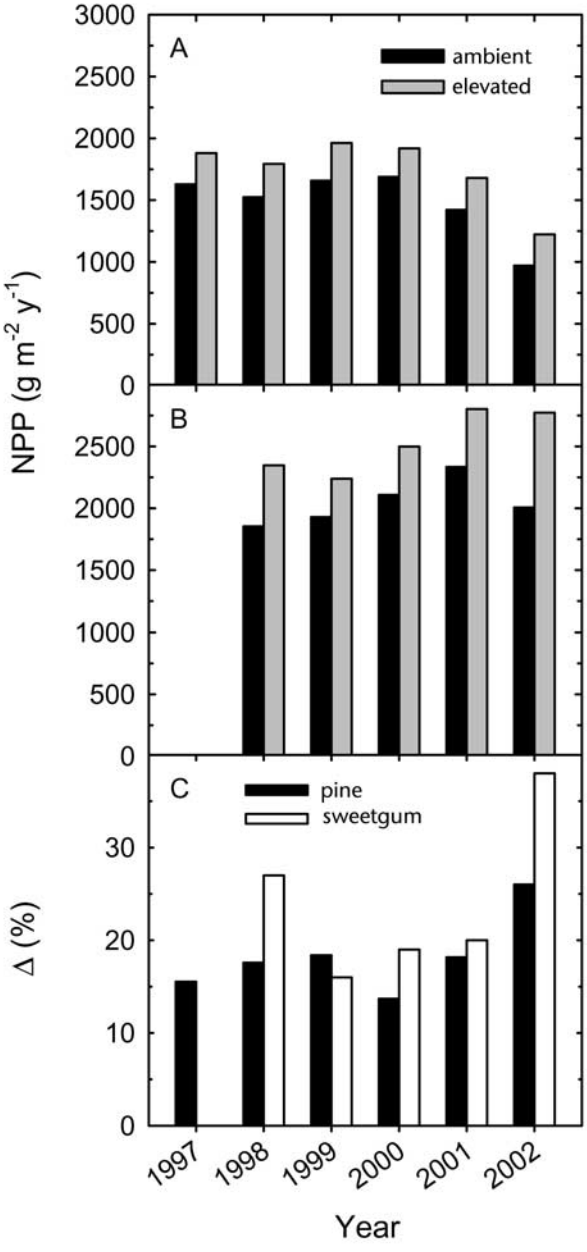

Figure 2. Apparent net primary production expressed per mass of dry matter (NPP; g m^{-2} yr^{-1}) for experimental plots in (a) a loblolly pine forest and (b) a sweetgum forest exposed to ambient (~370 μL L^{-1}; shaded bars) and elevated (~570 μL L^{-1}; black bars) levels of atmospheric CO_2. (c) Percentage stimulation. Apparent NPP was calculated as the sum of woody biomass increment (including coarse woody roots) and annual litterfall, as these were the only two components of NPP measured every year. 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 are from D. Moore, E. DeLucia, and R. Norby (unpublished data, 2004).

NPP in this forest (Moore et al., submitted manuscript, 2005). Thus half or more of the increase in NPP in the pine forest was allocated to relatively long-lived tissues. In contrast, the treatment caused a substantial shift in C allocation in sweetgum [*Norby et al.*, 2002, 2004]. 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. This change in allocation from long-lived woody tissues to shorter-lived fine roots may greatly reduce the capacity of sweetgum forests to store carbon in biomass, although C storage in soil is not precluded.

[19] Estimates of the mean residence time for woody tissues in the pine forest are from approximately 19 to 27 years, the former for wood developed under elevated CO_2, while the residence times for non-woody tissues (foliage and fine roots) are from 1.3 to 1.6 years [*Luo et al.*, 2003]. Using isotopic methods, *Matamala et al.* [2003] confirmed that the mean residence time of root C was 1.2 years for sweetgum and 4.2 years for pine, and may be much longer for some pine roots. Even at these longer residence times for pine fine roots, turnover of C in this pool is considerably shorter than woody biomass, leading to the inference that for the same stimulation of GPP, the pine ecosystem would store more C than the sweetgum ecosystem. However, this conclusion must be tempered by our incomplete understanding of the ultimate destination C released into the soil by the decomposition of fine roots.

[20] In both forests the increases in NPP with elevated CO_2 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 near 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; *Schäfer et al.*, 2003]. The stimulation of NPP without corresponding increases in LAI and light absorption resulted in 23–27% stimulation in radiation-use efficiency (ε), defined as NPP per unit absorbed photosynthetically active radiation. Values of ε for the sweetgum forest (2001, ambient plot: 2.01 g MJ^{-1}; 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). Exposure of aspen and birch trees to elevated CO_2 with FACE increased LAI, but the canopy had not yet closed in this young stand [*Karnosky et al.*, 2003]. Current evidence from the pine and sweetgum forests [*DeLucia et al.*, 2002; *Norby et al.*, 2003; *Schäfer et al.*, 2003], as well as from a high density poplar stand [*Gielen et al.*, 2003b] suggest that LAI and light absorption by closed-canopy forests is not likely to be affected by increasing CO_2.

