

COMMUNICATIONS

Ecological Applications, 12(5), 2002, pp. 1261–1266
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NET PRIMARY PRODUCTIVITY OF A CO₂-ENRICHED DECIDUOUS FOREST AND THE IMPLICATIONS FOR CARBON STORAGE

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Abstract. A central question concerning the response of terrestrial ecosystems to a changing atmosphere is whether increased uptake of carbon in response to increasing atmospheric carbon dioxide concentration results in greater plant biomass and carbon storage or, alternatively, faster cycling of C through the ecosystem. Net primary productivity (NPP) of a closed-canopy *Liquidambar styraciflua* (sweetgum) forest stand was assessed for three years in a free-air CO₂-enrichment (FACE) experiment. NPP increased 21% in stands exposed to elevated CO₂, and there was no loss of response over time. Wood increment increased significantly during the first year of exposure, but subsequently most of the extra C was allocated to production of leaves and fine roots. These pools turn over more rapidly than wood, thereby reducing the potential of the forest stand to sequester additional C in response to atmospheric CO₂ enrichment. Hence, while this experiment provides the first evidence that CO₂ enrichment can increase productivity in a closed-canopy deciduous forest, the implications of this result must be tempered because the increase in productivity resulted in faster cycling of C through the system rather than increased C storage in wood. The fate of the additional C entering the soil system and the environmental interactions that influence allocation need further investigation.

Key words: carbon allocation; carbon sequestration; CO₂ enrichment; FACE (free-air CO₂-enrichment) experiment; fine-root productivity; forest productivity; global change; heterotrophic respiration; *Liquidambar styraciflua* (sweetgum); net primary productivity.

INTRODUCTION

Much of the experimental research on the responses of plants to increased atmospheric CO₂ can be reduced to a simple, two-part question: Will rising [CO₂] increase the productivity of plants and ecosystems, and will increased productivity translate into increased carbon storage? It has long been recognized that elevated CO₂ should initially increase the rate of net C fixation in most plants and hence the net primary productivity (NPP) of plant communities. The critical uncertainty is whether the increase in NPP will lead to a substantial increase in plant biomass or, alternatively, an increase in the rate of turnover of leaves or roots and the cycling of C through the ecosystem without changing plant biomass (Strain and Bazzaz 1983). Increased plant biomass, particularly the woody biomass of forests, can

lead to C storage over time scales of several decades, and hence is relevant to policy decisions surrounding human perturbation of the global C cycle (Schulze et al. 2000).

Those alternatives set the central framework for an ongoing experiment in which a closed-canopy deciduous forest stand is exposed continuously to an elevated concentration of CO₂, and the responses of C pools and fluxes are measured. The 15-m-tall forest stand is a sweetgum (*Liquidambar styraciflua*) monoculture established in 1988 on the Oak Ridge National Environmental Research Park in eastern Tennessee, USA (Fig. 1) (Norby et al. 2001). Two 25-m diameter plots have been exposed to elevated CO₂ (3-yr daytime average of 537 μmol/mol) since April 1998 using the free-air CO₂-enrichment (FACE) system that is also employed in a *Pinus taeda* forest in North Carolina (Hendrey et al. 1999, DeLucia et al. 1999). The stand-level responses are compared to those in three control plots that receive no added CO₂.

Manuscript received 20 November 2001; accepted 30 January 2002.

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FIG. 1. The Oak Ridge FACE facility in a *Liquidambar styraciflua* plantation. The two rings of towers on the left surround plots receiving elevated CO₂, and the two plots on the right are control plots that receive no added CO₂. A third control plot without towers is not visible in the center. Each of the plots is 25 m in diameter. Details about the site and facility operations were presented by Norby et al. (2001).

NET PRIMARY PRODUCTIVITY, NPP

Methods

Net primary productivity (Clark et al. 2001) of the sweetgum stand was measured on an annual basis through independent measures of leaf, wood, and fine-root production. Net annual production of leaves was determined using baskets to collect leaves as they abscised, primarily in September and October (Norby et al. 2001). Annual wood increment (i.e., net wood production) of each plot was determined using an allometric equation that relates aboveground woody biomass increment to the change in basal area of each individual tree on the plot and to plot-averaged measurements of stem height, taper, and wood density (Norby et al. 2001). Coarse-root production was determined through an allometric equation relating root mass to tree basal area (Norby et al. 2001). Fine-root production was determined every two weeks from observations of root length production in five minirhizotron tubes (Johnson et al. 2001b) in each plot using a Bartz video camera system and ROOTS (Michigan State University, East Lansing, Michigan, USA) software. Data on root length production and disappearance per tube were converted to root mass per unit land area based on the root length density and the volume of soil

observed in each minirhizotron window. Root length density was determined from root samples extracted from soil in-growth cores. The estimation of fine-root standing crop from minirhizotron observations agreed well with the direct measurement from soil cores.

