Annual basal area increment and growth duration of *Pinus taeda* in response to eight years of free-air carbon dioxide enrichment

DAVID J. P. MOORE*[1], SUSANNE AREF†[2], RINGO M. HO†[3], JEFFREY S. PIPPEN‡, JASON G. HAMILTON§ and EVAN H. De LUCIA¶

*Program in Ecology and Evolutionary Biology, University of Illinois at Urbana – Champaign, Urbana, IL 61801, USA, †Department of Statistics, University of Illinois at Urbana – Champaign, Urbana, IL 61801, USA, ‡Nicholas School of the Environment and Earth Sciences, Duke University, Durham, NC 27708, USA, §Department of Biology, Ithaca College, Ithaca, NY 14850, USA, ¶Department of Plant Biology, University of Illinois at Urbana – Champaign, Urbana, IL 61801, USA

Abstract

Rising CO_2 is predicted to increase forest productivity, although the duration of the response and how it might be altered by variation in rainfall, temperature and other environmental variables are not well understood. We measured the basal area of rapidly growing *Pinus taeda* trees exposed to free-air CO_2 enrichment for 8 years and used these measurements to estimate monthly and annual growth. We used these measurements in a statistical model to estimate the start and end of growth in each year. Elevated CO_2 increased the basal area increment (*BAI*) of trees by 13–27%. In most years, exposure to elevated CO_2 increased the growth rate but not the duration of the active growth period. With the exception of 1 year following an extreme drought and a severe ice storm, *BAI* was positively correlated with the amount of rainfall during the active growth period. The interannual variation in the relative enhancement of *BAI* caused by elevated CO_2 was strongly related to temperature and rainfall, and was greatest in years with high vapor pressure deficit. There was no evidence of a systematic reduction in the stimulation of growth during the first 8 years of this experiment, suggesting that the hypothesized limitation of the CO_2 response caused by nitrogen availability has yet to occur.

Key words: carbon gain, climate change, dendrometer bands, forests, phenology, precipitation, stem growth, temperature

Received 8 August 2005; revised version received 14 March 2006; acceped 23 March 2006

Introduction

Forest ecosystems exchange vast quantities of CO_2 with the atmosphere and represent a large global sink for carbon (Schlesinger, 1997). Because trees use the C_3 photosynthetic pathway, it has been hypothesized that increasing amounts of CO_2 in the atmosphere, derived primarily from human activities, will cause a substantial increase in forest productivity (Strain & Bazzaz, 1983). This hypothesis can now be tested in large stature forests at realistic spatial and temporal scales using free-air CO_2 enrichment (FACE) technology (Hendrey & Kimball, 1994; Hendrey *et al.*, 1999). For rapidly growing pine, sweetgum, and poplar stands, exposure to CO_2 concentrations predicted for 2050 caused a median increase of 23% in net primary production (*NPP*; DeLucia *et al.*, 1999, 2005; Norby *et al.*, 2002; 2005; Calfapietra *et al.*, 2003). However, these analyses are limited to 3–5 years of CO_2 exposure and the stimulation of growth may decrease with time as nitrogen and other nutrients become limiting (Reich *et al.*, 1997; Oren *et al.*, 2001; Finzi *et al.*, 2002; Luo *et al.*, 2004).

In many models of the global carbon cycle, plant growth, and productivity increase with rising levels of

Correspondence: Evan DeLucia, tel. + 217 333 3261, fax + 217 244 7246, e-mail: delucia@uiuc.edu
[1]Present address: Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO 80301, USA.
[2]Present address: Department of Statistics, Virginia Polytechnic Institute and State University Blacksburg, VA 24061, USA.
[3]Present address: Department of Psychology, McGill University, Montreal, QC, Canada, H3A 1B1.

