

First-year growth response of trees in an intact forest exposed to elevated CO₂

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Abstract

Although elevated atmospheric CO₂ has been shown to increase growth of tree seedlings and saplings, the response of intact forest ecosystems and established trees is unclear. We report results from the first large-scale experimental system designed to study the effects of elevated CO₂ on an intact forest with the full complement of species interactions and environmental stresses. During the first year of exposure to $\approx 1.5 \times$ ambient CO₂, canopy loblolly pine (*Pinus taeda*, L.) trees increased basal area growth rate by 24% but understorey trees of loblolly pine, sweetgum (*Liquidambar styraciflua* L.), and red maple (*Acer rubrum* L.) did not respond. Winged elm (*Ulmus alata* Michx.) had a marginally significant increase in growth rate ($P=0.069$). These data suggest that this ecosystem has the capacity to respond immediately to a step increase in atmospheric CO₂; however, as exposure time increases, nutrient limitations may reduce this initial growth stimulation.

Keywords: climate change, elevated-CO₂, growth, *Pinus taeda*, understorey trees

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Introduction

Elevated atmospheric CO₂ increases growth of tree seedlings and saplings under artificial conditions (growth chambers, greenhouses, and open top chambers). A recent meta-analysis of 79 published studies of seedlings and saplings exposed to twice ambient CO₂ concentrations ($\approx 700 \mu\text{L L}^{-1}$) reports an average increase in total biomass of 29% (Curtis & Wang 1998). Greater biomass accumulation is related to substantial increases in photosynthesis and in some cases decreases in leaf dark respiration (Curtis & Wang 1998). The increase in biomass may be greater for deciduous trees (63%) than for conifer trees (38%; Ceulemans & Mousseau 1994), although Curtis & Wang (1998) report no statistical difference between these groups. However, it is unclear how rising levels of atmospheric CO₂ will affect growth of intact forest ecosystems or whether forests will serve as a sink for increasing CO₂.

Environmental stress can influence the magnitude of the CO₂ response. Although nutrient limitations tend to reduce CO₂-induced biomass increases, other stresses may increase the response (Curtis 1996). For example, the relative growth enhancement caused by $2 \times$ ambient CO₂

is increased from 29% to 52% when woody plants are grown in low light (Curtis & Wang 1998). By increasing the ratio of carboxylation to oxygenation of Rubisco, the first enzyme of carbon fixation, future elevated levels of atmospheric CO₂ may reduce photorespiration and therefore increase the quantum yield of photosynthesis (Long 1991). Understorey plants operate primarily in the quantum yield region of the light response curve; thus elevated CO₂ may be of particular benefit for understorey trees (Long & Drake 1991; Bowes 1993; Drake *et al.* 1997). Potential interactions of drought stress and elevated CO₂ are less clear. Elevated CO₂-induced increases in photosynthesis and decreases in stomatal conductance may increase plant water use efficiency (WUE), thus ameliorating water stress (e.g. Ceulemans & Mousseau 1994). However, Curtis & Wang (1998) report no consistent evidence for a significant effect of elevated CO₂ on stomatal conductance in trees. Intact ecosystems comprise complex sets of biotic interrelationships and interacting stresses; therefore, studies conducted on isolated, juvenile plants may not accurately represent responses of mature forest trees or understorey trees to elevated CO₂.

Free-Air CO₂ Enrichment (FACE) technology (Hendrey & Kimball 1994; Lewin *et al.* 1994; Ellsworth *et al.* 1995),

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Species	<i>n</i>		RBAI		<i>P</i>
	amb.	elev.	amb.	elev.	
Canopy					
<i>Pinus taeda</i>	103	100	0.097	0.120	0.023*
Understorey					
<i>Pinus taeda</i>	26	26	0.062	0.057	0.719
<i>Liquidambar styraciflua</i>	31	39	0.104	0.113	0.766
<i>Ulmus alata</i>	14	10	0.068	0.097	0.069
<i>Acer rubrum</i>	4	5	0.168	0.089	0.381

**P*-value calculated for BAI₉₇ – BAI₉₆—see text.

allows the application of elevated CO₂ treatments to plants growing under natural conditions in the field. The first large-scale experimental FACE system designed to study the effects of elevated CO₂ on an intact forest ecosystem was initiated on 27 August 1996 in a loblolly pine (*Pinus taeda* L.) plantation. The forest has been unmanaged since planting, and several hardwood species have become established in the understorey. The soils in this region are primarily clay-rich Alfisols of the Enon series and are low in available nitrogen and phosphorus. This system presents an opportunity to investigate the response of both established loblolly pine canopy trees and understorey trees to elevated CO₂ in an intact forest ecosystem.

