

The Changing Role of Forests in the Global Carbon Cycle: Responses to Elevated Atmospheric CO₂

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Summary

- The combustion of fossil fuels is injecting vast quantities of CO₂ in the atmosphere, altering the C cycle in ecosystems and driving an increase in global temperatures. Forests contribute half or more of global net primary production and approximately 80% of terrestrial productivity and thus play a central role in the global carbon cycle.
- Using free-air CO₂ enrichment technology to expose plots within intact forests to the level of CO₂ anticipated in 2050, it was discovered that net ecosystem productivity (NEP) and net primary productivity (NPP) in loblolly pine and sweetgum forests were substantially increased. This stimulation in the pine forest was greater in warm than in cool years.
- Greater plant respiration contributed to lower NPP in the sweetgum than in the pine forest.
- These forests responded differently to elevated CO₂. Where the pine forest added C to woody tissues, exposure to elevated CO₂ caused a large increase in fine root production in the sweetgum forest. Differences in allocation may alter the mean residence time of C in different forests.
- Imbalances in the N cycle may reduce the response of these forests to elevated CO₂ in the future. The stimulation of forest productivity will slow the accumulation of CO₂ in the atmosphere, but if these forests are representative of forests globally, the observed stimulation of productivity is insufficient to reverse the accumulation fossil-fuel derived C in the atmosphere.



Figure 1. Free-air CO₂ enrichment experiments (FACE) where plots in an intact loblolly pine forest (left) and an intact sweetgum forest (right) are exposed to ambient (~370 μl l⁻¹) and elevated (~570 μl l⁻¹) atmospheric CO₂.

Loblolly pine and sweetgum share similar life history characteristics but the difference in leaf and fine root longevity may directly alter the retention and cycling of C in these different forests. Foliage of loblolly pine, an evergreen species, lives for approximately 18 months, whereas sweetgum is a deciduous species, and the leaves live for 6 months or less. Similarly, longevity of loblolly pine fine roots is about 3.4 times longer than that of sweetgum fine roots (Matamala *et al.* 2003).

In the Duke Forest FACE experiment, 30-m diameter plots in a loblolly pine forest are exposed nearly continuously to ambient plus 190 μl l⁻¹ CO₂. This forest (35° 58' N, 79° 05' W) is on heavily weathered clay-rich Alfisol soils with relatively low nitrogen and phosphorus availability (Hamilton *et al.* 2002). The experimental sweetgum plantation located on the Oak Ridge National Environmental Research Park in Roane County, Tennessee, USA (35° 54' N, 84° 20' W) was established on moderately well drained silty-clay-loam soils classified as an Aquatic Hapludult; these soils are somewhat richer in nutrients than the pine forest in North Carolina (Norby *et al.* 2001). Daytime CO₂ concentration in the experimental plots averages 550 μl l⁻¹ during the growing season. Based on current projections, this CO₂ level is anticipated by 2050 (IPCC 2001). Both experiments use the same FACE technology (Hendrey *et al.*, 1999) and include fully instrumented control plots.

Annual C pools and fluxes were determined in each forest by biometric measurements and by extrapolating tissue-specific fluxes to the whole forest per year.

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DeLucia *et al.* 1999. *Science* 284:1177-1179; IPCC Third Assessment Report. 2001. Cambridge University Press, Cambridge, UK; Finzi *et al.* 2002. *Oecologia* 132:567-578; Hamilton *et al.* 2002. *Oecologia* 131:250-260; Hendrey *et al.* 1999. *Global Change Biology* 5:293-309; Norby *et al.* 2002. *Ecological Applications* 12:1261-1266; Matamala *et al.* 2003. *Science* 302:1385-1387

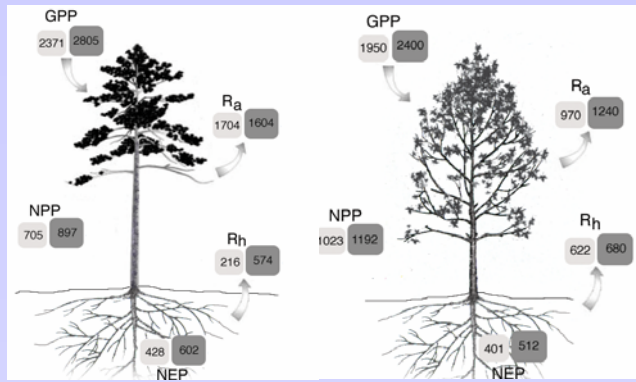


Figure 2. Carbon budget (gC m⁻² yr⁻¹) for a pine forest (left) and sweetgum forest (right) exposed to ambient (~370 μl l⁻¹; light bubbles) and elevated (~570 μl l⁻¹; dark bubbles) atmospheric CO₂. Gross primary production (GPP) represents annual photosynthesis; respiration from plants (R_a) and soil 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_a.

