Oecologia (2002) 131:250–260
DOI 10.1007/s00442-002-0884-x

ECOSYSTEMS ECOLOGY

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Forest carbon balance under elevated CO_2

Received: 30 July 2001 / Accepted: 3 January 2002 / Published online: 19 March 2002

Abstract Free-air CO_2 enrichment (FACE) technology was used to expose a loblolly pine (*Pinus taeda* L.) forest to elevated atmospheric CO_2 (ambient + 200 µl l^{-1}). After 4 years, basal area of pine trees was 9.2% larger in elevated than in ambient CO_2 plots. During the first 3 years the growth rate of pine was stimulated by ~26%. In the fourth year this stimulation declined to 23%. The average net ecosystem production (NEP) in the ambient plots was 428 gC m^{-2} $year^{-1}$, indicating that the forest was a net sink for atmospheric CO_2. Elevated atmospheric CO_2 stimulated NEP by 41%. This increase was primarily an increase in plant biomass increment (57%), and secondarily increased accumulation of carbon in the forest floor (35%) and fine root increment (8%). Net primary production (NPP) was stimulated by 27%, driven primarily by increases in the growth rate of the pines. Total heterotrophic respiration (R_h) increased by 165%, but total autotrophic respiration (R_a) was unaffected. Gross primary production was increased by 18%. The largest uncertainties in the carbon budget remain in separating belowground heterotrophic (soil microbes) and autotrophic (root) respiration. If applied to temperate forests globally, the increase in NEP that we measured would fix less than 10% of the anthropogenic CO_2 projected to be released into the atmosphere in the year 2050. This may represent an upper limit because rising global temperatures, land disturbance, and heterotrophic decomposition of woody tissues will ultimately cause an increased flux of carbon back to the atmosphere.

Keywords Carbon dioxide · Free-air CO_2 enrichment · *Pinus taeda* · Global carbon cycle · Carbon sequestration

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Introduction

Forests account for more than 75% of the carbon stored in terrestrial ecosystems and approximately 40% of the carbon exchange between the atmosphere and the terrestrial biosphere each year (Schlesinger 1997). Human activities are increasing atmospheric CO_2 concentrations with concomitant changes in global climate (Houghton et al. 2001). These changes have heightened interest in the potential for forests to sequester atmospheric carbon and in understanding how this potential may change as atmospheric CO_2 continues to increase during the next century. Elevated CO_2 stimulates tree growth and forest net primary production (NPP) in intact forest ecosystems (DeLucia et al. 1999; Norby et al. 2001). NPP represents the amount of carbon incorporated into biomass and is the difference between total carbon assimilated by photosynthesis (gross primary production or GPP) and that lost by autotrophic respiration (R_a). Thus, predicting the effects of elevated CO_2 on NPP under different environmental conditions requires understanding the effects of CO_2 on GPP and R_a. For example, an increase in NPP could be driven by increased fixation of carbon into the system (increased GPP), reduced flux of carbon out of the system (reduced R_a), or both.

The amount of carbon forests incorporate into biomass (NPP) is likely to increase transiently with increased atmospheric CO_2 (Comins and McMurtrie 1993; Luo and Reynolds 1999). However, this will not necessarily result in increased ecosystem carbon sequestration because a significant fraction of this carbon is lost to het-

erotrophic respiration (R_h) each year (Schlesinger 1997). Carbon potentially available for longer-term storage is represented by net ecosystem production (NEP), defined as the difference between NPP and R_h (Schlesinger 1997). In addition to such factors as the historic patterns of land use, NEP depends on the age of the forest. Young and old forests may have zero or even negative values of NEP (i.e. ecosystem carbon loss), whereas ~60% of NPP may become NEP for mid-aged stands (Arneth et al. 1998; Schulze et al. 2000). Because NEP depends on both NPP and R_h, an increase in NPP does not necessarily cause a corresponding increase in NEP.

The Duke Forest free-air CO_2 enrichment (FACE) experiment was established to examine the response of an intact loblolly pine forest to elevated atmospheric CO_2 (Hendrey et al. 1999). In this paper, we present the growth response of trees during 4 years of exposure to elevated CO_2. We use our results and values from the literature to calculate a carbon budget for 1 year. We selected 1998 because root biomass and increment data were available and the response of tree growth to elevated CO_2 was relatively constant from 1997 to 1999. Our objective was to quantify the major carbon pools and fluxes to evaluate the potential of this forest to sequester carbon and determine how this potential may be affected by elevated atmospheric CO_2.

Materials and methods

Site

The Duke Forest FACE experiment is located near Chapel Hill, North Carolina (35 58′N 79 05′W). The forest is dominated by loblolly pine (1,733 stems ha^{-1}; 92% of total woody biomass), with sweetgum (*Liquidambar styraciflua* L., 620 stems ha^{-1}) and yellow poplar (*Liriodendron tulipifera* L., 68 stems ha^{-1}) as subdominants (DeLucia et al. 1999). Forty-eight species of woody plants (trees, shrubs and vines) have established naturally in the understory of this forest (J. Pippen, unpublished data). The soil is a clay-rich Alfisol with low nitrogen and phosphorus availability (Schlesinger and Lichter 2001). This section of the Duke forest was farmed a century ago, and the current plantation was established in 1983 after a regenerating forest was clear-cut in 1979.

The FACE system increases atmospheric CO_2 concentration in 30-m diameter experimental plots within this continuous pine forest (Hendrey et al. 1999). Each FACE plot consists of a circular plenum that delivers air to an array of 32 vertical pipes. The pipes extend from the forest floor through the 14-m tall forest canopy and contain adjustable ports at 50-cm intervals. These ports are tuned to control atmospheric CO_2 concentration through the entire forest volume. Fumigation with CO_2 in three "elevated" plots (ambient + 200 µl l^{-1} or approximately 560 µl l^{-1}) began in August 1996. Three "ambient" control plots receive the same volume of air without additional CO_2. Each plot is ~100 m from its nearest neighbor. To control for topographic variation (~5 m) between plots and potential gradients in site fertility, the three control and three fumigated plots are arranged in three blocks.