Our objective was to quantify the growth of established loblolly pine trees in response to elevated CO₂ in an intact forest with the full complement of natural physical and biotic interactions in place. We also measured growth of four abundant understorey hardwood species to examine the potential interaction between light limitation and CO₂ enrichment. We report results for the first two years (pretreatment and the first year of CO₂ treatment) of this long-term CO₂-enrichment experiment.

Methods

A FACE (Free-Air CO₂ Enrichment) system was installed in Duke Forest, in an intact 15-year-old loblolly pine (*Pinus taeda* L.) plantation in the Piedmont region of North Carolina (35°97'N 79°09'W). The site contains three elevated CO₂ plots maintained at ambient plus 200 μL L⁻¹ CO₂ (≈ 550 μL L⁻¹) paired with three ambient plots. Forced air (ambient plots) and CO₂ are delivered to the forest via a large circular plenum and 32 vertical pipes that surround each 30-m diameter ring (plot). The pipes extend from the forest floor through the 15-m tall forest canopy and contain adjustable ports at 50-cm intervals. These ports are tuned to control atmospheric [CO₂] through the entire volume of forest. The injection of CO₂

Table 1 Sample size (*n*) and relative basal area increment (RBAI, cm² cm⁻² y⁻¹) of canopy (7.9–24.6 cm d.b.h.) and understorey (3.5–11.6 cm d.b.h.) trees during the first year of CO₂ treatment. RBAI was calculated as the slope (*b*₁) of the regression: BAI = *b*₀ + *b*₁ (BA_{min}), where BAI is the basal area increment (cm² increase in basal area for 1997) and BA_{min} is the minimum (initial) basal area (cm²) in 1996 for canopy trees and 1997 for understorey trees

was initiated on 27 August 1996. The FACE rings injected CO₂ for > 80% of the total time from that date to the end of 1997 and the CO₂ concentration in the pine canopy was, on average, within 10% of the set point of ambient plus 200 μL L⁻¹ CO₂.

All trees within the six experimental plots larger than 2.5-cm diameter at breast height (d.b.h., measured 1.4 m above ground level) were mapped, and the number of individuals and total basal area (BA) of stems determined. We measured diameter growth of the four most abundant species in the six experimental plots: loblolly pine (1733 trees ha⁻¹, BA = 26.3 m² ha⁻¹), sweetgum (*Liquidambar styraciflua* L.; 667 trees ha⁻¹, 1.2 m² ha⁻¹), winged elm (*Ulmus alata* Michx.; 226 trees ha⁻¹, 0.2 m² ha⁻¹), and red maple (*Acer rubrum* L.; 207 trees ha⁻¹, 0.2 m² ha⁻¹). These four species account for > 95% of total Basal Area in the six plots. Together, other species contribute 804 trees ha⁻¹ and 1.2 m² ha⁻¹ BA and include *Carpinus caroliniana* Walt., *Carya ovata* (Mill.) K. Koch, *Cercis canadensis* L., *Fraxinus americana* L., *Juniperus virginiana* L., *Liriodendron tulipifera* L., *Nyssa sylvatica* Marsh., *Ostrya virginiana* (Mill.) K. Koch, *Pinus virginiana* Mill., *Prunus serotina* Ehrh., *Quercus alba* L., *Quercus rubra* L., *Rhus typhina* L., and *Ulmus rubra* Muhl.

