Allometric determination of tree growth in a CO$_2$-enriched sweetgum stand

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Summary

• In a free-air CO$_2$ enrichment (FACE) study, above-ground growth of *Liquidambar styraciflua* (sweetgum) trees was measured in a closed-canopy stand to test hypotheses about long-term effects of rising [CO$_2$] in a deciduous forest.
• Allometric relationships were established between above-ground dry mass and basal area, height, taper and wood density for all trees in the 314-m^2 plots. Leaf area index was calculated from leaf litter mass.
• In the first year of exposure, elevated [CO$_2$] stimulated stand-level aboveground dry matter increment by 33%, but in the second year the growth stimulation was reduced to 15% and was no longer statistically significant. Leaf area index was not affected by CO$_2$ enrichment in either year.
• These results indicate that large trees that are no longer in an exponential growth phase retain the capacity to respond to elevated [CO$_2$]. The combined 2-yr response of a 24% increase in growth per unit leaf area is consistent with predictions from earlier studies. A longer-term data set is needed to resolve the reason for different responses in the 2 years.

Key words: allometry, basal area increment, elevated CO$_2$, forest productivity, free-air CO$_2$ enrichment (FACE), global change, *Liquidambar styraciflua* (sweetgum), tree growth.

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Introduction

It is now well established that tree species, like all C$_3$ plants, respond to an increased concentration of atmospheric carbon dioxide (CO$_2$) with higher rates of photosynthesis and faster growth rates. Most of the conclusions about CO$_2$ effects from short-term experiments with potted tree seedlings were supported by multiyear experiments with larger trees rooted in the soil in the field (Norby *et al.*, 1999). That is, the enhancement of photosynthesis persists through time, even as foliar nitrogen (N) concentrations are reduced, and plant growth rates are significantly increased. While the confirmation of our initial understanding is gratifying, there remain important impediments to applying this knowledge to questions about forest growth and metabolism in a future, CO$_2$-enriched atmosphere (Lee & Jarvis, 1995), and that is the ultimate objective of this research. The difficulty lies in questions of scale – how to scale the responses of small groups of individuals to the responses

of a forest stand, and how to predict processes and pools that change slowly in a forest, such as nutrient cycling or soil organic matter. The problems of scale are exacerbated by the experimental difficulties inherent in investigating forest ecosystems with large and long-lived plants.

An appreciation of developmental processes in trees has revealed the problem in extrapolating the effects of increased [CO$_2$] on biomass increment, of young trees in open-top chambers, to the scale of a mature forest stand (Ceulemans & Mousseau, 1994; Lee & Jarvis, 1995). The importance of leaf area as a controller of plant response to [CO$_2$] has been made clear in many experiments (Norby & O'Neill, 1989, 1991; Ceulemans *et al.*, 1995; Norby *et al.*, 1995; Tissue *et al.*, 1997; Curtis *et al.*, 2000). Young trees undergo a period of exponential growth in which an increased leaf area supports increased growth, which in turns supports production of more leaf area, and so on. The very large enhancements in tree growth that have been reported (Norby *et al.*, 1995; Idso & Kimball, 1997)

are a result of this compound interest effect, but when growth is normalized to a constant leaf area, the responses to elevated [CO_2] are similar across experiments and species (Norby, 1996; Norby *et al.*, 1999) and are consistent with many other data summaries of plant responses (Eamus & Jarvis, 1989; Ceulemans & Mousseau, 1994; Wullschleger *et al.*, 1997; Curtis & Wang, 1998).

It is appropriate to normalize growth by leaf area because as trees grow into a forest stand, leaf area reaches a relatively constant value as it becomes constrained by environmental limitations imposed by available water, nutrients, or light. Exponential growth is no longer possible, and trees enter a linear growth phase in which their growth increment is approximately constant each year (Kozlowski *et al.*, 1991). Can the responses of a closed canopy forest stand in a linear growth phase be predicted from experiments with small assemblages of exponentially growing trees? Rey & Jarvis (1997) concluded that the tree growth responses to [CO_2] are short-lived and not seen when equal-sized trees are compared. Alternatively, we have suggested that the effect of [CO_2] on annual stem growth increment per unit leaf area (growth efficiency (Waring & Schlesinger, 1985) or canopy productivity index (Norby, 1996)), which averages about a 26% increase at 650–700 ppm CO_2 (Norby *et al.*, 1999), is a robust response that should persist after canopy closure.

This hypothesis must be tested in a closed-canopy forest stand, and that is the primary objective of the Oak Ridge Experiment on CO_2 Enrichment of Sweetgum. This experiment uses free-air CO_2 enrichment (FACE) technology (Hendrey *et al.*, 1999) to expose a closed-canopy *Liquidambar styraciflua* forest plantation to elevated atmospheric [CO_2]. The forest stand is similar in age and stature to the *Pinus taeda* (loblolly pine) stand in another FACE experiment (DeLucia *et al.*, 1999), but the sweetgum experiment is in a deciduous forest stand with a more nutrient-rich soil and a less developed understory. The important features of this stand – its closed canopy, linear growth phase, fully occupied soil and uniformity – permit us to test hypotheses about responses of forests to elevated [CO_2], one of which is that the previously observed effect of elevated [CO_2] on annual growth per unit leaf area will persist after canopy closure. This experiment also enables us to measure the response of forest leaf area index (LAI) to CO_2 enrichment, a critically important issue that cannot be addressed in smaller-scale systems.

The objectives of this initial report from the Oak Ridge sweetgum experiment are to describe the site and experimental design, establish the analytical framework for assessment of above-ground growth and provide an initial evaluation of the growth response to elevated CO_2.

Methods

Site description

The experimental site is a planted sweetgum (*Liquidambar styraciflua* L.) monoculture located on the Oak Ridge National Environmental Research Park in Roane County, Tennessee, USA (35°54′ N, 84°20′ W). The plantation was established in spring 1988. One-year-old, bare-rooted sweetgum seedlings were planted at a spacing of 2.3 m × 1.2 m. A total of 1.7 ha was planted with sweetgum in two areas – a 185 × 70 m area and a smaller 85 × 50 area, separated by a stand of *Platanus occidentalis* L. Herbicide was used in 1989 and 1990 to control competition from weeds; no fertilizer has been added. The canopy has been closed at least since 1996, and the stand has differentiated into crown classes. Lower branches are being shed, and there has been some mortality of suppressed trees. Reproductive growth has not started except for a few trees (< 1%) that have produced a few fruit.