Carbon pools and increments

We define "pool" as a carbon reservoir in the ecosystem lasting 1 year or longer and "increment" as the annual change in the size of each pool. The annual net accumulation of carbon in wood above and belowground, foliage, fine roots and forest floor were included as increments.

At monthly intervals beginning in March 1996, we measured the circumference of 203 canopy loblolly pine trees distributed across the ambient and elevated plots using stainless steel dendrometer bands as in Naidu and DeLucia (1999). For each dendrometer tree, annual growth was expressed as relative basal area increment (RBAI), calculated as the annual change in basal area divided by the initial basal area for each year. RBAI values varied by less than 0.2% over the entire range of basal area in our plots and were, therefore, considered independent of the initial tree diameter (DeLucia et al. 1999; Naidu and DeLucia 1999). These values were used to estimate the annual change in diameter for the trees in each plot that were not measured with dendrometer bands.

In 1997, we also began measuring 112 subcanopy hardwood trees (*Acer rubrum* L., *Liquidambar styraciflua*, *Ulmus alata* Michx., *Cornus florida* L., *Liriodendron tulipifera*). The biomass of each tree by component (foliage, aboveground wood, coarse woody roots) was calculated from diameter measurements using site-specific allometric equations for the pines (Naidu et al. 1998; DeLucia et al. 1999) and equations from the literature for subcanopy hardwoods (Whittaker and Marks 1975; Martin et al. 1998). There was no difference in the relationship between tree height and diameter for loblolly pine after 3 years of exposure to elevated CO_2 (E. DeLucia, unpublished data), suggesting that the treatment did not affect the regression equations used to calculate biomass from tree diameter.

Standing carbon pools for pine wood and foliage were calculated from biomass data using tissue-specific carbon concentrations measured by micro-Dumas combustion (NA1500, Carlo Erba Instrumentazione, Milan, Italy). Standing carbon pools for wood and foliage of understory hardwoods were calculated using carbon concentrations measured in sweetgum (representing 43% of understory tree biomass). Fine root carbon pools and increments reported by Matamala and Schlesinger (2000) were derived from bi-weekly soil cores and include estimates of root mortality and decomposition. The increment of forest floor carbon from Schlesinger and Lichter (2001) was estimated as the average increase over the first 3 years of the experiment.

Changes in mineral soil C are difficult to estimate and were not included in our C budget. Following the transition from agriculture to a loblolly pine forest, Richter et al. (1999) estimated that the annual rate of accumulation of C in the mineral soil was 4.1 g m^{-2}. Values cited by Richter et al. for other forests varied from 21–55 g m^{-2} $year^{-1}$. Though the accumulation of C in the forest floor can be substantial, its accumulation in the mineral soil is likely to be small and did not vary between treatment and control plots in our experiment (Schlesinger and Lichter 2001).

Detritus production and losses of organic carbon

The production of detritus and other losses of organic C result in a transient change in pool sizes that lasts less than 1 year; litterfall, fine root mortality, and carbon losses from the canopy as dissolved organic carbon (DOC) in throughfall and from herbivory are included in this category. Litterfall (pine and deciduous foliage, branches, bark, reproductive structures) was collected once or twice a month in 12, 0.16-m^2 traps randomly placed on the forest floor of each plot as in Finzi et al. (2001). The turnover rates of fine roots were calculated as the sum of mortality and decomposition as in Matamala and Schlesinger (2000). Losses in the form of DOC from the canopy are from Lichter et al. (2000). Pine foliage herbivory was estimated as 1% of peak standing foliage mass (D. Lincoln, personal communication). Folivory in the understory (6.5% of foliage production) was measured on 486 randomly selected leaves from each of winged elm (*U. alata*), sweetgum (*L. styraciflua*) and red maple (*A. rubrum*) using digital photography and image analysis (J. Hamilton, unpublished data).

Data for carbon losses as volatile organic compounds (VOC) are currently unavailable for this site and were not included in the C budget. However, these fluxes are likely to be small. Assuming

a flux of 1 µg C gDW^{-1} h^{-1} for monoterpene emissions from loblolly pine (Kim 2001), and using the maximum foliage biomass in control and fumigated plots, we estimate that annual C losses as VOC would be less than 10 g m^{-2}. This value is similar to an independent estimate for a mixed deciduous-coniferous forest in northern Wisconsin (Isebrands et al. 1999).

Respiratory carbon losses

We define respiratory carbon losses as any flux of CO_2 or inorganic carbon leaving the ecosystem, including plant and microbial respiration. Respiratory losses from woody tissues, leaves and roots were partitioned into a temperature-dependent maintenance component (R_m) and a temperature-independent construction component (R_c) that were summed for the calculation of total respiration (McCree 1970; Thornley 1970; Amthor 2000). Rates of maintenance respiration were measured by gas-exchange techniques on non-growing tissue as in Amthor (1989). The temperature dependence of respiration was modeled as a Q_{10} response: $R_T=R_0\{\exp[T \ln(Q_{10})/10]\}$ where R_T is the total CO_2 efflux rate at temperature T, R_0 is the respiration rate at 0°C, and Q_{10} represents the change in respiration with a 10°C change in temperature. Total stand R_m was calculated for each tissue type by calculating rates every half hour using temperatures measured at the site, summing over 365 days for perennial tissues or 210 days for deciduous leaves, and multiplying by the appropriate biomass.

Except for fine roots (see below), construction cost in g glucose g^{-1} tissue was calculated from measured heat of combustion and the fraction of carbon, nitrogen and ash in each sample according to Williams et al. (1987). All values are expressed as CO_2 units. Construction respiration (an estimate of mass of carbon respired/mass tissue) was calculated from construction cost by subtracting the carbon content of the tissue (Nobel et al. 1992; Carey et al. 1996, 1997).