NPP of understory vegetation was estimated from destructive harvests. Plants in the understory, including grasses, forbs, and woody vines and tree seedlings, were harvested from subplots in 1999 and 2000. NPP was considered standing biomass for herbaceous taxa and 25% of standing biomass for woody perennials. We estimated understory production for 1998 by extrapolation based on the proportional change in biomass between 1999 to 2000, which is consistent with visual estimates of the plant cover and production in 1998.

Several other potential components of NPP (Clark et al. 2001) were not included in the calculation, but these are unlikely to influence the results. Branch litter was primarily from dead trees that did not contribute to NPP. There was very little foliar herbivory observed in this stand. Volatile emissions and canopy leaching are generally small components of NPP, and we had no measurements to support their inclusion. The importance of rhizodeposition and root herbivory is unknown, but assuming organic compounds released to

TABLE 1. Dry-matter components of net primary productivity (NPP) of *Liquidambar styraciflua* trees in ambient and elevated CO₂.

NPP component	Ambient CO ₂ (g·m ⁻² ·yr ⁻¹)	Elevated CO ₂ (g·m ⁻² ·yr ⁻¹)	E/A†	P‡
1998				
Leaf	361 ± 15	390 ± 28	1.079	NS
Stem	1140 ± 36	1514 ± 26	1.328	0.005
Coarse root	111 ± 1	133 ± 6	1.195	0.154
Fine root	202 ± 94	240 ± 62	1.186	NS
Total	1815 ± 52	2277 ± 58	1.254	0.005
1999				
Leaf	441 ± 13	502 ± 27	1.138	0.103
Stem	1083 ± 63	1246 ± 28	1.150	0.147
Coarse root	96 ± 2	103 ± 5	1.073	0.196
Fine root	257 ± 126	333 ± 52	1.297	NS
Total	1877 ± 138	2184 ± 46	1.163	0.187
2000				
Leaf	472 ± 5	525 ± 2	1.113	0.004
Stem	1283 ± 108	1374 ± 36	1.071	NS
Coarse root	104 ± 4	112 ± 5	1.077	NS
Fine root	261 ± 136	553 ± 166	2.117	0.054
Total	2120 ± 159	2564 ± 184	1.209	0.143
1998–2000 (average)				
Leaf	425 ± 10	472 ± 18	1.112	0.003
Stem	1169 ± 66	1378 ± 12	1.179	0.003
Coarse root	104 ± 2	116 ± 5	1.119	0.002
Fine root	240 ± 109	375 ± 64	1.563	0.019
Total	1937 ± 110	2341 ± 26	1.209	0.002

Note: Data are the means (±1 SE) of three ambient or two elevated-CO₂ plots.

† E/A is the ratio of the means in elevated vs. ambient CO₂.

‡ Statistical significance within a year was determined by two-tailed *t* test (NS = nonsignificant at *P* > 0.2). The experimental unit was the plot except for fine roots, where the experimental unit was the minirhizotron tube (5 tubes/plot) because of the very high spatial variability. Statistical analysis of the combined data set was by analysis of variance. Probabilities of a significant main effect of CO₂ are shown. Probabilities of a significant CO₂ × year effect are: leaf, *P* > 0.2; stem, *P* < 0.119; coarse root, *P* < 0.087; fine root, *P* < 0.147; and total, *P* > 0.2.

these routes are rapidly respired, they will be accounted for in the subsequent calculation of net ecosystem production (NEP). Changes in carbohydrate content of stems would not be captured by allometric analysis. Soluble carbohydrates were extracted from leaves, stems, and roots in aqueous 80% ethanol, dried in a nitrogen stream, converted to trimethylsilyl derivatives, and measured by gas chromatography–mass spectrometry. Changes (increases or decreases) in pool sizes of carbohydrates were transient and did not accumulate over time.