The soil at the site, which is classified as an Aquic Hapludult, developed in alluvium washed from upland soils derived from a variety of rocks including dolomite, sandstone and shale. It has a silty clay loam texture and is moderately well drained (Soil Conservation Service, 1967; van Miegroet *et al.*, 1994). The soil is slightly acid (water pH approximately 5.5–6.0) with high base saturation largely dominated by exchangeable Ca. Mean annual temperature (1962–93) is 13.9°C, and mean annual precipitation is 1371 mm, with a generally even distribution of precipitation throughout the year. Environmental monitoring at the site was described by Wullschleger & Norby (2001).

FACE apparatus

Six 25-m diameter plots were laid out in 1997, and construction of the FACE facility began thereafter, following the design employed at the loblolly pine FACE experiment in North Carolina (Hendrey *et al.*, 1999). Site disturbance was minimized during construction. Twelve aluminum towers on concrete foundations surround each of four plots, and two vent pipes were suspended from a cross-arm at the top of each tower. Therefore each plot is surrounded by 24 vent pipes spaced 3.3 m apart. Initially the towers were 15 m tall, but before the 1999 growing season they were extended to 18 m to accommodate the increased height of the trees. The vent pipes are connected to a plenum constructed of 38-cm diameter polyethylene pipe. A radial blower pushes air through the plenum at 2.0 m³ s⁻¹. A pneumatically activated valve, operated by compressed air from an air compressor and storage tank, is between the plenum and each vent pipe. In the two plots set up for elevated CO_2, pure CO_2 is introduced to the air flow immediately after the blower so that it is diluted before reaching the vent pipes. The CO_2 is delivered from a 50-ton capacity CO_2 tank with electrical vaporizers and a Kurz regulatory valve as described by Hendrey *et al.* (1999). The CO_2 comes from a natural gas source (BOC Gases) and has a $\delta^{13}C$ signature of −51‰.

Regulation of the CO_2 concentration is achieved using equipment and software designed at Brookhaven National Laboratory (Hendrey *et al.*, 1999). An air sample is drawn

Table 1 Initial characteristics of the plots. Plot 6 was excluded from subsequent analyzes. Taper index is defined as $1-A_4/A_{1.3}$, where A_x is cross sectional area at 1.3 and 4 m height. Soils were analyzed for total C and N on the Perkin-Elmer 2400 CHN Analyzer, exchangeable Ca^{2+}, Mg^{2+}, and K^+ by atomic absorption after extraction with 1 M ammonium acetate; and extractable P with 0.5 M HCl plus 1 M NH_4F followed by automated colorimetric analysis

Plot	Treatment	Soil C content (Mg ha^{-1})	Soil N content (Mg ha^{-1})	Soil extract. P (kg ha^{-1})	Soil exch. K (kg ha^{-1})	Soil exch. Ca (kg ha^{-1})	Soil exch. Mg (kg ha^{-1})	Tree height (m)	Stand basal area (cm^2 m^{-2})	Trees per plot	Taper index
1	Elevated	77	11	57	749	6690	997	12.0	27.2	84	0.435
2	Elevated	95	11	82	588	10920	1209	12.2	27.3	86	0.427
3	Ambient	54	8	99	635	5190	751	12.6	30.2	91	0.468
4	Control	76	12	82	717	8530	1294	12.6	28.6	86	0.453
5	Control	70	11	91	626	7030	964	12.8	30.5	95	0.494
6	Ambient	140	16	53	1146	16260	2406	11.7	22.6	68	0.413

from the middle of the plot near the top of the canopy and analyzed for CO_2 concentration with a LiCor 6252 infrared gas analyzer. The analyzer communicates with the central computer via fiber optic cable. Wind speed and direction are monitored with an anemometer and wind vane mounted above the canopy; the data also are communicated to the central computer via fiber optic cable. The appropriate flow rate of CO_2 into each of the treatment rings is calculated by a proportional-integral-differential (PID) algorithm using wind speed and the time-integrated departure of current $[CO_2]$ from the set point (Hendrey *et al.*, 1999); the result is communicated to the rotary valve once per second. The valves to the vent pipes are opened or closed based on wind direction such that the 10 vents in the upwind direction are open. When wind speed is < 0.4 m s^{-1}, every other vent pipe is opened. The system is shut off when wind velocity exceeds 6 m s^{-1} for more than 5 min; this occurs only rarely, usually in association with thunderstorms or in early spring before substantial canopy development.

The CO_2 treatment was initiated in April 1998, before bud break, although some initial problems and a lightning strike delayed reliable operation until May 11. The $[CO_2]$ set-point in 1998 was a constant 565 p.p.m. In 1999 a dual set-point (565 ppm day and 645 ppm night) was used to represent better the diurnal variation in ambient $[CO_2]$. Actual average $[CO_2]$ in 1998 was 528 during the day and 541 ppm at night (534 ppm overall); in 1999 the $[CO_2]$ was 538 ppm (day), 615 ppm (night), and 573 ppm overall. The daytime average of 533 ppm will be used to characterize the treatment. These averages include periods when there was no CO_2 enrichment because of equipment failure, interruptions in CO_2 supply, high winds, or deliberate suspension for experimental purposes (10% of the time in 1998 and 11% in 1999). The standard deviation of 1-min averages was 60 ppm, and 90% of the 1-min averages were within 20% of the set point. Average concentrations in the two elevated CO_2 plots differed by < 2 ppm. In ambient plots $[CO_2]$ near the top of the canopy was 394 ppm (day) and 454 ppm (night). These concentrations are higher than globally averaged $[CO_2]$ (368 ppm in 1999) because of

low dispersion of CO_2 released in soil respiration during generally low-wind conditions at night and early morning hours. Although the separation between plots was much less than recommended, there was no evidence of significant contamination of ambient plots by the CO_2 released to treatment plots. The $[CO_2]$ in the upper canopy of ambient plots averaged only 10 ppm higher over the growing season than ambient $[CO_2]$ measured distant from the FACE array and was only 5 ppm lower on days when there was no CO_2 release to the elevated plots. In the worst case when the wind was from the north-west quadrant (which occured 17% of the time), $[CO_2]$ in ambient plots was elevated by 18 ppm over distant ambient.