Leaf R_m and Q_{10} for loblolly pine and sweetgum were taken from Hamilton et al. (2001). The values of Q_{10} used for the seasonal extrapolation were measured in mid June. The mean value of leaf R_m for ambient and elevated CO_2 was used because there were no significant differences between treatments. Respiration rates varied with canopy position, so we recalculated season-average R_0 (basal leaf respiration at 0°C) for the top (0.000212 µmol g^{-1} s^{-1}) and bottom (0.000144 µmol g^{-1} s^{-1}) of the canopy. R_m for the pine canopy was then calculated by applying these rates to the total pine leaf biomass partitioned as 75% sun foliage and 25% shade foliage. For hardwoods, rates for sweetgum shade leaves were applied to all hardwood leaf biomass. Leaf mitochondrial respiration is suppressed in the light, so we assumed that the respiration rate during the day was 60% of the rate during the night (Kirschbaum and Farquhar 1984; Ryan et al. 1996). The total mass of respiring pine foliage is not constant over a year because loblolly pine needles live an average of 19 months (Finzi et al. 2001). From January through March, we used half the peak biomass minus half the yearly increment; from April through September we used the peak biomass; from October through December, we used half the peak biomass plus half the yearly increment. Rates of construction respiration from Hamilton et al. (2001) were extrapolated to the canopy using the peak standing biomass minus litterfall.

We measured pine bole R_m after the cessation of diameter growth in October on five trees in each plot. Gas exchange was measured with two automated open-system infrared gas-analysis systems (Model 6262, LiCor Lincoln, Neb.) that permitted sequential measurements of five trees at 10-min intervals in each of two plots (Carey et al. 1996). CO_2 efflux was measured using Plexiglas cuvettes (0.6 l) attached to boles 1.5 m above the soil. After sterilizing the boles with 4% $CuSO_4$, cuvettes were sealed with non-hardening, gas-tight putty to the northwest side of trees. Air inside each cuvette was mixed rapidly with fans and an external pump operating at 1 l min^{-1} controlled airflow through each cuvette. Higher flow rates caused an increase in pressure inside the cuvettes resulting in lower rates of CO_2 efflux (E. Carey and S. Naidu, unpublished data). Bole temperature was measured in each cuvette with a copper-constantan thermocouple inserted 0.5 cm into the sapwood. Each tree was measured at 1-s intervals for 10 min each hour for at least two consecutive 24-h periods. The two systems were run simultaneously in paired ambient and elevated plots. Diurnal variation in measured values was used to calculate the relationship between respiration and bole temperature. Q_{10} was calculated as the slope (β) of the natural log of respiration plotted against sapwood temperature ($Q_{10}=\exp^{(10\cdot\beta)}$; Ryan 1990), and the values of Q_{10} measured in October were used to estimate bole respiration at all times of year. Rates of bole R_m for hardwood trees were taken from Wullschleger et al. (1995).

Following the pine bole respiration measurements, a core was extracted from under each cuvette and stained with bromcresol green to identify the heartwood-sapwood boundary. Respiration rates were expressed per unit sapwood volume under the cuvette, where sapwood volume was the difference between the total wood volume and the heartwood volume of a sector with radius equal to half the diameter (minus bark thickness) under the cuvette.

Entire stand R_m of woody tissue for the pines was calculated using total volume of woody components (boles, branches, coarse roots) in each plot calculated as the sum of each component over all trees in each plot using site-specific regressions of sapwood versus diameter at breast height (DBH) for loblolly pine (S. Naidu, unpublished data). Respiration rates of coarse roots were assumed to be the same as for bole wood, but yearly rates were calculated using half-hour soil temperatures. Respiration rates for branch sapwood were assumed to be 2.52 times higher than bole sapwood as in Mairer et al. (1998). Rates for hardwood bole, branch and coarse root R_m were assumed to be the same, and were extrapolated to the stand using masses derived from allometric equations in the literature (Whittaker and Marks 1975; Martin et al. 1998).

In 1997, four to five pine trees in each plot were cored, and the 1997 growth ring was used to calculate construction respiration (R_c) by microbomb calorimetry as in Hamilton et al. (2001). Nitrogen and carbon fractions of the wood were determined by micro-Dumas combustion. Construction respiration for coarse root and branch wood was assumed to be the same as for bole wood and was extrapolated to the stand level using the appropriate biomasses. For hardwood woody tissues, R_c was taken from Wullschleger et al. (1997) and extrapolated with the appropriate biomasses.

Rates of fine root respiration were measured with roots still attached to the tree using a portable gas exchange system (LiCor 6400, Lincoln, Neb.) in July 2000 (George 2001). The change in biomass of fine roots was small during July (Matamala and Schlesinger 2000), so measured rates were assumed to represent R_m. Roots were exposed by gently removing leaf litter, rinsed with water, blotted dry, and placed in the gas exchange cuvette. Each measurement (n=10 per plot) was done on a mat of roots including all roots ≤2 mm in diameter. The CO_2 level in the cuvette was held at the atmospheric level for that plot to minimize diffusion between the interior of the cuvette and the atmosphere. Additional experiments showed no direct suppression (sensu Amthor 1991) of respiration rates by elevated CO_2. The average rate of root respiration, measured at 25°C was 8.9±1.3 (1 SD) nmol CO_2 g^{-1} $s^{-1}$and 6.9±0.6 nmol CO_2 g^{-1} s^{-1}, for ambient and elevated plots, respectively. This 22.6% reduction in the specific rate of root respiration was statistically significant (P<0.05) and may have been related to a trend in reduced root nitrogen content for roots in the enriched plots (George 2001).

The Q_{10} value for fine roots (2.08) was calculated as an average of literature values for evergreen species (Sowell and Spomer 1986; Ryan et al. 1996, 1997; Clinton and Vose 1999; Tjoelker et al. 1999). This value of Q_{10} was used to convert measured fine root respiration rates to basal respiration rates (R_0; ambient 0.00144 µmol CO_2 g^{-1} s^{-1}, elevated 0.00111 µmol CO_2 g^{-1} s^{-1}). The basal rates were extrapolated to the stand-level using yearly average biomass plus half the yearly increment (Matamala and Schlesinger 2000). Roots in the 2–3 mm size class have much lower respiration rates than roots less than 2 mm (R. Matamala, personal communication) and were grouped with coarse roots. Fine root R_c was calculated as 25% of total yearly fine root production as in Ryan et al. (1996).