[21] Microbial respiration from the soil (R_h) returned approximately 9–37% of GPP to the atmosphere in these

forests (Figure 1). Nearly continuous records of CO_2 efflux from the soil surface are available for both sites [*King et al.*, 2004; J. S. Pippen, unpublished data, 2005], but calculation of R_h is problematic, as it requires differentiating C derived from plant roots from that derived from soil microorganisms [*Kelting et al.*, 1998; *Edwards and Norby*, 1999; *Hanson et al.*, 2000]. 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 $R_{fine\ root}$, where R_{soil} was measured as CO_2 efflux from the soil surface [*Andrews and Schlesinger*, 2001] and $R_{fine\ root}$ was calculated as the product of standing root biomass and temperature-adjusted respiration rates measured on unearthed but attached roots [*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 (W. Cheng, personal communication, 2004) as per *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 (5%; Figure 1).

[22] 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 leaf litter inputs of C to the soil in the pine forest relative to the sweetgum forest thereby providing more substrate for soil microbial populations near the surface. Though *Zak et al.* [2003] were unable to demonstrate a significant change in microbial N or nitrogen mineralization rates with elevated CO_2 in these forests, greater respiration [*Andrews and Schlesinger*, 2001; *Phillips et al.*, 2002] suggests that microbial activity may have been stimulated under trees exposed to elevated CO_2 without a corresponding increase in microbial biomass. In the sweetgum stand, elevated CO_2 stimulated fine root input, thereby adding substrate deeper in the soil profile. 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].

[23] The nutrient contents of pine and hardwood leaf litter in the pine forest was 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].

[24] Elevated CO_2 stimulated net ecosystem production (NEP), and the absolute values were comparable between these forests (Figure 1). However, caution is warranted with regard to NEP calculated for a single year, especially for ecosystems in which C influx and efflux are changing after a perturbation [*Luo et al.*, 2003]. For the pine experiment, it was assumed that there was no change in soil C [*Schlesinger and Lichter*, 2001], and NEP was calculated as C accumulating at the site by summing tree C increments plus the increase in forest floor C [$I_{wood} + I_{leaf} + I_{coarse\ root} + I_{fine\ root} + I_{forest\ floor}$]. (The increment in forest floor C ($I_{forest\ floor}$) was measured directly [*Schlesinger and Lichter*, 2001] and is functionally equivalent to ($D_{litterfall} + D_{fine\ root}$) $- R_h$.) 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 a potentially important inconsistency. While this estimate of NEP calculated by summing increments 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 (e.g., NPP $- R_h$) is only ~54% of the value presented in Figure 1. This discrepancy suggests that the estimate of $R_{fine\ root}$ 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 reported by *Schäfer et al.* [2003].

[25] Ecosystems accumulate C as NEP, and over time a portion of this C may be released to the atmosphere by fire or human-induced changes in land cover. Following these losses, the rate of C storage by terrestrial ecosystems is called net biosphere production (NBP [*IGBP Terrestrial Carbon Working Group*, 1998]). There is considerable uncertainty about the contribution of CO_2 fertilization of NEP, and ultimately NBP, to the terrestrial C "sink" of ~2.8 Gt yr^{-1}. Recent evidence suggests that reforestation and aforestation 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. However, their approach has been criticized for not being sufficiently robust to estimate small changes in growth [*Joos et al.*, 2002].

[26] Though NBP and not NEP represents C storage by landscapes, the percentage stimulation of the latter may reveal the potential contribution of CO_2 fertilization to the observed terrestrial sink. On the basis of the observed stimulation in these forests (Figure 1) and assuming the response of NEP to CO_2 is linear, the ~55 $\mu L\ L^{-1}$ increase in CO_2 between 1930 and 1995, the approximate interval examined by *Caspersen et al.* [2000], should have contributed to an 8–12% stimulation in C seques-

tration. Though young forests may have considerable capacity to respond to increases in atmospheric CO_2, 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 CO_2-induced growth stimulation.

[27] The Duke and the Oak Ridge FACE experiments provide novel insights into the response of forest ecosystems to an increase in atmospheric CO_2, but the picture they paint is incomplete. Both experiments exposed trees to a step-change in CO_2, where suddenly and in one step it was increased 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 versus step increases in atmospheric CO_2 [*Luo et al.*, 2003; *Klironomos et al.*, 2005]. Hence we cannot assume that the effect of CO_2 enrichment on the stimulation of NPP and NEP in these experiments will persist.