Experimental design

Initially six plots were laid out (two with elevated $[CO_2]$, two with towers and blowers but no added CO_2, and two with no FACE apparatus), but we subsequently learned that the soil in one of the no-blower plots is substantially different from that of the other five plots. Bulk density is lower and total C, N, K, Ca, and Mg contents are higher (Table 1). In addition, the trees on this plot were planted with wider spacing. Because of these differences, which could confound the interpretation of future soil or biological responses, this plot was excluded from the experiment. The responses in this plot during the 2 yrs of measurement did not differ substantially from those in the other plots in ambient $[CO_2]$, and removing data from this plot does not alter or bias any of our conclusions about the effects of elevated $[CO_2]$.

The subsequent experimental design comprises two plots with elevated $[CO_2]$ and three plots with ambient $[CO_2]$. Statistical analysis was by ANOVA with plot as the experimental unit. We have seen no effects of the blowers on environmental conditions or biological responses, justifying the combination of the two plots with blowers and the one plot without. For example, temperature over 30 d at a height of 2 m in the center of the plots averaged 13.67°C in control plots with blowers and 13.69°C in plots without blowers.

Tree growth assessment

Measurements of tree growth began in April 1997, 1 yr before the onset of CO_2 exposure. Every tree within 10 m of plot center was measured. A steel dendroband encircled the bole at a height of 1.3 m, held on with a spring. The initial circumference was measured, and the distance between two holes in the band was measured periodically with digital calipers to track increases in circumference. (The distance measured between the two index holes actually was the chord; the arc distance was determined by a simple geometric formula.) Measurements were made at approximately monthly intervals between April and December. Tree basal area (BA) was calculated from circumference, and plot BA was the sum of BA of all live trees within the 314 m^2 measurement area.

The calculation of aboveground tree mass from the basal area data set required allometric equations. These were established from 12 trees that were cut down during FACE ring construction in 1997 to accommodate the vent pipe towers and 10 larger trees from the plantation (between plots) cut down in August 1999. Bole circumference was measured at 0.5 m, 1.3 m and at the base of the live crown. Leaves were removed and the fresh mass of the bole and branches was determined. Subsections of bole and branches were cut, weighed fresh and then oven-dried and weighed again so that above-ground woody dry mass (DM) could be calculated. Aboveground tree mass was linearly related to BA ($r^2 = 0.91$, Fig. 1a). Branch mass was 10.6% of total above-ground tree mass.

The root systems of the 10 trees harvested in 1999 were excavated using a power winch and hand tools. The roots were washed free of soil with a high-pressure hose, oven-dried, and weighed. There was a linear relationship ($r^2 = 0.85$) between BA and root dry mass (Fig. 1c). Woody root mass was about 18.7% of whole-tree mass. Although root mass is not included in subsequent analyzes, conclusions about whole-tree growth should closely parallel those about above-ground growth.

The relationship between BA and above-ground DM implicitly assumes a constant relationship between BA and tree volume, and between tree volume and DM. Growth in elevated CO_2 could alter either of these relationships and thereby alter the regression between BA and DM. Since we could not harvest trees from the experimental plots without compromising the long-term experiment, nondestructive approaches were necessary. To address the relationship between BA and volume, we measured tree height and taper. Tree height of a subset of 20 trees per plot was measured at the end of each growing season with a clinometer in 1997 and 1998 and with an ultrasonic hypsometer in 1999. An index of taper (T) was calculated as $1 - A_4/A_{1.3}$ where A_x is the cross-sectional area (square centimeters) at height x. Bole circumference at 4 m height was measured annually on a subset of eight trees per plot. In 1999 the measurement of A_4 was extended to 20 trees per plot; there was excellent agreement with the original
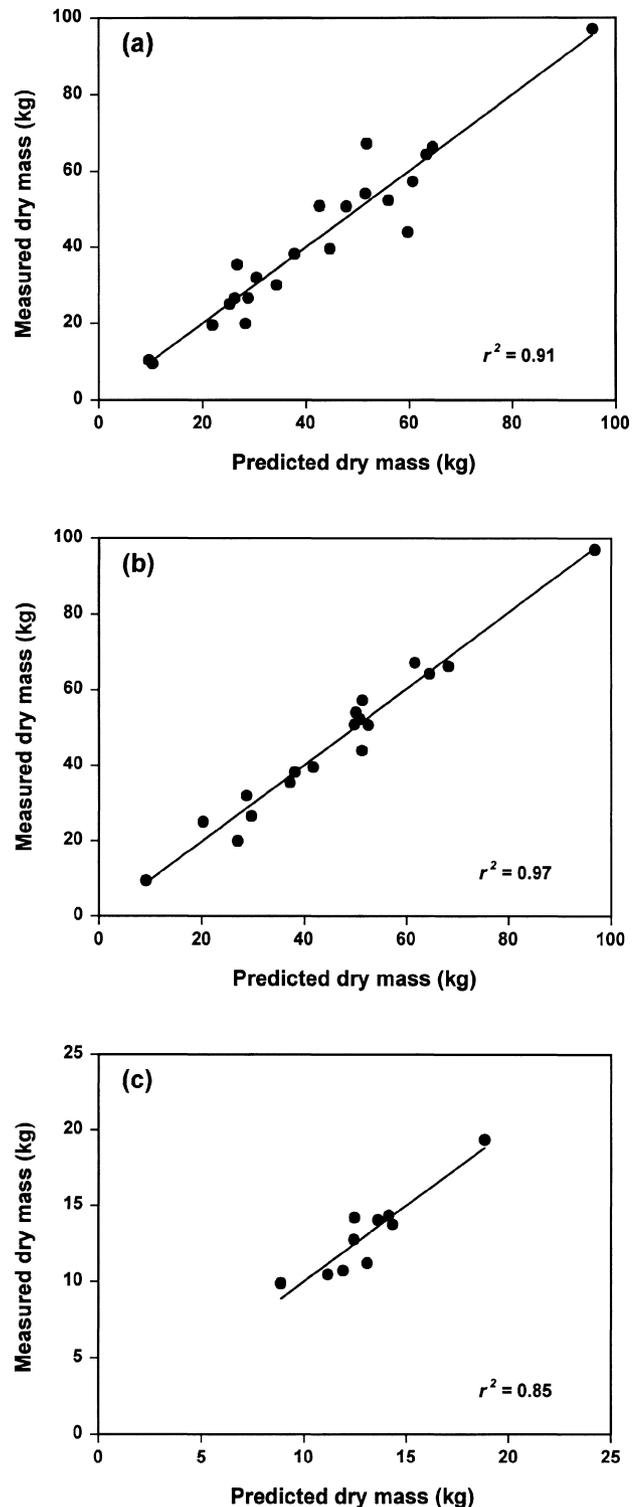