Dissolved inorganic carbon in soil water (DIC) was considered a respiratory loss from roots and soil microbes. It was apportioned between these two sources in the same ratio as root respiration to soil microbial respiration (22% from soil microbes in ambient plots; 47% in elevated plots). DIC was calculated from carbonate equilibria and bi-weekly measurements of the concentrations of dissolved CO_2, bicarbonate, and carbonate; and soil CO_2 concentration, temperature, and soil solution pH. Total soil CO_2 efflux was measured with a field-portable infrared gas analyzer affixed to PVC couplings permanently inserted into the soil. Values for DIC and total soil CO_2 efflux are from Andrews and Schlesinger (2001).

Productivity

We previously reported NPP for the forest during the first two complete years of CO_2 fumigation (DeLucia et al. 1999). In the present paper, we use the standing pool of biomass in 1998 and recent measurements of fluxes to calculate a complete carbon budget including NPP, GPP, and NEP. NPP was calculated as the sum of all increments, including detritus production and other losses of organic C: wood, foliage and fine root increments; litterfall; fine root mortality and decomposition; DOC and herbivory. NEP was calculated as carbon accumulating at the site: wood, foliage and fine root increments and forest floor accumulation. Accumulation of C in mineral soil was not included in NEP. GPP was calculated as NEP plus total ecosystem respiratory loss (R_e: soil CO_2 efflux; DIC; canopy and woody respiration; and herbivory) plus DOC. Total autotrophic respiration (R_a) was calculated as the sum of all plant respiratory components (some of the CO_2 respired from roots goes directly into DIC but the calculation of root respiration is from tissue-specific rates so DIC is not included in the calculation of R_a). Soil microbial respiration ($R_{\text{soil microbes}}$) was calculated as total soil CO_2 efflux minus fine and coarse root respiration plus the proportion of DIC attributed to microbes (see above). Total heterotrophic respiration (R_h) was calculated as $R_{\text{soil microbes}}$ plus losses to herbivory.

Statistical analyses

Inferential statistical analyses were applied to the values for wood and foliage increment, as well as the tissue-specific rates of respiration (wood and foliage). Measurements of chemical constituents used in the calculation of construction respiration also were subject to statistical comparisons. For these analyses, values for all trees in each ring were averaged. Plots were blocked and a paired *t*-test was applied with plot as the replicate (n=3 per treatment). Unless otherwise noted, all tests were two-tailed and $P \leq 0.05$ was chosen as the level of significance. We relied on the statistical inferences from Matamala and Schlesinger (2000) and Finzi et al. (2001) for comparisons of fine root increment with turnover and litterfall, respectively.

The production estimates (GPP, NPP, NEP) and the respiratory fluxes extrapolated to the ecosystem level (R_a, R_h) each represent the sum of several components. Because of the possibility that errors may accumulate in calculating these highly derived variables, statistical probabilities applied to the plot means and variances may not reflect the true uncertainty in our estimates. Therefore, we did not apply statistical methods to these derived variables, but instead presented the mean and range for each value.

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Results

Previously we reported that the percentage increase in basal area of loblolly pine trees (relative to their size in April 1996) was 4.5% greater in the elevated than in the ambient plots after 2 years of exposure to elevated CO_2 (DeLucia et al. 1999). This difference increased to 7.2% in 1999 and 9.2% by the end of 2000 (Fig. 1). Pre-treatment growth rates (RBAI) of loblolly pine trees were not statistically different (ambient 0.0939; elevated 0.0982; Fig. 2). Between 1997 and 1999, the stimulation of RBAI was relatively constant at ~26%, although the absolute values varied by year (1997: ambient 0.0759, elevated 0.0950; 1998: ambient 0.0536, elevated 0.0681; 1999: ambient 0.0623, elevated 0.0788). The stimulation of RBAI was somewhat lower in 2000 (23.4%; ambient 0.0593, elevated 0.0732). The RBAI of each species of understory hardwood tree responded differently to elevated CO_2 (data not shown). Because of small sample size, and because understory hardwoods made up only 8% of the total biomass, we calculated an average stimulation (15%) over all hardwood species and over all 4 years to use for extrapolation to whole-system estimates.

The total pool of plant carbon in the ambient plots was 6,129 g m^{-2} (Table 1), which is comparable to other loblolly pine plantations in the region (Schiffman and Johnson 1989). Approximately 90% of the total carbon pool was in pine tissues and the rest in hardwoods. Fo-

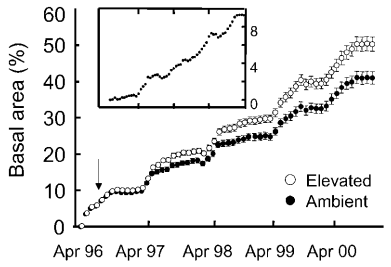

Fig. 1 Average percentage increase in basal area (±1 SE), relative to basal area measured in April 1996, for loblolly pine trees growing in ambient (n=102) and elevated (n=101) CO_2. The *inset* shows the absolute difference between the percentage increase in basal area for trees in elevated and ambient plots and the *arrow* indicates when the CO_2 fumigation was initiated

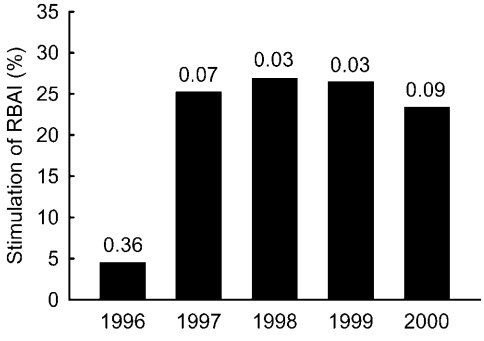

Fig. 2 Stimulation in relative basal area increment (RBAI) for loblolly pine trees growing in ambient and elevated CO_2 plots. The percentage stimulation was calculated as $[(RBAI_{elevated}-RBAI_{ambient})/RBAI_{ambient}]$. The average RBAI was calculated for 30–40 trees in each plot. Numbers above bars indicate *P*-values for comparison of ambient and elevated plots using a paired-sample *t* test (one-tailed, n=3)

liage and fine roots were 9% and 6% of the total carbon pool, respectively, and the remainder was woody tissue.