Results

NPP (dry matter) of the sweetgum trees in ambient CO₂ was 1815 g/m² in 1998 (Table 1). Aboveground woody biomass increment accounted for 63%, and belowground woody increment (coarse roots) was 6% of total sweetgum NPP. Leaf litter and fine-root production comprised 20% and 11%, respectively. NPP was similar in magnitude in 1999 and increased substantially in 2000, a year with more favorable weather (Gunderson et al. 2002); most of the increase was attributable to the woody increment. NPP was 25% higher in CO₂-enriched plots than in controls during the first year of treatment, 16% higher in 1999 and 21%

higher in 2000 (Table 1). Over the three years of treatment, the increase in sweetgum NPP in elevated [CO₂] averaged 21% (*P* < 0.002), and although year was also a significant effect, there was no CO₂ × year interaction. The physiological basis for the enhanced NPP resides in the consistent and sustained stimulation of leaf-level photosynthesis throughout the canopy (Gunderson et al. 2002), with no indication of photosynthetic downregulation. Total canopy photosynthesis (gross primary production, GPP) in 1999 was 27% higher in elevated CO₂, based on calculations from canopy conductance (Wullschlegel et al. 2002); NPP was 35% of GPP.

A 21% stimulation of NPP in an atmosphere with 537 μmol/mol CO₂ is generally consistent with observations of CO₂ effects on other ecosystems, smaller trees, and projections from models. A *Pinus taeda* stand in North Carolina, USA, had a 25% increase in NPP in response to CO₂ enrichment in a similarly designed FACE experiment (DeLucia et al. 1999). Trees in field exposure chambers exhibited a 26% increase in aboveground biomass increment (normalized to constant leaf area) in 600–700 μmol/mol CO₂ (Norby et al. 1999). The CO₂-enrichment response can be expressed as a biotic growth factor (β, Amthor and Koch 1996), which

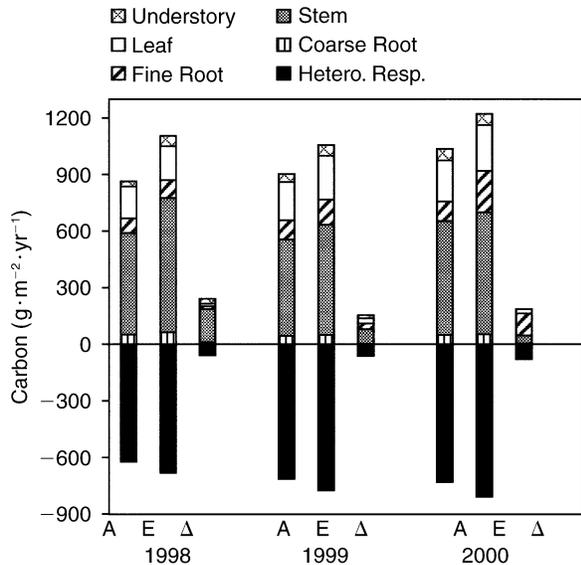


FIG. 2. Allocation of C in NPP (net primary production) and heterotrophic respiration in ambient (A) and elevated (E) CO₂, and the increase in C in elevated CO₂ (Δ) over three years in a 15-m-tall sweetgum forest stand, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA. Carbon contents were calculated from dry mass and C concentrations of 46.3% in foliage, 47.1% in wood, and 39.6% in fine roots, based on analyses on an NA 1500 nitrogen analyzer (CE Instruments, Milan, Italy).

here is calculated as the proportionate increase in NPP (0.21) divided by the natural log of $[\text{CO}_2]_{\text{elevated}}/[\text{CO}_2]_{\text{ambient}}$, using the $[\text{CO}_2]$ from 1000 to 1600 hours (542 and 374 $\mu\text{mol/mol}$). The β of the sweetgum stand over 3 yr was 0.57, which is at least as much as predicted from experiments with smaller and younger trees and exceeds the values (0.3–0.5) used in most global models (King et al. 1995).