Fig. 1 Allometric equations developed to estimate woody biomass of *Liquidambar styraciflua* trees. (a) Aboveground (bole and branch) mass predicted from cross-sectional area at 1.3 m height ($A_{1.3}$, cm2) by the equation dry matter (DM) = $-2.24 + 0.355 * A_{1.3}$; (b) aboveground mass predicted from $A_{1.3}$ (cm2) × tree height (H, m) and taper index (T) by the equation DM = $30.25 + 0.0174 * A_{1.3} * H - 56.81 * T$; (c) dry mass of woody roots predicted from $A_{1.3}$ by the equation DM = $0.049 * A_{1.3} + 4.91$.

set of eight trees. Taper index also was determined on the 18 of the 22 harvested trees that were used for establishing the allometric equations.

The relationship between tree volume increment and dry mass increment (DMI) is a function of the density of the wood formed in a given year. Wood density was measured from increment cores that were collected in February 2000 and separated into wood formed in 1997, 1998 and 1999. The dimensions (length and diameter) of the fresh segments were measured with calipers, and the segments were oven-dried and weighed, enabling the calculation of dry mass per unit fresh volume. Wood density of the harvested trees was determined on cross sections of the boles of seven of the 22 harvested trees.

The regression in Fig. 1(a) was improved by the inclusion of height and taper (Fig. 1b). Other models combining $A_{1.3}$, H and T in various ways had non-significant coefficients or lower r^2 values. Above-ground dry matter increment was calculated as the change in DM from one year to the next. The influence of differences in wood density was included as a correction factor on DMI. This correction factor was the relative difference between wood density for a plot × year and the average density of trees used to establish the regression equation (0.51 g cm^{-3}).

Leaf area index was determined beginning in 1996, 2 yr before the onset of CO_2 exposure. Leaves were collected after they fell into baskets placed 1 m above the ground. In 1996–98 there were five 0.17-m^2 baskets per plot; in 1999 these were replaced with seven 0.19-m^2 baskets. Leaves were collected throughout the growing season, but most came down between mid-September and early November. During this period leaves were removed from the baskets every 2 wk, dried and weighed.

The conversion of leaf mass per unit ground area to LAI was problematic because of the wide range of specific leaf area (SLA) within the canopy. To calculate a whole-canopy SLA,

leaves were collected from each meter increment of height in the canopy in August of each year, and their area and dry mass measured. The SLA of each canopy layer was weighted by the relative distribution of leaf area by canopy height, which had been determined on the trees harvested for determination of allometric relationships. Litter SLA was assumed to be 7% greater than green leaf SLA due to dry matter loss during senescence (Norby *et al.*, 2000). This method of calculating canopy SLA assumes that the leaf area distribution determined on trees grown in ambient [CO_2] also applies to CO_2-enriched trees. Measurements of light penetration through the canopy in the experimental plots have not indicated any shift in the leaf area distribution in response to CO_2 enrichment (C. A. Gunderson, unpublished), and even a large shift (e.g. 20% of the leaf area in one layer moved up to the next layer) would result in only a 3% change in the predicted LAI. This method of leaf mass-to-area conversion was checked by an alternative approach. Freshly fallen leaves were collected from the forest floor of each plot whenever litter was collected from the baskets, and their area, dry mass, and SLA determined. Hence, a different SLA was used for each leaf collection in each plot. This approach was prone to errors associated with the determination of the area of senescent leaves and possible sampling bias, but the resulting calculation of LAI in 1999 nevertheless agreed to that from the first approach within 2% on average.

Results

Tree ring analysis of 24 trees cut down in 1997 during construction of the FACE apparatus (including 12 of the trees used to establish allometric relationships) indicates that the trees had been in a linear growth phase since 1993 (Fig. 2). At the start of the 1997 growing season, BA in the plots 1–5
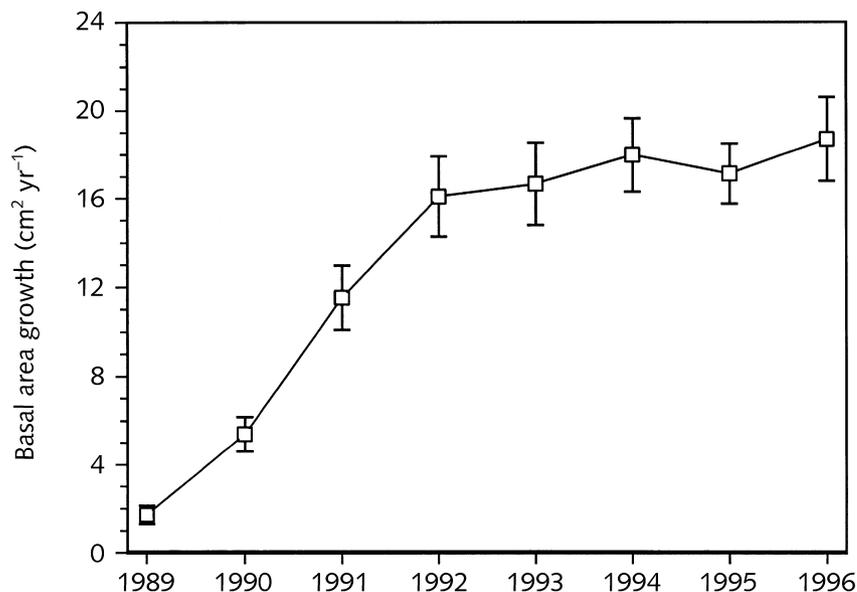

Fig. 2 Chronology of basal area increment reconstructed from tree ring analysis of 24 trees (± SE) cut down during construction of the FACE exposure system in 1997.

ranged from 27.2 to 30.5 cm^2 m^{-2} (Table 1), corresponding to a calculated wood dry mass of 6.4–7.0 kg m^{-2}. Average tree height and taper index differed between plots, and both were linearly related to the number of trees per plot. The differences in number of trees per plot can be attributed to mortality that probably occurred shortly after planting, except in plot 6 where the trees were originally planted with wider spacing. The effect of plot differences in tree density on tree form (height and taper) gives reason for inclusion of these terms in the allometric equation.