Elevated CO_2 increased all increments and litterfall (Table 2). Allometry-derived yearly increments of wood, including coarse roots, and foliage were 27% higher in fumigated than control plots. Matamala and Schlesinger (2000) reported a 78% increase in the increment of fine roots, but did not detect an increase in mortality and decomposition (Table 2). Total litterfall was 25% higher and remained higher in 1999 (19%; data not shown).

There were no detectable differences in total respiratory losses from the canopy or aboveground woody tissues (bole and branch); the mean values for ambient and elevated plots differed by not more than 6% (Table 3). For extrapolation, we used a constant Q_{10} measured in mid-June. Q_{10} has sometimes (Paembonan et al. 1991; Stockfors and Linder 1998), but not always (Cropper and Gholz 1991), been found to vary seasonally, increasing during colder months. If this were the case, our estimate of canopy respiration would be an underestimate of total yearly canopy respiration.

In situ measurements of fine roots revealed an approximately 23% reduction in the specific respiration rate at 25°C in fumigated compared with ambient plots [8.93±1.3 (1 SD) nmol g^{-1} s^{-1}, ambient; 6.91±0.6 nmol g^{-1} s^{-1}, elevated; n=30, P<0.05; George 2001]. Because of large inter-plot variation in fine root mass, there was no detectable difference in the extrapolated values of fine root respiration expressed per unit ground surface (Table 3). The tissue-specific rates of fine root respiration that we used to scale to ecosystem fluxes were approximately twice as high as those reported for the same site by Matamala and Schlesinger (2000). Differences in the measurement technique may have been responsible for part of this difference. In a recent literature survey, George (2001) found that respiration rates of severed roots, as in Matamala and Schlesinger (2000), consistently were lower than those for attached roots.

Total plant respiration was very sensitive to temperature because R_m made up the bulk of the respiratory flux for each component (Table 3). The contribution of R_m ranged from 81% to 97% of total respiratory flux for each plant component.

We found no statistically significant differences between treatments for pine bole basal respiration rates (R_0), the respiratory temperature response (Q_{10}), or construction respiration (R_c; Table 4). Therefore, we used

Table 1 Carbon pools of a 15-year-old loblolly pine forest in the Duke Forest FACE experiment. Data are maximal annual values for 1998 averaged over the three plots in each treatment. The standard deviations are shown in parentheses

Species	Tissue	Ambient gC m^{-2} $year^{-1}$	Elevated gC m^{-2} $year^{-1}$
Loblolly pine			
	Foliage[a]	496 (109)	494 (129)
	Bole[b]	3,614 (869)	3,654 (929)
	Branch[b]	683 (153)	680 (180)
	Coarse root[b]	601 (135)	590 (151)
Hardwoods			
	Foliage[c]	53 (18)	61 (32)
	Bole[d]	238 (117)	292 (194)
	Branch[e]	44 (21)	55 (38)
	Coarse root[f]	60 (29)	72 (49)
Both			
	Fine root[g]	340 (66)	375 (48)
	Total	6,129 (1053)	6,273 (1092)

[a] Carbon fraction 0.47 (ambient) and 0.49 (elevated) from Hamilton et al. (2001)
[b] Density 0.427 g cm^{-3} from Naidu et al. (1998); carbon fraction 0.49 this study
[c] Carbon fraction 0.47 (ambient) and 0.47 (elevated) from Hamilton et al. (2001)
[d] Density 0.509 g cm^{-3} from Forest Products Laboratory (1940); carbon fraction 0.45 from Wullschleger et al. (1997)
[e] Density 0.509 g cm^{-3} from Forest Products Laboratory (1940); carbon fraction 0.46 from Wullschleger et al. (1997)
[f] Density 0.509 g cm^{-3} from Forest Products Laboratory (1940); carbon fraction 0.44 from Wullschleger et al. (1997)
[g] Carbon fraction 0.41 from Matamala and Schlesinger (2000)

Table 2 Annual carbon increments, detritus production and other losses of organic C for a 15-year-old loblolly pine forest in the Duke Forest FACE experiment. Mean values are for 1998 and the standard deviations are shown in parentheses. The percentage difference between ambient and elevated CO_2 plots is indicated in the last column, and values followed by an asterisk are significantly different (P<0.05)

Parameter	Components	Ambient gC m^{-2} $year^{-1}$	Elevated gC m^{-2} $year^{-1}$	% Difference
Increments				
	Wood and foliage[a]	367 (43)	465 (45)	27*
	Fine roots[b]	18 (5)	32 (5)	78*
	Forest floor[c]	44	104	136
Detritus production				
	Litterfall[d]	287 (50)	358 (57)	25*
	Fine roots[b]	14 (11)	21 (14)	50
	Other[e]	18	23	28

[a] This study; includes coarse roots
[b] Data from Matamala and Schlesinger (2000)
[c] Annual average rate of forest floor accumulation from 1997 through 1999 from Schlesinger and Lichter (2001). Total forest floor C after 3 years of CO_2 enrichment was significantly greater in the enriched (884 g m^{-2}) than in the ambient (701 g m^{-2}; P=0.014) plots
[d] Statistical analyses from Finzi et al. (2001)
[e] Includes DOC from Lichter et al. (2000) and herbivory from this study

Table 3 Respiratory losses of carbon for a 15-year-old loblolly pine forest in the Duke Forest FACE experiment. Mean values are for 1998 and the standard deviations are in parentheses. The percentage of total respiration for each component that is maintenance respiration is designated $\%R_m$. The percentage difference in mean values between ambient and elevated CO_2 plots is indicated in the last column. None of the values were significantly different ($P<0.05$)

Component	Ambient gC m^{-2} $year^{-1}$	% R_m	Elevated gC m^{-2} $year^{-1}$	$\%R_m$	% Difference
Canopy[a]	492 (80)	81	463 (94)	85	–6
Bole and branch[b]	488 (75)	88	519 (94)	86	6
Coarse root[b]	61 (12)	88	64 (16)	87	5
Fine root[c]	662 (172)	97	555 (50)	96	–16
DIC[d]	16		22		38
Soil CO_2 efflux[d]	928 (19)		1,176 (132)		27
Soil microbes[e]	208 (186)		565 (80)		171