atmospheric CO_2 (Cramer *et al.*, 2001), but the availability of mineral nutrients may limit potential growth enhancements at higher CO_2 concentrations (Luo & Reynolds, 1999; Medlyn *et al.*, 2000; Hungate *et al.*, 2003). Exposure of a *Pinus taeda* forest to elevated CO_2 for 6 years caused an increase in basal area (*BA*) growth and productivity (DeLucia *et al.*, 1999; Hamilton *et al.*, 2002; Schäfer *et al.*, 2003; Finzi *et al.*, 2006). However, there has been no corresponding increase in the rate of nitrogen mineralization in plots exposed to elevated CO_2 (Finzi *et al.*, 2002; 2006) and nitrogen has become increasingly immobilized in biomass and organic soil (Finzi *et al.*, 2006), suggesting that the growth stimulation may decline in the future. If nitrogen limitation causes the stimulation of growth by elevated CO_2 to diminish over time, projections of a sustained increase in the size of the terrestrial carbon sink will prove false (Hungate *et al.*, 2003; Lenton & Huntingford, 2003).

The capacity of forests to absorb atmospheric carbon may be altered by variation in weather, particularly temperature and precipitation. While a number of environmental factors affect tree growth, the potential effects of temperature and water availability on the response to elevated CO_2 rests on a firm mechanistic foundation. Based on the kinetics of the primary carboxylating enzyme, the stimulation of photosynthesis by elevated CO_2 should increase proportionally with rising temperature (Jordan & Ogren, 1984; Long, 1991). Also, many woody plants make more efficient use of water when grown in elevated CO_2 (Drake *et al.*, 1997; Curtis & Wang, 1998), so the relative stimulation in growth may be greater in times of low rainfall. Thus, fluctuations in temperature and rainfall from year to year could alter the effect of CO_2 on tree growth and productivity.

The objective of this study was to quantify the interannual variation in the effect of elevated CO_2 on growth of *P. taeda* trees and to determine whether the growth response observed previously (DeLucia *et al.*, 1999; Naidu & DeLucia, 1999; Hamilton *et al.*, 2002; Finzi *et al.*, 2006) has been sustained over 8 years. Fluctuations in the relative enhancement of tree growth are placed in the context of interannual variation in weather. A second objective was to determine if an increase in the duration of *BA* growth in trees exposed to elevated CO_2 could be responsible for part of the observed stimulation in *NPP* reported in this forest (DeLucia *et al.*, 1999; Hamilton *et al.*, 2002; Finzi *et al.*, 2006). This experiment was conducted at the Forest Atmosphere Carbon dioxide Transfer and Storage-1 (FACTS-1) research site – a long running experiment where intact forest plots are exposed to elevated CO_2 without confounding chamber effects or constraining rooting volume.

Materials and methods

Site description

The FACTS-1 research site at Duke Forest is located in the Piedmont region of North Carolina (35°58′N 79°05′W). This facility uses FACE technology to increase the CO_2 concentration in three of six experimental plots within a continuous unmanaged *P. taeda* plantation (Hendrey *et al.*, 1999). Each 30 m diameter plot consists of a circular plenum that delivers air to an array of 32 vertical pipes. The pipes extend from the forest floor to above the 18 m tall forest canopy and contain adjustable ports at 50 cm intervals that allow control of atmospheric CO_2 through the entire forest volume.

CO_2 enrichment occurred 80% of the time as it was switched off when air temperature was below 5 °C or when wind speed exceeded $5 \, \mathrm{m \, s^{-1}}$. The average CO_2 concentration (24 h average) in the three fully instrumented control plots during the first 6 years of the experiment was 386 ± 21 (SD) μmol mol^{-1} and three experimental plots were maintained at ambient plus 196 μmol mol^{-1} CO_2 ($582 \pm 79 \, \mu$mol mol^{-1}). From 2003 onwards fumigation was switched off at night leading to an average daytime CO_2 concentration of $\sim 383 \pm 26 \, \mu$mol mol^{-1} in the ambient plots while the elevated plots were maintained at plus 194 μmol mol^{-1} CO_2 ($\sim 577 \pm 80 \, \mu$mol mol^{-1}). Recent evidence suggests that there is no direct effect of elevated CO_2 on plant respiration (Davey *et al.*, 2004) and turning off the injection gas at night represented a considerable financial savings. *P. taeda* seedlings were planted in 1983 in 2.4 m × 2.4 m spacing. Since that time a number of hardwood species have become established in the understory (Naidu & DeLucia, 1999).