We found no evidence of an effect of $[CO_2]$ on tree height growth, taper, or wood density (Fig. 3), but initial differences between plots persisted through time. As trees grew taller, the taper index declined, and it declined similarly in plots 1–4; the taper index did not decline in plot 5, the plot with the highest tree density.

The seasonal pattern of basal area increment (BAI) is shown in Fig. 4. There was no difference in basal area growth between plots before the onset of the CO_2 treatment, and the annual dry matter increment in 1997 also was very similar (Fig. 5). Therefore there was no pretreatment bias to confound subsequent effects of $[CO_2]$ on growth. The effect of elevated $[CO_2]$ in 1998 was apparent primarily during the mid-summer period of most active growth. In 1999 growth started later in CO_2-enriched plots than in ambient CO_2 plots, and the mid-summer enhancement was smaller (Fig. 4). BAI was increased 19% by elevated $[CO_2]$ in 1998 ($P < 0.02$) and 7% in 1999 (not significant).

The estimate of above-ground dry matter increment (DMI) and its relative response to elevated $[CO_2]$ depends on the regression equation used (Table 2). Using the best and most comprehensive equation (Fig. 1b with a correction for wood density), aboveground DMI in 1998 was 33% higher in the two CO_2-enriched plots than in the three plots with ambient $[CO_2]$, and the difference was statistically significant at $P < 0.005$ (Fig. 5a). In the second year of treatment, however, DMI was only 15% higher in elevated CO_2, and the difference was not statistically significant ($P > 0.15$). LAI varied year to year, but there were no significant treatment effects either before or after the onset of CO_2 exposure (Fig. 5b). With no difference in LAI, the response of growth per unit leaf area was very similar to the response of DMI. The combined growth increment (and growth per unit leaf area) over the 2 yr of CO_2 enrichment was 24% higher in elevated CO_2 ($P < 0.02$).

Although plot-level DMI is the appropriate measure of stand-level response to elevated $[CO_2]$, it also is instructive to analyze individual tree growth patterns. BAI was linearly related to initial basal area (Fig. 6); that is, bigger trees grew more. The positive x-intercept indicates that the smallest, suppressed trees did not grow at all. Otherwise, the relative effect of $[CO_2]$ in 1998 was similar across all size classes, as indicated by the larger slope compared with trees in ambient $[CO_2]$ and the uniform distribution of points along the regressions. Hence, there were no artifacts of differential size class distribution
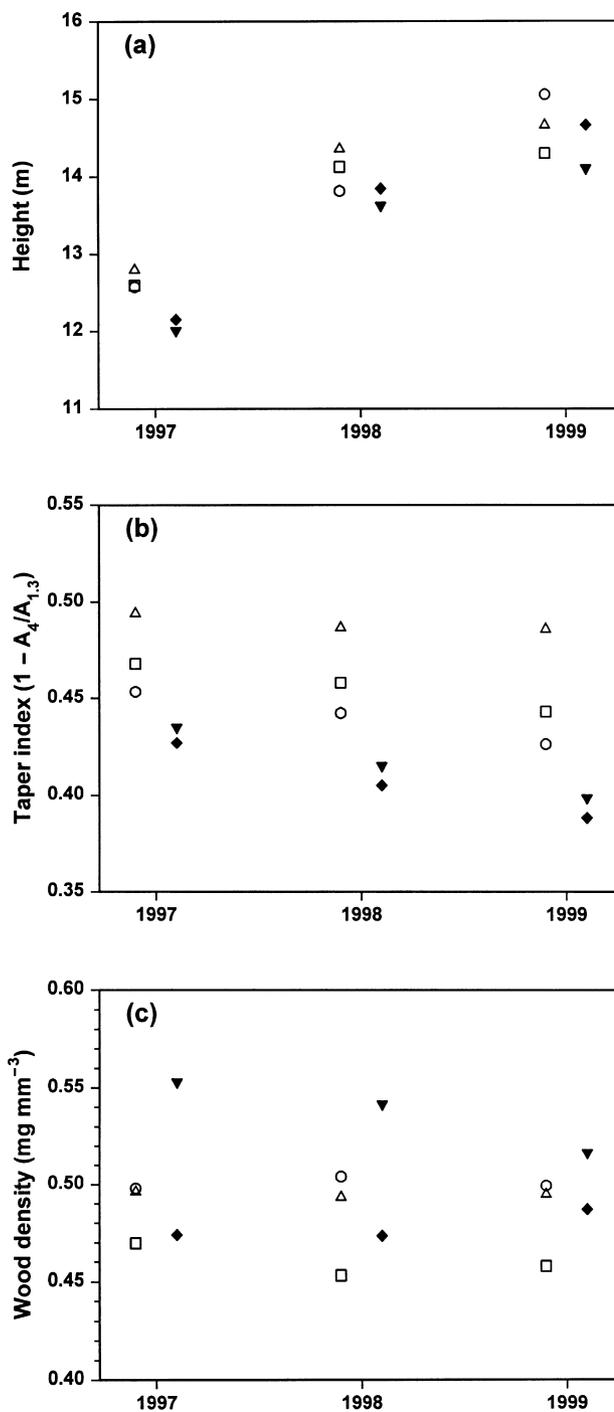

Fig. 3 (a) Tree height (b) taper index, and (c) wood density by plot based on a subset of trees in each plot. Open symbols are for plots in ambient $[CO_2]$ (open square, plot 3; open circle, plot 4; open triangle, plot 5). Closed symbols are for plots in elevated $[CO_2]$ (closed trianlge, plot 1; closed square, plot 2). Tree height was calculated as the average of a subsample of 20 trees per plot; sampling error (SE) was 0.3 m. Taper index for a plot was calculated from the mean values of $A_{1.3}$ and A_4 from a subsample of eight trees per plot (1997 and 1998) or 20 trees per plot (1999); there is no estimate of sampling error. Wood density was calculated as the average of three trees per plot; sampling error was 0.02 g mm^{-3}.

