

Forest Sensitivity to Elevated Atmospheric CO₂ and its Relevance to Carbon Management

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Experimental research investigating the responses of forest trees to rising concentrations of atmospheric CO₂ has for the past two decades been justified on the basis of the prominent role of forests in the global carbon cycle. The C cycle regulates the airborne fraction of CO₂ from fossil fuel combustion, and, therefore, the rate of increase of CO₂ in the atmosphere and the associated effects on global climate. As the atmospheric CO₂ concentration increases, the rate of uptake of CO₂ by the terrestrial biosphere—particularly forests—may increase via so-called “CO₂ fertilization”. Our ability to balance the global C cycle depends in part on different assumptions about the degree of CO₂ fertilization. Experiments with trees and forest stands exposed to future concentrations of CO₂ have helped to define and quantify the physiological and ecological processes involved in the CO₂ fertilization effect and their representation in ecosystem models.

Recent interest in the use of forests for C sequestration has thrust elevated CO₂ research into a new role, often a role that was not intended in experimental designs. Headlines describing the absence of an additional growth pulse in response to additional CO₂ inaccurately blare “Mature Forests Not Necessarily CO₂ Sinks,” and “Role of Trees in Curbing Greenhouse Gases Is Challenged”. Here we will consider what current research is saying about the sensitivity of forests to rising CO₂ and whether that information should be an important factor in forest management plans for enhancing C sequestration.

Forest Sensitivity to Increased CO₂

Trees, like most plants, respond to increased concentrations of CO₂ with an increase in the rate of photosynthesis. This response is widely documented and well understood. From this primary response of a tree to atmospheric CO₂ derive myriad secondary and tertiary responses that can alter how the tree interacts with its environment¹. Increased productivity in elevated CO₂ is widely documented in seedlings and young saplings of numerous species, measured as increased plant mass at the end of the experiment. The average response to twice-ambient CO₂ from many experiments with tree seedlings was a 29% increase in plant dry mass². If such responses were maintained in forest trees over many decades, it would imply a substantial potential for forests to store an increasing fraction of the excess C emitted to the atmosphere. However, there are many reasons to presume that tree productivity responses to high CO₂ will be less for mature trees in a closed forest, and a major research challenge has been to find meaningful ways to interpret experimental data so they are relevant to the long-term responses of a forest. Some of the critical issues are whether growth stimulation persists after canopy closure, how much the nitrogen cycle will constrain CO₂ fertilization effects, and whether any increased C uptake will be allocated to long-lived pools or simply cycle through the ecosystem faster¹.

Ongoing experiments using free-air CO₂ enrichment (FACE) are starting to provide answers to these questions. In a closed-canopy deciduous forest in Oak Ridge³ (a sweetgum plantation), photosynthesis is stimulated and net primary productivity (NPP) is about 21% higher in 20-m diameter plots exposed to 540 ppm CO₂, and this response has been sustained for three years. Although this forest stand is taking up more C, there has been a progressive change in how the extra C is allocated, which alters its retention by the ecosystem (Figure 1). In the first

year of CO₂ enrichment, aboveground stem biomass increased 33%, but in subsequent years the response of wood increment has been smaller and not significant. Instead, the extra C is being allocated to leaf litter and fine roots—C pools that turnover rapidly and do not accumulate in the ecosystem. Although leaf litter and fine roots add C to the soil, most of this is respired by soil organisms and returned to the atmosphere. Similar conclusions have emerged from a FACE experiment in a loblolly pine stand, where the loss in stimulation of woody increment was attributed to a N limitation⁴. These results from two experiments suggest that increasing atmospheric CO₂ concentration will have a limited direct impact on sequestration of C into long-lived pools. It should not be overlooked, however, that regardless of the fate of the *extra* C taken up by these systems, both of these rapidly-growing tree plantations are sequestering substantial amounts of C under current conditions.

Forest sensitivity to atmospheric CO₂ may be important in ways other than the direct effects on photosynthesis and NPP. In many trees, stomatal conductance is reduced, and water-use efficiency is increased, in elevated CO₂. While there has been much speculation that these responses could confer a measure of drought resistance to trees, evidence for this has generally been lacking. Scale is paramount here—in the sweetgum FACE experiment stomatal conductance of leaves was lower in elevated CO₂, but when integrated over the whole year and across the whole canopy, the effect of CO₂ on transpiration rate was small⁵. Nevertheless, when we speculate about and model forest responses to droughts in the future, an interaction with CO₂ should not be ignored.

Climatic warming, an indirect effect of rising CO₂ and other greenhouse gases, is likely to have more profound effects on forests. Temperature affects all biological processes, but the responses are non-linear, time-dependent, and highly dependent on initial conditions. Warming can have both negative and positive effects on tree growth, as demonstrated in an experiment with maple trees. Warming increased productivity of the maples by simulating photosynthesis and extending the length of the growing season, but the increased productivity was not realized because of the negative effects of high temperature stress during one particularly hot, dry summer period⁶. This specific experimental result reflects the general conclusion of the U. S. National Assessment of global change effects on forests: modest warming is expected to increase C storage in most forests ecosystems, yet under some warmer scenarios forests could experience drought-induced losses of C. Increased CO₂, however, will probably ameliorate many of the negative responses to warming.