A dominance hierarchy has established among pines and individual crowns were classified as either emergent, codominant or suppressed based on their position relative to the average canopy height in each plot (Naidu *et al.*, 1998). When fumigation began in August 1996, *P. taeda* trees were ~ 14 m tall and comprised more than 90% of the *BA* of the stand. This analysis was restricted to the *P. taeda* as this species accounts for over 85% of *NPP* in this forest (Hamilton *et al.*, 2002), and variation in the average *BAI* of *P. taeda* was the main factor controlling variation in *NPP* ($NPP = 56.23 \times BAI + 750.08$; $R^2 = 0.79$, $P < 0.01$; Finzi *et al.*, 2006).

Tree growth

In 1996, spring-loaded stainless steel dendrometer bands for measuring circumference were fitted to the boles of trees approximately 1.4 m above ground level (Keeland & Sharitz, 1993; Naidu *et al.*, 1998; DeLucia

et al., 1999; Naidu & DeLucia, 1999). Trees were randomly selected within each of the three height classes. Circumference was measured at approximately monthly intervals on between 31 and 34 trees in each plot (105 in the ambient plots and 104 in elevated plots) representing a sample size of between 25% and 52% of the total number of pines in each plot. Tree size is expressed as BA (Naidu et al., 1998). The data set from 1996 to 2004 consisted of more than 18 000 measurements of tree BA. Monthly basal area increment ($mBAI$) was normalized to a 30-day period ($BAI_{monthly} = [BA_{t1} - BA_{t0}]/[t1 - t0] \times 30$). Annual BAI was calculated as the difference between BA from the end of 1 year to the next, where BA at the end of any given year was the average of BA measured during the winter months (November through January).

Estimating the duration of the active growth period

To determine whether the CO_2 treatment and annual variation in weather affected the timing and duration of basal area growth in P. taeda, a statistical model was used to estimate the start, end, and duration of growth in each year. A model was necessary to estimate the day that growth was initiated or ceased as BA was measured monthly. Two independent models (Proc Nlin, SAS v. 9.0, Cary, NC, USA) for the start of growth and the end of growth, respectively, were fitted to the basal area measurements of each tree for each year of the experiment (Fig. 1).

For the period before the start of growth, BA was defined as $BA = a$; and after growth started $BA = a + b$ (days) $+ c$ (days^2), where a is the initial basal area, b is the slope of the linear portion of the increase in basal

area and c is the curvature of that increase. The start day was calculated iteratively as the intersection between these two functions (Fig. 1).

The end of growth was estimated in the same way except that the end day was the intersection between the growth curve and the final basal area (Fig. 1) and curvature (c') was constrained to be $-0.5(b')/(\text{end day})$. Because the stop model estimated the end of growth asymptotically and for other considerations explained below, we defined the end of the active growth period as the day when BA was 90% of the annual maximum.

Meteorological data

To examine the potential influence of interannual variation in weather on the response of tree growth to elevated CO_2, precipitation and temperature data were compiled from measurements made at the FACTS-1 research site (from April 1997) and from the State Climate Office of North Carolina at NC State University (before April 1997, source station: Chapel Hill 2 W, NC, approximately 16 km from the field site). Other environmental variables were measured on site from April 1997 onwards. Relative humidity, soil moisture, and photosynthetically active radiation (PAR) incident on the forest canopy were measured as in Schäfer et al. (2003) and data were provided by R. Oren.