[a] Tissue-specific rates from Hamilton et al. (2001)
[b] Tissue-specific rates from this study and from literature; see Materials and methods
[c] Tissue-specific rates from George (2001); biomasses from Matamala and Schlesinger (2000)
[d] Dissolved inorganic carbon; data from Andrews and Schlesinger (2001)
[e] Calculated as [soil CO_2 efflux-(fine root respiration+coarse root respiration)+(22% DIC ambient or 47% DIC elevated]

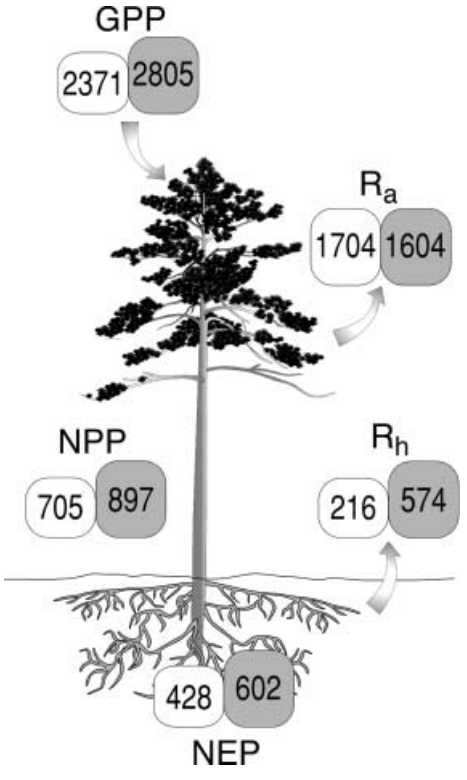

Fig. 3 Carbon budget (1998; gC m^{-2} $year^{-1}$) for a loblolly pine forest under ambient and elevated atmospheric CO_2. Each value is an average for the three ambient (*light boxes*) and three elevated CO_2 (*dark boxes*) plots. The range in values for each variable for the ambient and elevated plots, respectively, are as follows: gross primary production (GPP): 2226–2510 and 2788–2833; net primary production (NPP): 653–766 and 876–928; net ecosystem production (NEP): 392–477 and 578–635; autotrophic respiration (R_a): 1617–1765 and 1570–1645; heterotrophic respiration (R_h): 22–393 and 487–644. GPP was calculated as NEP plus R_e plus DOC, where R_e was the sum of C losses by total soil CO_2 efflux, DIC, canopy respiration, woody respiration and herbivory. NEP was the sum of wood and foliage increment, fine root increment and the accumulation of C in the forest floor. NPP was calculated as the sum of wood and foliage increment, fine root increment, litterfall, fine root detritus production, DOC, and C losses by herbivory. R_h was the sum of microbial respiration and herbivory; where microbial respiration was the difference between total soil CO_2 efflux and total root respiration (fine plus coarse root respiration) plus (22% DIC in ambient plots or 47% DIC in fumigated plots). Note that NEP does not equal NPP minus R_h for the elevated plots (see Discussion)

Table 4 Respiration and chemical composition of sapwood for loblolly pine measured in October 1997 in the Duke Forest FACE experiment. Each value is an average for the three ambient or three elevated CO_2 plots, and the standard deviations are in parentheses. There were no significant differences among mean values for any variable ($P<0.05$) (H_c the ash-free heat of combustion, R_0 respiration rate at 0°C)

Parameter	Ambient	Elevated
R_0 (μmol m^{-3} s^{-1})	8.9 (2.0)	8.1 (1.7)
Q_{10}	2.1 (0.2)	2.7 (0.4)
H_c (KJ g^{-1})	19.3 (0.4)	19.3 (0.2)
N%	0.12 (0.05)	0.12 (0.05)
C%	48.4 (1.5)	48.9 (1.5)
Construction cost (mol CO_2 kg^{-1} tissue)	48 (1.0)	48 (0.5)
Construction respiration (mol CO_2 kg^{-1} tissue)	7.7 (1.5)	7.1 (1.4)

the average of values for the ambient and elevated plots for extrapolating to the stand-level.

Elevated atmospheric CO_2 resulted in an 18% increase in GPP (Fig. 3) and there was no overlap in the range of values for the ambient and elevated plots. Total autotrophic respiration (R_a) was similar between treatments, but NPP, driven primarily by increased growth of the pines, was 27% higher under elevated CO_2. Values for NPP among ambient and elevated plots varied by 6–17% but, as for GPP, there was no overlap in the range of values. Total heterotrophic (R_h) respiration showed an increase of 165% (Table 3). NEP calculated as the increase in carbon residing at the site was stimulated by 41% in the elevated plots.

Discussion

During 1998, the rate of carbon accumulation in the ambient plots was 428 gC m^{-2} $year^{-1}$. This estimate of NEP was similar to values for other warm-temperate coniferous forests (Table 5). For example, Valentini et al. (2000), using eddy-covariance measurements, reported a value for net ecosystem exchange (the equivalent

Table 5 Carbon fluxes and pools for several different conifer forests. The mean values and ranges (in parentheses) for the three ambient CO_2 plots in the Duke FACE experiment are shown in the first column (R_e total ecosystem respiration)

Parameter		Pine[a]	Conifer[b]	Spruce[c]	Pine[d]	Pine[e]	Pine[f]	Pine[g]
Location:		N.C., USA	France	Canada	Australia	Ore., USA	N.C., USA	New Zealand
Stand age (years):		15	29	115	20	mixed	11	8
Flux (g C m^{-2} $year^{-1}$)								
	GPP	2,371 (2,226–2,510)	1,230	963	2,100	901–1,262	–	1,780
	NPP	705 (653–766)	–	517	903	405	500–1,235	960
	NEP	428 (392–477)	430	68	242	266	–100–721	600
	R_e	1,932 (1,800–2,023)	800	895	–	894–996	–	1,180
	R_h	216 (22–393)	–	449	–	134	351–744	310
	Soil CO_2 efflux	928 (916–949)	–	592	–	683	1,263–1,576	950
	Total root respiration	723 (567–904)	–	143	274	–	663–1,062	640
	Aboveground plant respiration	981 (860–1049)	–	303	794	211	–	–
NPP/GPP		0.3	–	0.5	0.4	0.3–0.4	–	0.5
Pool (g C m^{-2})								
	Aboveground C	5128 (4026–5899)	–	4920	5890	9826	1045–2220	3199
	Belowground C	1001 (923–1087)	–	1080	1169	–	305–675	–