In March 1996, dendrometer bands were installed on 31–39 loblolly pine trees (7.9–24.6 cm d.b.h.) in each plot (*n* = 103, ambient; *n* = 100, elevated). To minimize soil compaction from frequent visits, we selected canopy emergent, dominant, and suppressed (e.g. Barnes *et al.* 1998) individuals growing near the central boardwalk in each plot. Following Liming (1957) bands were constructed of 127-μm thick, 1.27-cm wide spring-tempered stainless steel and 0.79-cm OD, 7.62-cm long (0.071-cm stainless steel wire) extension springs. The vernier scale on the bands allowed changes in circumference to be read to the nearest 0.0254 cm (converted from inches).

In March 1997, understorey trees (3.4–11.4 cm d.b.h.) of loblolly pine, sweetgum, winged elm, and red maple were fitted with miniature dendrometer bands. Trees were selected arbitrarily and were fairly evenly distrib-

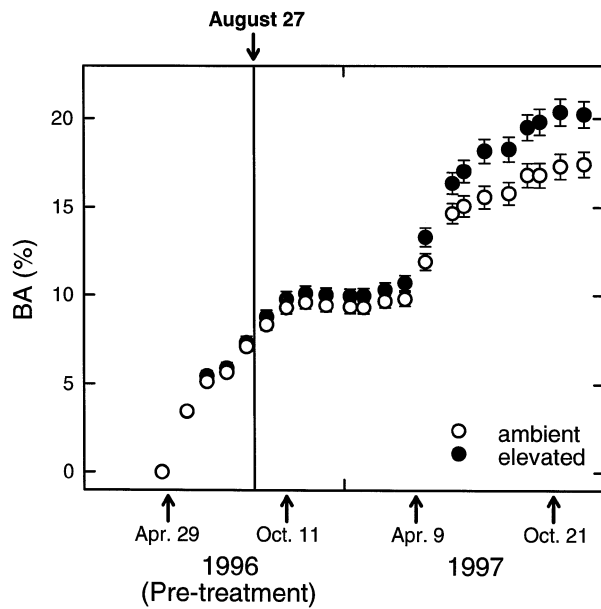


Fig. 1 Percent increase over initial values (measured in April 1996) of Basal Area (BA) for loblolly pine trees growing in ambient (open circles; $n=103$) and elevated (filled circles; $n=100$) plots for 1996 (pretreatment) and 1997 (the first year of treatment). The date of initiation of the elevated CO₂ treatment is indicated by the vertical line. Approximate dates of initiation and cessation of growth are indicated by arrows on the bottom axis. Error bars are plus or minus one standard error of the mean.

uted between plots, except there were no winged elm trees large enough to band in plot 1. Sample sizes are reported in Table 1.

Dendrometer bands on canopy trees were read monthly and the minibands on understorey trees were read when installed and in January 1998. Growth rate of canopy trees during 1996 (pretreatment) and canopy and understorey trees during 1997 (first year of treatment) was calculated as Basal Area Increment: $BAI = (BA_{max} - BA_{min}) / \text{year}$, where BA_{max} and BA_{min} are the yearly maximum and minimum basal area, respectively, calculated from the measured circumferences. When BAI is graphed vs. BA_{min} , the slope of the resulting regression line (BAI/BA_{min}) is the Relative Basal Area Increment (RBAI) and normalizes for initial differences in size.

To account for potential differences in growth rates between control and treatment plots prior to initiating the treatment, statistical analysis was performed on the difference between BAI_{1997} and BAI_{1996} for canopy trees. The lack of pretreatment data prevented this analysis for understorey trees. Nested analysis of covariance (ANCOVA) was used with BA_{min} (for 1996 for the canopy trees) as the covariate. Tests were performed with Proc GLM (SAS for Windows, version 6.12; Cary, NC).

Results and Discussion

Diameter growth of established canopy trees of loblolly pine in an intact forest, increased during the first year of exposure to $\approx 1.5 \times$ ambient atmospheric CO₂ concentration. To account for differences in initial size, the increase in basal area over time is graphed as the percentage increase over initial (April 1996) values (Fig. 1). Basal area growth of canopy loblolly pine trees began in April and ended in October with a slightly longer growing season in 1997 than in 1996 (Fig. 1). Increased growth under elevated CO₂ may have begun quite soon after the treatment was initiated and is evident by May 1997 and throughout the remainder of the first year of CO₂ treatment.