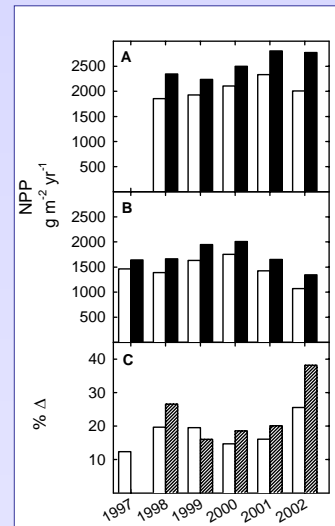
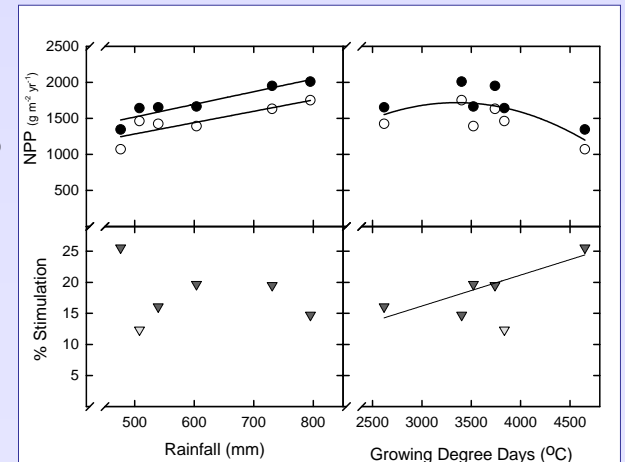


Figure 3. Net primary production (NPP, gDM m⁻² yr⁻¹) for experimental plots in a loblolly pine (A) and sweetgum forest (B) exposed to ambient (~370 μl l⁻¹; light bars) and elevated (~570 μl l⁻¹; closed bars) levels of atmospheric CO₂. The percent stimulation of NPP (pine, open bars; sweetgum, hatched bars) is illustrated in "C". NPP was calculated as the sum of woody biomass increment and annual litterfall. In the pine forest the treatment was initiated in August 1996 and some of the 1997 litter was formed before the initiation of the treatment. Data are from D. Moore, E. DeLucia and R. Norby (unpublished).

Figure 4. Net primary production (NPP, gDM m⁻² yr⁻¹) for loblolly pine forest plots exposed to ambient (open symbols, ~370 μl l⁻¹) and elevated atmospheric CO₂ (~570 μl l⁻¹, closed symbols), and its percent stimulation, plotted as a function of total rainfall during the growing season and growing degree days. Data are for the Duke FACE experiment and each point represents a mean value for a given year (1997-2002). Data are from D. Moore and E. DeLucia, unpublished.



Conclusions

At least early in stand development, loblolly pine and sweetgum forests on nutrient deficient soils and experiencing the full suite of biological interactions and variation in the environment have considerable capacity to respond to changes in atmospheric CO₂ derived from the combustion of fossil fuels. The experimental simulation of plus 190 μl l⁻¹ CO₂ caused an additional 174 gC m⁻² to be stored in the pine forest, representing a 41% stimulation of NEP, and an additional 111 gC m⁻² to be stored in the sweetgum forest, representing a 28% stimulation of NEP (Fig. 2). There is considerable inter-annual variation in its absolute magnitude and enhancement of the responses to CO₂. Net primary production in the pine forest was greater in years with more precipitation than in dry years, and this response to precipitation was not altered by elevated CO₂. In contrast, elevated CO₂ lessened somewhat the decrease in NPP observed at elevated temperature (Fig. 4). Forest productivity is likely to be stimulated by increasing atmospheric CO₂, at least early in stand development, and for pine forests this increase will be greater in warm than in cool years.

Respiratory fluxes return large quantities of C to the atmosphere and are important determinants of the total C sequestration in ecosystems, yet the magnitude and regulation of these fluxes remains poorly understood. In the pine and sweetgum stands R_a alone returned 50 – 72% of GPP to the atmosphere and greater R_a in the sweetgum forest than in the pine forest may explain its lower NPP (Fig. 2). Further research on the different components of respiration, with an emphasis on understanding season variation in its temperature dependence and the interaction of temperature dependence with the rate of substrate supply, will greatly enhance our understanding of the forest C cycles.

Differences in how forests respond to elevated CO₂ will alter their capacity to store additional C. In the pine forest exposed to elevated CO₂ additional C was allocated to boles and branches, whereas the sweetgum forest responded with a disproportional increase in fine root production. These tissues have profoundly different mean residence times potentially altering the duration of C storage. The residence time of C is longer in wood than in fine roots suggesting that the pine forest offers a longer-term storage of atmospheric C than the sweetgum forest. This statement must be tempered by our lack of understanding of the fate of C derived from decomposition of sweetgum roots. Insofar as this C becomes incorporated in recalcitrant soil organic matter, its residence time in the soil can be greatly extended.

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