Fig. 4 Basal area growth rate per unit land area during the pretreatment year (1997) and two years of CO_2 enrichment. Open triangle, ambient [CO_2]; closed triangle, elevated [CO_2].
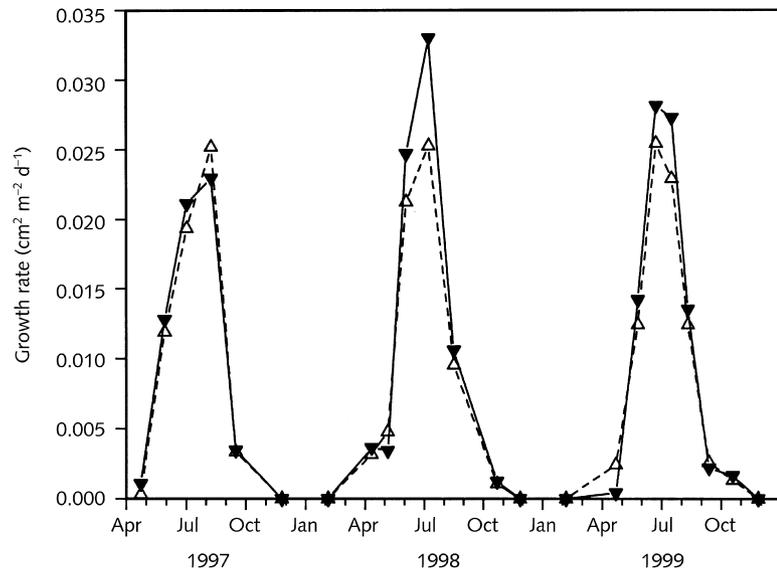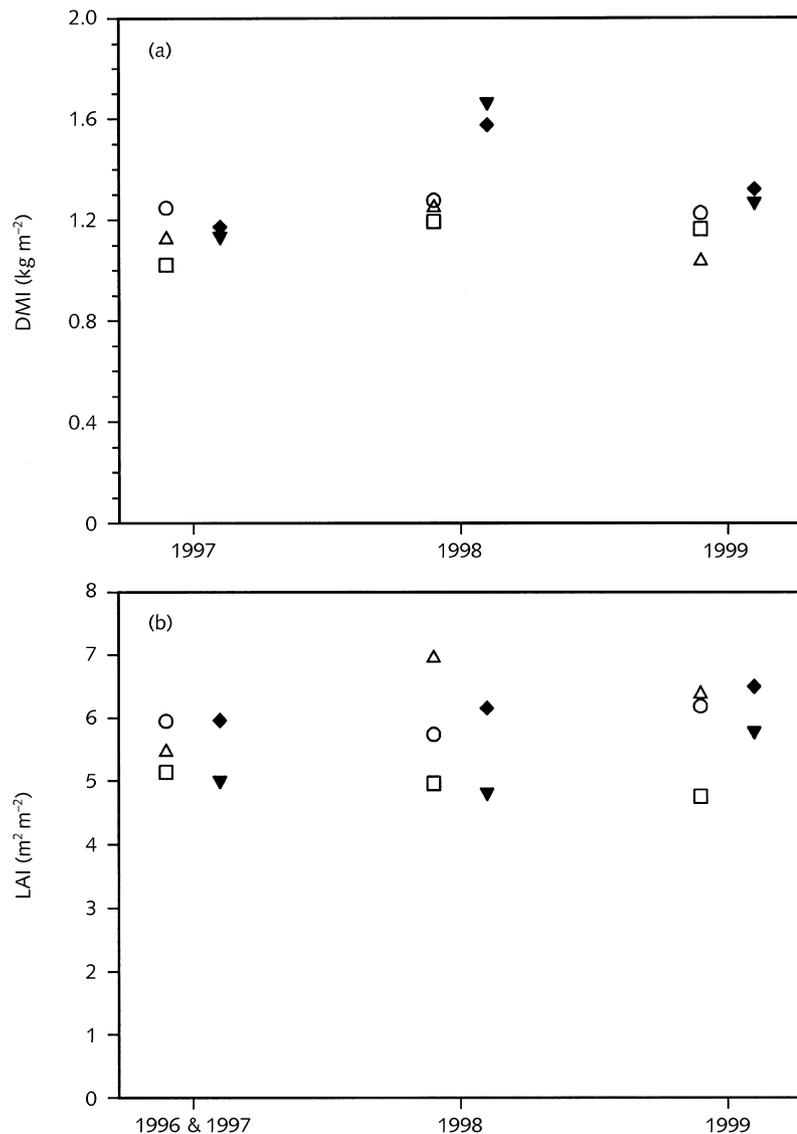

Fig. 5 (a) Dry matter increment (DMI) (aboveground) per unit land area and (b) leaf area index (LAI) by plot during the pretreatment years (1996, 1997) and 2 yr of CO_2 enrichment. Open symbols are for plots in ambient [CO_2] (open square, plot 3; open circle, plot 4; open triangle, plot 5). Closed symbols are for plots in elevated [CO_2] (closed triangle, plot 1; closed triangle, plot 2).