Relative basal area increment is analogous to relative growth rate and was calculated as the slope of the regression of BAI on BA_{min} (Fig. 2). In 1996, there appeared to be a small initial difference in RBAI for established loblolly trees growing in what were to become ambient ($RBAI=0.124 \text{ cm}^2 \text{ cm}^{-2} \text{ y}^{-1}$) and elevated ($RBAI=0.138 \text{ cm}^2 \text{ cm}^{-2} \text{ y}^{-1}$) CO₂ plots (Fig. 2); however, in 1997, RBAI for trees in elevated plots was 24% greater than trees in ambient plots (Table 1). To account for potential differences in BAI prior to treatment initiation, ANCOVA was performed on the difference between BAI in 1997 and 1996. The resulting values are primarily negative because growth rate was less in 1997 than in 1996, likely a result of a drought during the summer of 1997. This analysis indicates that RBAI of trees exposed to elevated CO₂ was significantly greater than that of trees exposed to ambient levels of CO₂ ($P=0.023$; Table 1).

After correcting for initial differences in BA between trees in control and treatment plots, mean basal area of loblolly pine was 14% greater by December 1997, than BA of trees exposed to elevated CO₂ (Fig. 1). Assuming a linear response, the observed growth stimulation would be 17.5% at $2 \times$ ambient CO₂. This stimulation in BA was similar to growth increases reported by Strain & Thomas (1992) for potted loblolly pine seedlings growing under $2 \times$ ambient CO₂ but with suboptimal soil nutrients (16–19% biomass increase after one growing season, 9% increase after two growing seasons). Under similar low nutrient and $2 \times$ ambient CO₂ conditions, others have reported no change (Griffin *et al.* 1993) or 35% (Gebauer *et al.* 1996) stimulation of growth for loblolly pine. Alternatively, $2 \times$ ambient CO₂ and high nutrients increase loblolly pine biomass 33–90% (Strain & Thomas 1992; Griffin *et al.* 1993; Tschaplinski *et al.* 1993; Gebauer *et al.* 1996; Groninger *et al.* 1996), a 2–6 times greater growth response than we observed at $1.5 \times$ ambient CO₂. These results suggest that within the first year of exposure to elevated CO₂, canopy loblolly pine trees

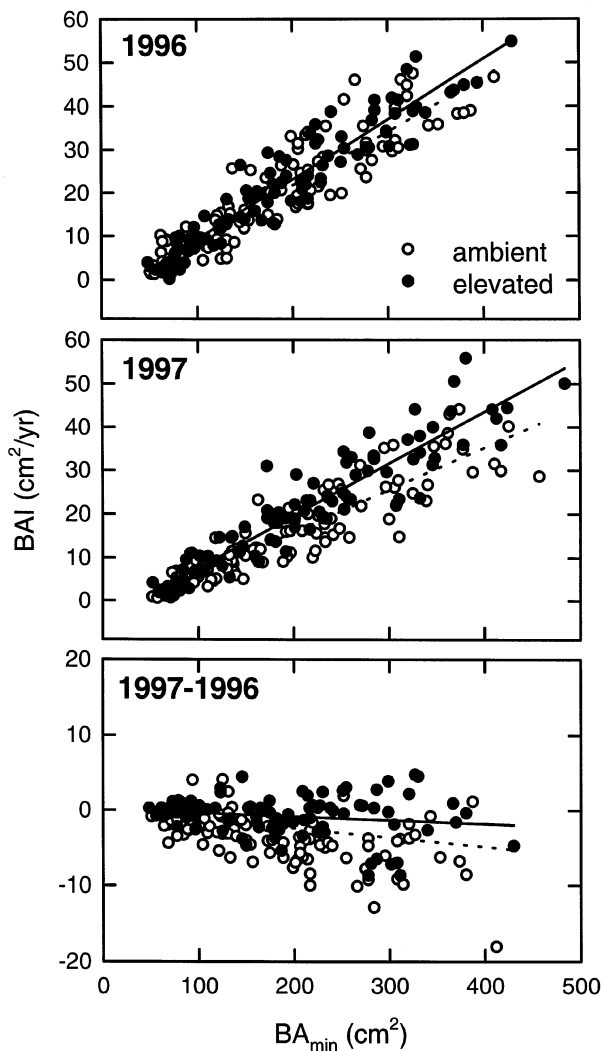


Fig. 2 Basal Area Increment (BAI) regressed against minimum BA of loblolly pine trees growing in ambient (open circles, dotted lines; $n=103$) and elevated (filled circles, solid lines; $n=100$) plots during 1996 and 1997. The bottom panel is $BAI_{1997} - BAI_{1996}$, the value on which statistical analysis was performed.