[a] *Pinus taeda* in the ambient plots (this study) in the Duke FACE experiment
[b] Mixed conifer stand (Valentini et al. 2000)
[c] *Picea mariana* (Malhi et al. 1999)
[d] *Pinus radiata* (Ryan et al. 1996)
[e] *Pinus ponderosa* (Law et al. 1999, 2000)
[f] *Pinus taeda* (Maier and Kress 2000)
[g] *Pinus radiata* (Arneth et al. 1998)

of NEP) for a coniferous forest in France of 430 gC m^{-2} $year^{-1}$. Other comparable forests range from 242 to 721 gC m^{-2} $year^{-1}$. NPP at our site (705 gC m^{-2} $year^{-1}$) was about 30% higher than the modeled regional average for loblolly pine forests reported by McNulty et al. (1996), but was within the range reported for an 11-year-old loblolly pine forest in North Carolina and slightly lower than *Pinus radiata* D. Don stands in New Zealand (Table 5).

NEP is the difference between GPP and total ecosystem respiration (R_e). Valentini et al. (2000) concluded that differences in forest NEP across a latitudinal gradient were determined primarily by variation in R_e as opposed to GPP. At our site, soil CO_2 efflux provided the largest contribution to R_e (48% in the ambient plots), with approximately equal contributions from foliage (25%) and aboveground woody tissues (25%). Our results for the contribution of total soil CO_2 efflux and foliage respiration to R_e were within the range reported in other studies (soil: 48%–76%, foliage 18%–43%; Lavigne et al. 1997; Law et al. 1999). However, our estimate of the contribution of aboveground woody tissues to R_e (25%) was higher than that of many other studies (5–15%; Lavigne et al. 1997; Law et al. 1999). This difference appears to have resulted from higher tissue-specific rates of respiration for loblolly pine (Table 4) than in these other studies.

GPP in the ambient plots (2,371 gC m^{-2} $year^{-1}$) was at the high end of many estimates for other coniferous forests, but similar to a 20-year-old *P. radiata* stand in New Zealand with comparable above- and belowground carbon pools (Table 5). Our estimate of GPP was considerably higher than values reported by Valentini et al. (2000) for a mixed conifer forest and by Luo et al. (2001) for this forest. In both cases, it appears that large differences in R_e caused the difference in GPP.

For our ambient plots, Luo et al. (2001) estimated GPP at 1,250 gC m^{-2} $year^{-1}$. This estimate is significantly lower than ours, partly because they used much lower values for the temperature response of respiration (Q_{10}). A lower value of Q_{10} would lead to a lower estimate of ecosystem respiration and, in turn, to a lower estimate of GPP. Compared with other coniferous forests, our relatively high estimates of GPP appear to have been caused by our high estimates of total ecosystem respiration (R_e). But our estimates of NPP are also at the high end, as would be expected for a rapidly growing early-successional pine forest. The NPP/GPP ratio, which incorporates production and respiration, may provide the best measure of the efficiency by which forests convert carbon fixed by photosynthesis into biomass carbon (Ryan et al. 1997). Our ambient NPP/GPP ratio of 0.3 is at the low end but within the range of other coniferous forests (Table 5 : 0.3–0.5), as well as within the range reported for a number of boreal forest communities (0.23–0.36; Ryan et al. 1997). The similarity of our estimate of NPP/GPP with these other studies suggests that our estimate of R_e is reasonable.

Elevated atmospheric CO_2 caused a 41% stimulation of NEP that resulted in an additional 174 gC m^{-2} $year^{-1}$ accumulating in the elevated compared with the ambient plots. Most of this stimulation (57%) resulted from in-

creased carbon storage in plant biomass; 35% resulted from forest floor accumulation, and 8% from increased fine root increment. Values for NEP did not include C in mineral soil (see Methods), and only a portion of the relatively labile material included in our estimate of NEP will ultimately become recalcitrant soil C. We consider our measurement of NEP more robust than estimates of GPP, NPP and R_e, as it was calculated from the fewest and most accurate measurements (the sum of carbon accumulating in wood, foliage, and fine root increment, and forest floor) and was free of the potentially large errors associated with extrapolating physiological measurements to the entire ecosystem.

Compared with ambient plots, elevated atmospheric CO_2 caused 27% stimulation in NPP that resulted in an additional 192 gC m^{-2} $year^1$ in plant biomass. Although it relied on more measurements than NEP, most of the largest quantities that go into the calculation of NPP (wood and foliage increment, and litterfall) are relatively easy to measure accurately. However, estimates of fine root increment, mortality and decomposition were included in the calculation of NPP and NEP (increment only) and these estimates are fraught with methodological problems (Vogt et al. 1998). The data we used from Matamala and Schlesinger (2000) indicated that root increment was a small component of the C budget and, therefore, did not contribute substantially to the uncertainty in our estimates of these production values. Pritchard et al. (2001) used a different methodology at the same site to produce estimates of root increment and production that were considerably larger than those of Matamala and Schlesinger (2000), but these estimates were still at the low end for other temperate and boreal forests. Though errors in estimating root increment and turnover probably did not affect our estimate of the CO_2 effect on NPP, uncertainties in quantifying belowground processes continue to hamper our ability to compare production across different forest ecosystems.