CARBON ALLOCATION

Returning to the original question currently confronting global-change biologists, Did the stimulation of net primary productivity (NPP) observed in this experiment cause an increase in plant biomass or faster cycling of C through the ecosystem? In the first year of the experiment, elevated $[\text{CO}_2]$ resulted in a large (33%) increase in aboveground woody increment. However, the effect of $[\text{CO}_2]$ on stem growth declined in the second (15%) and third years (7%), giving rise to alternate hypotheses about the physiological basis for the apparent loss in response of these trees (Norby et al. 2001). The possible explanations included down-regulation of canopy photosynthesis, limitation by N or another nutrient, an artifact of the step increase in $[\text{CO}_2]$, year-to-year variation associated with weather conditions, and changes in C allocation. Analysis of the components of NPP (Table 1) clearly indicates a change in allocation of the extra photosynthate in CO₂-enriched trees, resulting in differences in dry-matter

distribution. In units of C, and including the small (6% or less) contribution of the understory vegetation, annual ecosystem NPP in ambient CO₂ ranged from 866–1036 g C·m⁻²·yr⁻¹ over the 3 yr (Fig. 2), and increased by 154–240 g C·m⁻²·yr⁻¹ in elevated CO₂ (Table 2). Most (80%) of the additional net C taken up by this sweetgum ecosystem in CO₂-enriched plots was allocated to woody biomass in the first year of exposure, but this proportion declined steeply in subsequent years (54% in 1999 and 25% in 2000). The declining response of wood increment was matched by an increasing response of fine-root production (Table 1, Fig. 2). We interpret this allocation shift following the step increase in CO₂ and photosynthate production as a delayed response of fine-root production until carbohydrate availability in structural roots increased sufficiently to support new fine-root production, which is episodic in nature. We observed an increased accumulation of soluble carbohydrates in coarse roots in elevated CO₂ at the end of the 1999 growing season, prior to the large increase in fine-root production in 2000.

While increased tree biomass was the expected response to elevated CO₂ (Norby et al. 1999), other field studies also have failed to show such a response. Young *Liriodendron tulipifera* trees exposed to elevated CO₂ for three years in field chambers showed no significant increase in plant dry mass or leaf area (Norby et al. 1992) despite the sustained increase in leaf-level net C assimilation (Gunderson et al. 1993). Tree-ring analysis suggested a declining response of aboveground wood increment to elevated CO₂ of *Quercus ilex* trees at a natural CO₂ spring (Hättenschwiler et al. 1997). Aboveground woody increment in the FACE (free-air CO₂-enrichment) experiment in a *Pinus taeda* stand, however, was significantly enhanced and has remained so for five years (DeLucia et al. 1999, and E. H. DeLucia, personal communication), although stem growth enhancement was not sustained in the longer-running prototype FACE plot at the same site (Oren et al. 2001). Hence, it is not yet clear whether the apparent difference in response of the pine stand and the sweetgum stand represents a fundamental difference related to

TABLE 2. Increases in ecosystem net primary productivity (NPP), heterotrophic respiration (R_H), and net ecosystem productivity (NEP) in response to CO₂.

Measure	1998	1999	2000	Total
Increase in NPP (g C/m ²)	240	154	187	581
In fast pools (%)	20.4	46.2	75.0	44.8
In slow pools (%)	79.6	53.8	25.0	55.2
Increase in R_H (g C/m ²)	58	61	78	197
Increase in NEP (g C/m ²)	182	93	109	384
Fraction in stem (%)	96.4	82.2	39.4	76.9

Notes: Fast pools are defined as leaves, fine roots, and non-woody understory vegetation. Slow pools are defined as stem wood, coarse roots, and the woody component of the understory.

species or site characteristics, or rather a difference in the rate of adjustment to the perturbation. The key difference may be in how the additional NPP is allocated. Enhanced production of fine roots instead of aboveground biomass has been previously observed in tropical mesocosms (Körner and Arnone 1992) and in *L. tulipifera* in field chambers, where it was interpreted as a compensatory response to N limitation (Norby et al. 1992). Although there is no clear evidence yet of an N (or other nutrient) limitation in the sweetgum site, foliar N concentration has been reduced 8% in CO₂-enriched trees, and total N uptake has not increased commensurately with increased NPP (Johnson et al. 2001a). The [N] of wood in the dormant period (measured in increment cores collected in February) was lower after the 2000 growing season compared to previous years, which might suggest an impending N limitation to growth. An expected response to N limitation would be preferential allocation of extra C to fine-root production, which models suggest can lead to a decrease in long-term stem production (Comins and McMurtrie 1993).