growing under nutrient limitations in the field have similar growth responses to potted seedlings and saplings growing in similar low nutrient conditions.

Possibly because of the drought during the summer of 1997, RBAI was consistently lower than in 1996. In August of 1996 precipitation was close to the 50 year average, but in August 1997 it was $\approx 90\%$ below average. Under drought conditions, elevated CO₂ may ameliorate water stress by increasing water use efficiency (Ceulemans & Mousseau 1994) and thus may compensate for drought-induced growth limitations. However, Tschaplinski *et al.* (1993) and Groninger *et al.* (1996) report no interaction of elevated CO₂ with water stress. Therefore, the August

drought of 1997 may have limited growth in both treatments, but the relative magnitude of the CO₂-induced growth increase is unlikely to have been influenced by the drought.

Although many studies have investigated the interactions of nutrient and water limitations and elevated CO₂, irradiance is a major resource limitation that has rarely been examined in conjunction with elevated CO₂. Elevated atmospheric CO₂ may decrease photorespiration, thus increasing maximum quantum yield of photosynthesis (Long 1991). Since plants in forest understories function near the light compensation point, this increase in quantum yield would substantially increase net carbon gain (Long & Drake 1991; Bowes 1993; Drake *et al.* 1997). Elevated CO₂ therefore may be of particular importance for understory trees. In contrast to canopy loblolly pine trees, loblolly pine, sweetgum, and red oak trees in the understory did not increase growth rate in response to elevated CO₂, although there was a marginally significant ($P=0.069$) increase in RBAI for winged elm trees (Table 1). Elevated CO₂-induced increases in carbon gain under low light have been demonstrated in understory herbs (Hättenschwiler & Körner 1996) and tree seedlings (Kubiske & Pregitzer 1996), although increased growth in tree seedlings is more pronounced under high nutrient conditions (Bazzaz & Miao 1993). In the present study, nutrient limitations may have minimized any CO₂-induced growth increases; however, small sample sizes resulted in highly variable BAI values and this, coupled with the lack of pretreatment data for these trees, may have made small differences difficult to detect. Furthermore, suppressed trees in the understory tend to increase height rather than diameter growth, which lessens the risk of becoming overtopped by their neighbours (King & Loucks 1978; Naidu & DeLucia 1998). Thus potential growth increases may not have been detected by d.b.h. measurements used in this study.

Despite presumed nutrient limitations, a drought, and competition with neighbours, the first year of exposure to a step-increase in atmospheric CO₂ caused a significant increase in diameter growth of large loblolly pine trees. The growth stimulation was similar to that observed for seedlings grown under controlled conditions but with limited nutrient supply. A step-increase in CO₂ may yield a larger growth response, especially in the first year of exposure, than a gradual increase in CO₂. This could create a resource imbalance that may hasten the loss of the CO₂ response with time. For seedlings and saplings of loblolly pine (Strain & Thomas 1992; Tissue *et al.* 1996) and other tree species (Ceulemans & Mousseau 1994; Curtis 1996), the growth stimulation is often transient and appears to abate under conditions of nutrient limitation or via down-regulation of photosynthesis over

time in response to sink limitations (Ceulemans & Mousseau 1994; Drake *et al.* 1997). A recent study of oaks growing adjacent to a natural CO₂ vent also indicates that the growth stimulation occurs early and diminishes rapidly (Hättenschwiler *et al.* 1997). We therefore predict that the growth enhancement observed in this first year will diminish with time thus limiting the capacity of this forest to sequester atmospheric carbon.