Table 2 Estimates of above-ground dry matter increment (DMI) and the ratio of DMI in elevated vs. ambient [CO₂] (E/A) using different allometric relationships to predict tree (bole annd branch) dry mass from basal area (BA), taper (T), and height (H). The regressions including T are based on 18 harvested trees; those without T are based on 22 trees. In the last model, the estimate is adjusted by the wood density (d) in the increment relative to density of trees used in the regression. Only models in which all coefficients were highly significant are shown

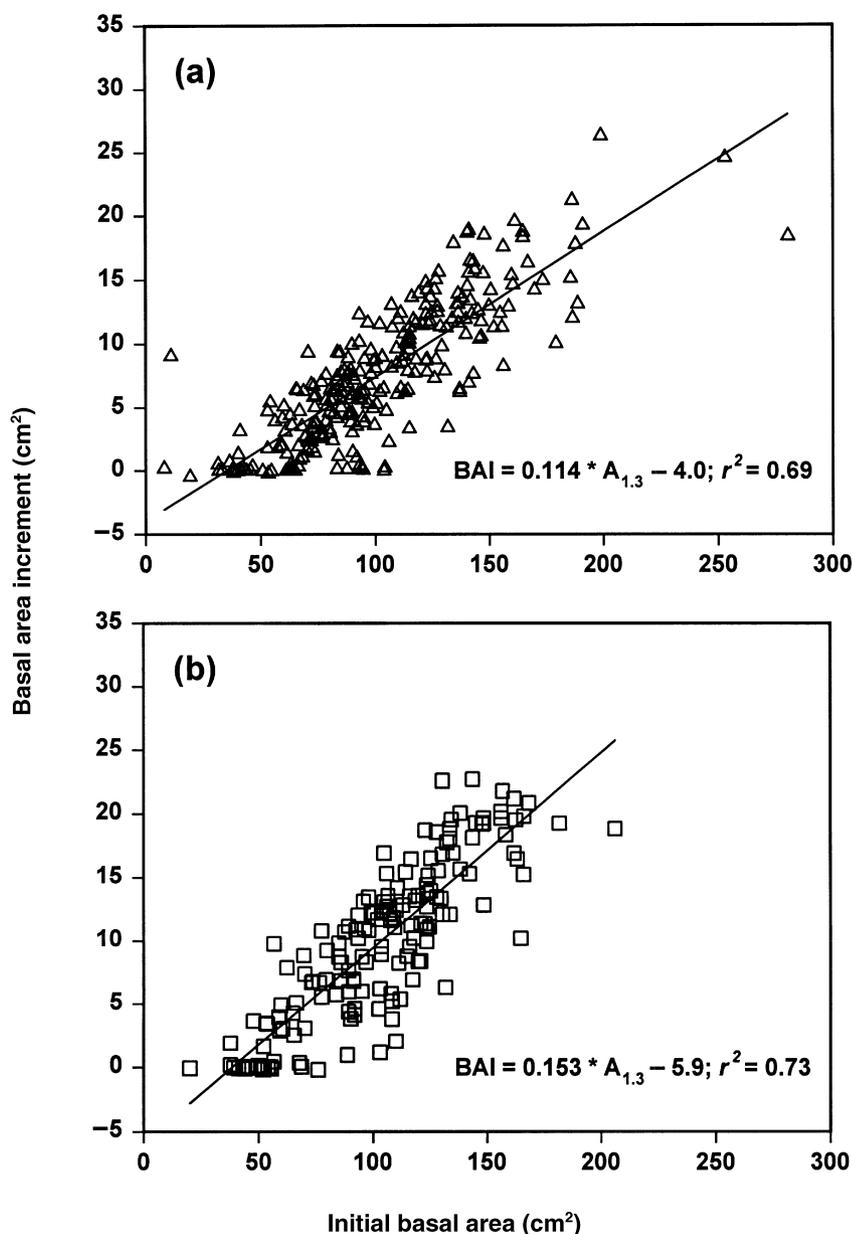| Model	r^2	DMI (kg m^{-2}) in ambient [CO₂]			E/A		
		1997	1998	1999	1997	1998	1999
f (BA)	0.91	0.782	0.808	0.699	1.016	1.195	1.070
f (BA, T)	0.95	0.846	0.870	0.794	1.015	1.381	1.177
f (BA*H)	0.94	1.114	1.299	1.138	0.962	1.147	1.050
f (BA*H, T)	0.97	1.072	1.211	1.150	0.976	1.269	1.111
f (BA*H, T) * d	0.97	1.019	1.140	1.083	1.019	1.328	1.150

Fig. 6 Relationship between basal area increment (BAI) of individual trees during 1998 and their basal area ($A_{1.3}$) at the start of the experiment in 1997. (a) Trees in ambient [CO₂] (plots 3, 4, and 5); (b) trees in elevated [CO₂] (plots 1 and 2).

between plots, and the stand-level response to CO_2 cannot, for example, be ascribed to the response of a few large trees. The response to CO_2 also was uniform with respect to distance from plot center and azimuth (not shown), indicating that there were no artifacts of differential CO_2 exposure.

Discussion

The responses of tree growth to elevated [CO_2] have been demonstrated many times, mostly in studies of several months to several years duration with seedlings and young saplings. These studies were designed to inform us about how forests will respond to a gradually changing atmosphere over decades and the feedback that forests provide to the atmosphere through the global carbon cycle. The experimental approach, however, has necessarily been to examine the responses of components of the forest ecosystem such as individual trees and specific processes. The current challenge is to measure the integrated response of an intact forest with a focus on stand-level mechanisms. We must determine whether relatively short-term studies of individual plants adequately represent the responses that will obtain in forests that have fully acclimated to a higher CO_2 concentration. Given this perspective, it is especially important that the initial responses to a large step-change in [CO_2] be interpreted cautiously.

The 24% increase in aboveground tree growth during the first 2 yr of exposure to 533 ppm CO_2 is consistent with the 29–30% increase that has been observed in experiments with tree seedlings exposed to higher concentrations (600–700 ppm) of CO_2 (Wullschleger *et al.*, 1997; Curtis and Wang, 1998). The 24% increase in growth per unit leaf area in our sweetgum experiment also is consistent with the responses of young saplings in open-top chambers (Norby *et al.*, 1999) and in support of our hypothesis that this response would be sustained after canopy closure. Comparable results from forest stands include the 25% increase in above-ground growth rate (relative BAI) of loblolly pine trees exposed to *c.* 560 ppm CO_2 for 2 yr (DeLucia *et al.*, 1999). The tree-ring record of a *Quercus ilex* stand exposed for 35 yr to elevated [CO_2] in the vicinity of a natural CO_2 spring in Italy, as reported by Hättenschwiler *et al.* (1997), apparently showed a sustained 19% increase in BAI relative to trees in a reference plot (interpretation of Norby *et al.*, 1999), but more extensive tree ring sampling at the site showed no response to elevated [CO_2] (Tognetti *et al.*, 2000).