Forest Management Decisions and Elevated CO₂

Should a forest manager alter any management decisions based on the certainty of rising CO₂ concentrations? Forest management must have a long-term perspective, and trees that are planted today will see substantially higher CO₂ concentrations in the future. If a case could be made that some tree species will take better advantage of the increased CO₂ than others, perhaps decisions would be altered as to what species to plant for the best economic return. Although there have been many attempts to classify different tree species as to their CO₂ responsiveness, and differences between experimental results are often attributed to species differences, there really is little basis for making any such classification. For example, the growth response of seven tree species to CO₂ enrichment spanned a very large range, but when growth was normalized to constant leaf area (as is appropriate for consideration of responses in a mature forest), the responses were remarkably similar⁷. Proper species selection for a given site is an important aspect of forest management, but response to elevated CO₂ is likely to be much less

important than environmental factors such as fertility, drought, cold temperature, and disease tolerance.

The sensitivity of forests to CO₂ also is unlikely to be an important factor is evaluation of the prospects for C sequestration in tree plantations. Consider the Oak Ridge FACE experiment. The sweetgum plantation was established in 1988 on abandoned agricultural land. In 2000 net ecosystem productivity (i.e., C storage) was about 300 g C m⁻² yr⁻¹, a large increase over that of adjacent old-fields, although it will probably decline as heterotrophic respiration of recent inputs to the soil catches up with new production. The increase due to growth in 540 ppm CO₂ was calculated to be 114 g C m⁻² during 2000, but less than 40% of this was in long-lived pools (i.e., wood). This amount would need to be discounted further for a new plantation ramping up to the 540 ppm atmosphere over the next 60 years. Hence, in a tree plantation established today, the gain in C sequestration attributable to rising CO₂ would be a small and highly uncertain part of the total C sequestration potential. Of course, the absence of a substantial response to elevated CO₂ certainly does not *diminish* the capacity of this fast-growing tree plantation to store C, but given the many other uncertainties, CO₂ fertilization need not be considered part of the evaluation of a C sequestration project.

FACE Studies Can Aid Sequestration Analysis

FACE and other CO₂ enrichment studies were not designed to evaluate forest management plans for enhanced sequestration, and as we have seen, they may have little direct bearing on this discussion. Nevertheless, they are important for providing input and understanding needed in the models and assessments of forest responses to atmospheric and climatic change, which provides the context for C sequestration projects. These intensive studies in tree plantations also are a valuable resource for improving our understanding of environmental controls of tree growth and C cycling processes and developing better protocols for measuring C sequestration. Some of the methodological opportunities are in non-destructive measurement of tree growth, fine root turnover, CO₂ efflux from the soil surface, and the use of stable isotopes to track C cycling in soil, all of which may be important in future efforts to document C storage in forests.

References

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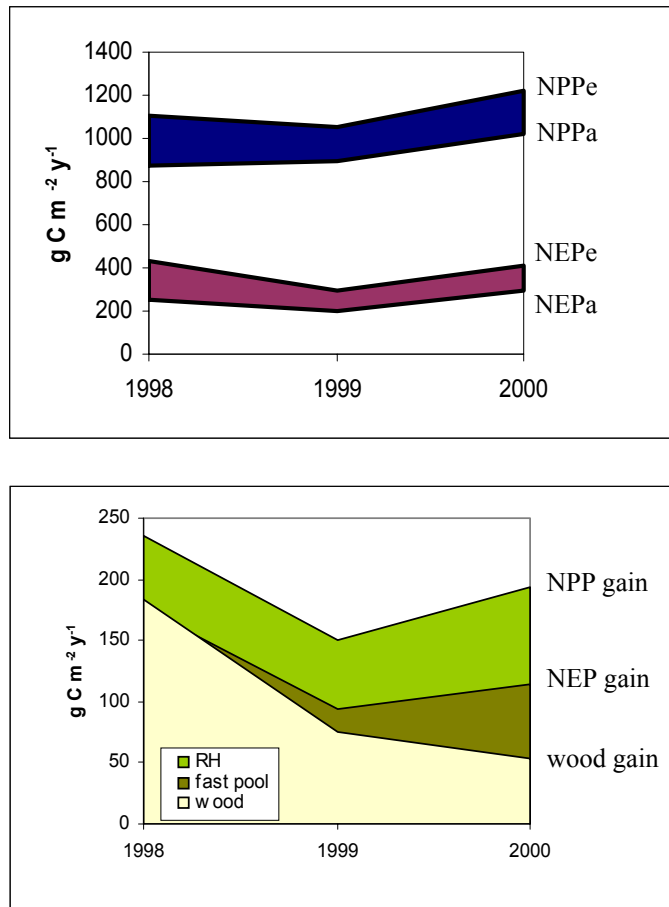


Figure 1. Responses to elevated CO_2 in a sweetgum plantation. *Top:* NPP and NEP in ambient and elevated CO_2 , and the gain due to elevated CO_2 (shaded portions). *Bottom:* the gain in NPP (blue area from top panel) is apportioned into the C allocated to heterotrophic respiration (R_H), fast-turnover pools (fine roots and leaves), and wood.