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References

- Barnes BV, Zak OR, Denton SR, Spurr SH (1998) *Forest Ecology*, 4th edn. John Wiley and Sons, New York, 774pp.
- Bazzaz FA, Miao SL (1993) Successional status, seed size, and responses of tree seedlings to CO₂, light, and nutrients. *Ecology*, **74**, 104–112.
- Bowes G (1993) Facing the inevitable: plants and increasing atmospheric CO₂. *Annual Review of Plant Physiology and Plant Molecular Biology*, **44**, 309–332.
- Ceulemans R, Mousseau M (1994) Effects of elevated atmospheric CO₂ on woody plants. *New Phytologist*, **127**, 425–446.
- Curtis PS (1996) A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon-dioxide. *Plant, Cell and Environment*, **19**, 127–137.
- Curtis PS, Wang W (1998) A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia*, **113**, 299–313.
- Drake BG, González-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO₂. *Annual Review of Plant Physiology and Plant Molecular Biology*, **48**, 609–639.
- Ellsworth DS, Oren R, Huang C, Phillips N, Hendrey GR (1995) Leaf and canopy responses to elevated CO₂ in a pine forest under free-air CO₂ enrichment. *Oecologia*, **104**, 139–146.
- Gebauer RLE, Reynolds JF, Strain BR (1996) Allometric relations and growth in *Pinus taeda*: the effect of elevated CO₂ and changing N availability. *New Phytologist*, **134**, 85–93.
- Griffin KL, Thomas RB, Strain BR (1993) Effects of nitrogen supply and elevated carbon dioxide on construction cost in leaves of *Pinus taeda* (L.) seedlings. *Oecologia*, **95**, 575–580.
- Groninger JW, Seiler JR, Sedaker SM, Berrang PC (1996) Effects of CO₂ concentration and water availability on growth and gas exchange in greenhouse-grown miniature stands of loblolly pine and red maple. *Functional Ecology*, **10**, 708–716.
- Hättenschwiler S, Körner C (1996) Effects of elevated CO₂ and increased nitrogen deposition on photosynthesis and growth of understory plants in spruce model ecosystems. *Oecologia*, **106**, 172–180.
- Hättenschwiler S, Miglietta F, Raschi A, Körner C (1997) Thirty years of *in situ* growth under elevated CO₂: a model for future forest responses? *Global Change Biology*, **3**, 463–471.
- Hendrey GR, Kimball BA (1994) The FACE program. *Agricultural and Forest Meteorology*, **70**, 3–14.
- King D, Loucks OL (1978) The theory of tree bole and branch form. *Radiation and Environmental Biophysics*, **15**, 141–165.
- Kubiske ME, Pregitzer KS (1996) Effects of elevated CO₂ and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiology*, **16**, 351–358.
- Lewin KF, Hendrey GR, Nagy J, LaMorte RL (1994) Design and application of a free-air carbon dioxide enrichment facility. *Agricultural and Forest Meteorology*, **70**, 15–29.
- Liming FG (1957) Homemade Dendrometers. *Journal of Forestry*, **55**, 575–577.
- Long SP (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: Has its importance been underestimated? *Plant, Cell and Environment*, **14**, 729–739.
- Long SP, Drake BG (1991) Effect of the long-term elevation of CO₂ concentration in the field on the quantum yield of photosynthesis of the C₃ sedge, *Scirpus olneyi*. *Plant Physiology*, **96**, 221–226.
- Naidu SL, DeLucia EH (1998) Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. *Canadian Journal of Forest Research*, **28**, 1116–1124.
- Strain BR, Thomas RB (1992) Field measurements of CO₂ enhancement and climate change in natural vegetation. *Water, Air, and Soil Pollution*, **64**, 45–60.
- Tissue DT, Thomas RB, Strain BR (1996) Growth and photosynthesis of loblolly pine (*Pinus taeda*) after exposure to elevated CO₂ for 19 months in the field. *Tree Physiology*, **16**, 49–59.
- Tschaplinski TJ, Norby RJ, Wullschlegel SD (1993) Responses of loblolly pine seedlings to elevated CO₂ and fluctuating water supply. *Tree Physiology*, **13**, 283–296.