Despite the sustained increase in NPP in elevated CO₂, the allocation of the additional carbon to fine roots rather than to wood reduces the C sequestration potential of this sweetgum forest. Wood is the plant C pool with the slowest turnover and hence the most important determinant of the capacity of this system to sequester additional C over the policy-relevant time frame of several decades. Wood increment (stem growth) also is the most visible and easily quantifiable component of a forest system. Fine roots generally have high turnover rates and do not accumulate as a store of C, although radiocarbon evidence suggests that small roots (up to 2-mm diameter, in contrast to the sweetgum fine roots, which are mostly <0.5 mm) may persist for many years (Gaudinski et al. 2001). Increased fine-root productivity does add additional C to the soil and creates the possibility of an increase in long-lived soil organic-matter pools, but there is no straightforward link between NPP and soil C accretion (Körner 2000), and detection of increases in soil C will be much more difficult than detecting increases aboveground (Schlesinger and Lichter 2001).

CARBON CYCLING

We evaluated the cycling of C through the soil system by measuring the CO₂ efflux from soil, from which heterotrophic respiration (R_H) and net ecosystem production (NEP) (or annual C storage) was calculated. Heterotrophic respiration is the sum of non-root CO₂ efflux from litter-free soil and the C loss from decomposing litter. Analysis of the ¹³C content of CO₂ efflux in July 2000 indicated that at this stage of the stand's development about 45% of the soil respiration was respiration by roots or of recently-derived root exudates, following the approach of Andrews et al. (1999). We then assumed the annual root contribution to soil CO₂

efflux was proportional to fine-root production. Rates of mass loss of leaf litter were determined on litter samples in mesh bags and applied to the litter production of the previous year.

This young, fast-growing sweetgum plantation had a positive C balance, with an NEP in ambient CO₂ of 191–307 g C·m⁻²·yr⁻¹, similar to that of temperate deciduous forests in the eastern United States (Curtis et al. 2002). Although R_H was higher in elevated CO₂, offsetting some of the gain in NPP, total NEP over 3 yr was 384 g C/m² higher in CO₂-enriched plots (Fig. 2, Table 2). Of this gain in ecosystem C, 77% was in aboveground wood, but this percentage was declining steeply, and the overall contribution of wood to C sequestration can be expected to become progressively smaller as the experiment continues. As long as NPP continues to be enhanced by CO₂ enrichment and more C enters the ecosystem, it will be necessary to look to the soil for evidence of C sequestration. The consequences of increased allocation of the extra C to fast-turnover pools will not be immediately apparent because of the time lags between production, entry into the soil organic pools, and subsequent mineralization. For example, sweetgum fine roots from this site die about one year after they are produced, and lose ~35% of their mass during the next year, based on measurements of CO₂ efflux from dead fine roots incubated in soil at 20°C.

These initial estimates of R_H and NEP, and their response to CO₂ enrichment, should not be extrapolated into the future without regard to the likelihood of transient effects, such as lags between photosynthesis and soil respiration (Luo and Reynolds 1999, Schulze et al. 2000, Luo 2001). Lags in physiological response (such as the delayed response of fine-root production) may be equally important and a reason for caution in the interpretation of the initial responses of vegetation to step increases in CO₂. Adjustments to the step increase may have occurred sooner in this fast-growing plantation than would be the case in other experimental systems, although larger adjustments may ultimately occur at a more nutrient-poor site.

Conclusions

This experiment has provided the first evidence that CO₂ enrichment can increase productivity in a closed-canopy deciduous forest. The interpretation of the results, however, must be tempered by the observed shift in allocation of the extra C from aboveground wood production to fast-turnover pools that enter the soil system. This allocation shift reduces the potential of the stand to store the additional C in biomass and points toward the need for more detailed investigations of soil C processes and the controls on environmental interactions (e.g., N cycling) that influence allocation.

ACKNOWLEDGMENTS

This research was supported by the Office of Biological and Environmental Research, U.S. Department of Energy.

Oak Ridge National Laboratory is managed by UT-Battelle, LLC, for the U.S. Department of Energy under contract DE-AC05-00OR22725. This work contributes to the Global Change and Terrestrial Ecosystems Core Project of the International Geosphere-Biosphere Programme.

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