[28] By compiling several data sets including growth measurements of trees next to natural CO_2 springs, *Idso* [1999] concluded that the growth stimulation caused by elevated CO_2 attenuates strongly with time. Much of this attenuation is attributable to the transition from the exponential growth phase of the young trees, wherein both increasing leaf area and higher growth per unit leaf area contribute to the growth response [*Norby*, 1996], to a linear growth phase after canopy development is complete. However, N feedbacks also are thought to lead to an attenuation of response over time; on nutrient deficient soils, the stimulation of tree growth should abate as forests outpace the capacity of soils to provide N and other nutrients [*Zak et al.*, 1993; *Luo et al.*, 2004].

[29] In an experiment conducted in Italy, more inorganic N was removed from the soil by a densely planted popular stand exposed to free air CO_2 enrichment for 3 years than plots exposed to ambient air [*Calfapietra et al.*, 2003]. In the loblolly pine FACE experiment, tree growth is colimited by CO_2 and N, and it appears that rates of N mineralization may become growth limiting under elevated CO_2 at some point in the future [*Oren et al.*, 2001; *Finzi et al.*, 2002]. However, at least at this early stage of development, N mineralization has not responded to elevated CO_2 in either stand [*Zak et al.*, 2003]; N uptake by trees has increased with CO_2 enrichment [*Finzi et al.*, 2002; *Johnson et al.*, 2004], but the growth enhancement has not abated in either forest (Figure 2).

[30] In addition to substantial interannual variation in the absolute value of NPP, the percentage stimulation caused by elevated CO_2 also varied from 14 to 26% for the loblolly pine forest and from 16 to 38% for the sweetgum forest (Figure 2). Most of the variation in the absolute values of NPP in the pine forest was related to differences in precipitation during the growing season, with greater NPP in wet years. In this forest, variation in percentage stimulation of NPP was not, however, correlated with interannual changes in water availability (Moore et al., submitted manuscript, 2005). NPP also varied with average summer temperature and growing season degree-day totals and was greatest in moderate years, but lowest in warm and cool years. The percentage stimulation in NPP was positively correlated with the average temperature during the growing season and growing-degree days (Moore et al., submitted manuscript, 2005). Similar relationships between NPP and environmental factors have not yet been described for the sweetgum stand.

[31] A second but no less important limitation of these experiments is that trees were exposed to elevated CO_2 but without the intimately related increase in air temperature that is expected as greenhouse gases accumulate in the atmosphere, leaving the question unresolved of how elevated CO_2 and temperature interact to affect C cycling. Elevated temperatures potentially affect C cycling in forest ecosystems [*Clark et al.*, 2003] by directly affecting photosynthesis and respiration [*Long*, 1991; *Myers et al.*, 1999; *Cox et al.*, 2000; *Cramer et al.*, 2001; *McGuire et al.*, 2001], or indirectly by affecting soil moisture availability and the rates of nutrient mineralization [*McNulty et al.*, 1997; *Aber et al.*, 2001]. The relationship between pine NPP and growing-degree days (Moore et al., submitted manuscript, 2005) suggests that NPP may decline as temperature increases, but may decline somewhat less under elevated levels of CO_2.

4. Conclusions

[32] Early in stand development, loblolly pine and sweetgum forests on unfertilized soils and experiencing the full suite of biological interactions and variation in the environment have the capacity to respond to increasing atmospheric CO_2. The experimental simulation of plus 200 $\mu L\ L^{-1}$ CO_2 caused an average 14–26% stimulation of NPP in the pine forest and an average 16–38% stimulation of NPP in the sweetgum forest over several years of exposure. In the one year when the complete C budget was calculated for each forest, an additional 174 $gC\ m^{-2}$ was stored in the pine forest exposed to elevated CO_2, representing a 41% stimulation of NEP, and an additional 128 $gC\ m^{-2}$ was stored in the sweetgum forest, representing a 44% stimulation of NEP (Figure 1). At least for the pine forest, there is evidence that exposure to elevated CO_2 accelerates the rate of forest development [*LaDeau and Clark*, 2001], and the long-term balance between accelerated C cycling associated with more rapid forest development and additional C storage in these forests remains unknown. A full evaluation of the capacity of these forests to store additional C will require information about the accumulation of soil humus and the accumulation of woody biomass through the life of the forest.

[33] Respiratory fluxes returned large quantities of C to the atmosphere and were important determinants of the total C sequestration in these ecosystems, yet the magnitude and regulation of these fluxes remains poorly understood. Though not examined in these experiments, the magnitude of these respiratory fluxes may increase with projected increases in temperature in the future.

[34] 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, much of the additional C was allocated to boles, branches, and coarse woody roots, whereas the sweetgum forest responded with a dispropor-

tional increase in fine root production. 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.

[35] The imbalance between the rate of N supply and utilization in the pine forest [*Finzi et al.*, 2002] suggests that the stimulation of net primary production and other aspects of C cycling by elevated CO_2 may 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, though not yet evident, may appear in the future. The stimulation of net ecosystem production observed in these experiments may slow the rate of increase of CO_2 in the atmosphere; however, the contribution of CO_2 fertilization to the terrestrial C sink is likely to be small compared to projected changes in land use.

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