GPP was stimulated 18% by elevated CO_2. The estimate of GPP is more uncertain than either NPP or NEP because it cannot be measured directly but requires separate measurements of NEP and component respiratory carbon fluxes (soil CO_2 efflux, DIC, canopy respiration, woody respiration, DOC, and herbivory). Recently, Luo et al. (2001) used a combination of modeling and eddy-flux measurements to calculate that GPP was stimulated by 43% in the fumigated plots in the Duke Forest FACE experiment. Their results suggest that autotrophic respiration (R_a) was stimulated 62% by elevated CO_2, but we found no such stimulation (Fig. 3).

An alternative method of calculating NEP revealed both corroboration and discrepancies in our carbon budget. The estimates of NEP presented in Fig. 3 relied only on measurements of changes in carbon pools (carbon in live tree biomass and forest floor; see Materials and methods). Alternatively, we calculated NEP as the difference between NPP and the sum of heterotrophic respiratory losses of carbon ($R_{\text{soil microbes}}$, herbivory) and DOC losses (Schlesinger 1997). This yielded NEP estimates of 478 gC m^{-2} $year^1$ in the ambient plots and 311 gC m^{-2} $year^{-1}$ in the fumigated plots. The two calculations of NEP are in excellent agreement for ambient plots (11% difference). However, for the fumigated plots, the alternative calculation of NEP is about 48% lower than the calculation including only changes in carbon pools. The estimate of NEP derived only from changes in carbon pools is probably more accurate than the one that includes both pools and fluxes because of uncertainties in extrapolating specific respiratory rates to the stand-level. Thus, we conclude that our estimate of $R_{\text{soil microbes}}$ in the fumigated plots may be too large by about 290 gC m^{-2} $year^{-1}$.

Whereas we found a 171% stimulation of $R_{\text{soil microbes}}$ by elevated CO_2, to reconcile the alternative calculations of NEP, $R_{\text{soil microbes}}$ in the fumigated plots would have to be only about 30% higher than in the ambient plots. Allen et al. (2000) found no difference in microbial biomass between ambient and elevated plots at this site, suggesting that a small stimulation of $R_{\text{soil microbes}}$ is more likely. $R_{\text{soil microbes}}$ was calculated as the difference between total soil CO_2 efflux and total root respiration and a small contribution from DIC. Therefore, in the fumigated plots, either our measurements of soil CO_2 efflux are approximately 25% too high, our estimates of root respiration are approximately 47% too low, or some combination of these. Andrews et al. (1999) used carbon-13 labeling at this site to estimate that roots contribute 55% of total soil respiration in the fumigated plots. This is in close agreement with our estimate of 48%, suggesting no large systematic error in our estimate of either soil CO_2 efflux or root respiration. Further, our estimates of soil respiration and root respiration are in close agreement with those for other forests with similar litterfall carbon input (Raich and Nadelhoffer 1989). It is probable that small errors in both quantities contribute to this discrepancy.

Our estimates of NPP do not include carbon in root exudates. If elevated CO_2 significantly increased root exudation, our estimates of NPP in the fumigated plots would be too low. This could account for some of the discrepancy between the two methods of calculation. There is conflicting evidence regarding the stimulation of root exudation under elevated CO_2. Some studies have found no significant increases in root exudation in plants grown under elevated CO_2 (Norby et al. 1987; Cheng et al. 2000; Uselman et al. 2000), whereas others have found increased exudation (Rouhier et al. 1994; Jones et al. 1998). In our experimental plots, Schlesinger and Lichter (2001) reported apparently higher percent carbon in the mineral soil of fumigated plots (albeit non-significant) with no evidence for higher percent nitrogen. A plausible explanation for this observation is increased carbohydrates delivered to the soil via root exudation.

Considering the implications for global carbon cycle, we found large stimulations of tree growth (more than 23% for 4 years) and NPP (27%) for forest plots exposed to elevated CO_2. Model simulations predict that this stimulation will decline as tree growth exceeds rates of

nitrogen mineralization resulting in increasing nitrogen limitation (Comins and McMurtrie 1993; Luo and Reynolds 1999). Further, current rates of nitrogen and phosphorus mineralization fall below the demand invoked by the enhanced productivity of the trees (Finzi et al. 2001; Oren et al. 2001). We observed a small decline in CO_2-induced growth stimulation of loblolly pine in 2000 (Fig. 2), but it is not yet possible to determine whether this is the beginning of a downward trend or natural inter-annual variability. The stimulation of NPP under elevated CO_2 will likely affect short-rotation forestry of loblolly pine (Groninger et al. 1999).

At the Duke Forest FACE site, the increase in NPP without proportional increases in ecosystem respiration led to an increase in NEP. Thus, our results suggest that elevated atmospheric CO_2 increases carbon sequestration in young, productive forests and are consistent with a North American carbon sink that may have strengthened over the past 10 years (Schimel et al. 2001). The growth stimulation and, therefore, the stimulation in NEP, probably represents the maximal response of forests to elevated atmospheric CO_2 (DeLucia et al. 1999). To estimate an upper-bound for additional carbon sequestration in temperate forests resulting from elevated atmospheric CO_2, we assumed the stimulation of NPP and the ratio of NEP/NPP from the present study applied to the global area of temperate forest (9.2×10^{12} m^2; Schlesinger 1997). In such a scenario, an extra 1.47 PgC $year^{-1}$ would be sequestered in temperate forests by the CO_2-induced stimulation in production. This would account for less than 10% of yearly emissions of CO_2 from fossil fuel combustion in the year 2050 (Houghton et al. 1995). CO_2-induced stimulation of productivity of forests in their current state is small (Caspersen et al. 2000; Schimel et al. 2000) and will be insufficient to take up enough CO_2 to offset future anthropogenic emissions. The capacity of forests as a carbon sink may be further reduced by future increases in global temperatures and deforestation.

Acknowledgements We gratefully acknowledge G.R. Hendrey, K.F. Lewin and J. Nagey (Brookhaven National Laboratory) and the staff of Duke Forest for operation of the FACTS-1 experiment. We thank J. Pippen for field assistance, G. Kennedy for help constructing the carbon budgets, and R. Matamala for providing fine root biomass and turnover data. Comments on the manuscript from members of the DeLucia laboratory are much appreciated. The U.S. Department of Energy, the National Aeronautics and Space Administration, and the National Science Foundation provided financial support for this research.

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