Conclusions from our sweetgum experiment based on the combined response over 2 yr are not robust because the response was much larger (33%) in the first year than the second (15%). While it might be considered noteworthy that there was a fast response in this system, the fast response is not relevant to global change analysis because the step-change in [CO_2] from 370 to 533 ppm in the experiment cannot be considered an analog for the gradual increase in [CO_2] in the atmosphere. Nevertheless, these results indicate that large trees have the capacity to respond to elevated [CO_2] just as much as younger trees that are in exponential growth.

The loss of a significant response in the second year of exposure cannot be taken as evidence that there will be no sustained response in this system. The long-term response remains unresolved – clearly more than 2 yr of data are necessary to describe long-term response in a forest system. However, it is important to suggest explanations for the difference between the two years and thereby provide an analytical framework for future analyzes. We suggest and evaluate five possible reasons that the large and statistically significant increase in growth that occurred in the first year of exposure to elevated [CO_2] did not occur in the second year:

1. Recognizing that the rate of leaf photosynthesis was higher in elevated [CO_2] in both years and throughout the canopy, with no evidence for acclimation or down regulation (C. A. Gunderson, unpublished), it might still have been the case that canopy photosynthesis acclimated to elevated [CO_2] in the second year through a reduction in LAI. A compensatory reduction in relative plant leaf area was the explanation for the limited aboveground growth response of *Liriodendron tulipifera* saplings to elevated [CO_2] (Norby *et al.*, 1992). However, LAI of our sweetgum stand has not responded to [CO_2], and the reduced growth response cannot be ascribed to reduced LAI.

2. Ecosystem models (Mooney *et al.*, 1999) and general speculation (Bazzaz & Fajer, 1992) suggest that short-term growth increases in forests in response to elevated [CO_2] will not be sustained because of nutrient feedbacks that limit growth. It seems unlikely that a nutrient feedback could have occurred so quickly in this relatively nutrient-rich system, and preliminary measurements have suggested that no changes in nutrient cycling have yet occurred (Johnson *et al.*, 2001).

3. The first-year response could have been an artifact of the 'square wave' phenomenon (the large step-change in [CO_2]), and the second (or subsequent) year response is more indicative of the eventual long-term response. The response may have been driven by conditions set in the year before exposure, such as the number of leaf primordia in the overwintering buds or the quantity of stored nutrients or carbohydrates. The long-term response of forests to global change will be driven by a year-to-year [CO_2] increase of about 1.5 ppm, whereas the first year increase in this experiment was 144 ppm Although there are no observations that support the 'square-wave' explanation, it cannot be dismissed until there are more years of data.

4. The difference in response might be attributable to differences in weather during the 2 yr and an interaction between the influences of weather and [CO_2]. For example, the responses to elevated [CO_2] during an 8-yr experiment in a native tallgrass prairie varied substantially depending on year-to-year differences in the degree of drought (Owensby *et al.*, 1999). In our sweetgum study, most of the effect of elevated [CO_2] occured in mid-summer when growth rates were highest. However, peak growth rates in ambient [CO_2] were similar each year, which argues against important interannual differences

in growing conditions that could explain the difference in response to $[CO_2]$ in 1998 and 1999. There were small differences in early season growth response (the onset of basal area growth was delayed in elevated $[CO_2]$ in 1999), but there were no obvious weather conditions to explain this observation. Again, a longer-term record is needed to elucidate $CO_2 \times$ weather interactions.

5. If there was a change in carbon allocation in CO_2-enriched trees between the first and second years of exposure, the response of net primary productivity might not be reflected in aboveground stem mass increment. For example, a relative increase in fine root production, as was suggested in an experiment with *L. tulipifera* saplings (Norby *et al.*, 1992) might have been at the expense of carbon storage in stem wood, much as predicted by the ecosystem model G'DAY in response to decreased foliar [N] in elevated $[CO_2]$ (Kirschbaum *et al.*, 1994). This hypothesis will be evaluated when the data on fine root production and other components of net primary productivity are available.

An important rationale for investigating the responses to elevated $[CO_2]$ in a closed-canopy forest stand was the opportunity to determine whether forest LAI changes with $[CO_2]$. Leaf area is an important controller of forest growth, as it represents the opportunity for interception of solar radiation. Differences in leaf area development can explain much of the variation in the growth response to elevated $[CO_2]$ of young trees in open-top chambers (Norby, 1996; Norby *et al.*, 1999). However, leaf area responses in smaller-scale systems, such as experiments in open-top chambers, primarily reflect developmental patterns and do not predict LAI after canopy closure. The sweetgum trees in this experiment had been in a linear growth phase for several years before the initiation of CO_2 exposure, and LAI was relatively stable. Hence, growth responses can be evaluated without the confounding influence of developmental rate during exponential growth. We saw no evidence for an effect of elevated $[CO_2]$ on LAI of the sweetgum stand during the 2-yr exposure, and none of the growth response (or change in growth response between 1998 and 1999) can be ascribed to effects on LAI. The response of LAI in the *Pinus taeda* FACE experiment currently is uncertain; there may be a small but nonsignificant increase in plant area index in elevated $[CO_2]$ (Lichter *et al.*, 2000). No effects of $[CO_2]$ on LAI were apparent in the trees at the Italian CO_2 springs sites (Hättenschwiler *et al.*, 1997).

The evaluation of above-ground growth response in this experiment was dependent on the establishment of an appropriate allometric relationship. We have confidence in this approach because BA of every tree on the experimental plots was measured (no sampling error) and, since there were no pretreatment differences between plots, there was no need to express the results in relative terms. The allometric relationship we used was robust and incorporated elements that might be altered by CO_2 enrichment. Nevertheless, the uncertainty in this approach is apparent in the variation in estimated biomass and relative effect of $[CO_2]$ on biomass increment caused by using different regression equations (Table 2). For example, the allometric relation with BA was very acceptable ($r^2 = 0.91$) but resulted in estimates of DMI that were 30–55% different from the values we used in this analysis. Regional assessments of terrestrial carbon stocks and fluxes are similarly dependent on allometric relationships between DM (or carbon content) and an easily measured parameter such as diameter or BA (Whittaker & Woodwell, 1968; Wirth *et al.*, 1999). These relationships are then applied across broad regions (Dixon *et al.*, 1994; Schulze *et al.*, 1999), introducing additional errors. It is sobering to recognize this potential for substantial error in assessments of forest carbon budgets given their importance in the quantification of the global carbon budget.

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