We assumed that environmental conditions immediately before the onset of basal area growth may have affected growth rate through their influence on early season carbon assimilation and water status; conversely, because growth had nearly ceased for the year, we assumed that conditions immediately before its cessation would have a small effect on the annual basal area
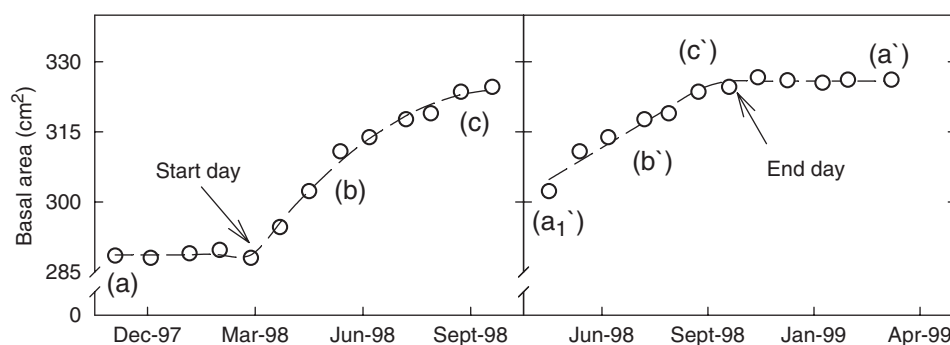

Fig. 1 Basal area (BA) for a typical Pinus taeda tree from December 1997 through April 1999. BA was calculated from measurement of bole circumference. The symbols represent measured values and the lines represent functions fit to the data. Two functions were used to describe the progression of growth from winter into summer and autumn (left panel). In winter, BA (basal area) $= a$ (constant), and during summer and autumn, $BA = a + b(\text{day}) + c(\text{day}^2)$; where b is the initial increase in tree size and c is the curvature of growth late in the season. The intersection of these two functions defined the 'start day'. The progression of growth from summer into the following winter was also described by two functions (right panel). During summer and autumn, $BA = a_1' + b'(\text{day}) + c'(\text{day}^2)$ and during the following winter, $BA = a'$. The intersection of these two functions defined the 'end day'. The 'end day' was then modified to accommodate the gradual cessation of growth late in the year (see 'Materials and methods').

increment. To calculate temperature and rainfall totals which would have the most influence on tree growth we defined the active period for basal area growth as 15 days before the onset of growth until the day the trees reached 90% of their annual maximum. Precipitation totals were estimated by summing daily rainfall measurements and the mean temperature was calculated for the same period. Monthly values for the Palmer Drought Severity Index for climate division NC 3102 were obtained from the National Climatic Data Center located in Asheville, NC.

Statistical analysis

Statistical analyses followed a randomized complete block design and were conducted with the SAS System for Windows (SAS v. 9.0). We used a repeated measures mixed model ANOVA (Proc Mixed) to estimate the fixed effects of CO_2 treatment (two levels: ambient and elevated), year (eight levels: 1997–2004) on the start, end, and duration of the active growth period. The block was considered a fixed factor while block by treatment, block by year effects were considered random and the degrees of freedom were calculated using the containment method (Littell *et al.*, 2002). The subject of the repeated measure was the individual plot and the covariance structure was modeled using a compound symmetric variance–covariance matrix. To account for variation in tree size the relationships between initial size and onset and cessation of growth were tested but were found not to contribute to the variance.

Variation in annual BAI ($cm^2 yr^{-1}$) for *P. taeda* growing under ambient and elevated CO_2 was estimated using a repeated measures mixed model ANCOVA (Proc Mixed). The year effect included each calendar year from 1997 to 2004. The covariate in the BAI model was the BAI of each tree before the commencement of fumigation in 1996. Crown class represents whether the trees were suppressed, dominant or emergent from the canopy (as defined by Naidu *et al.*, 1998), and the treatment was either elevated or ambient CO_2. The subject of the repeated measure was the individual tree and the covariance structure was modeled using a heterogeneous autoregressive variance–covariance matrix. Denominator degrees of freedom were calculated using the Kenward–Rogers approximation (Kenward & Rogers, 1997; Littell *et al.*, 2002). Upper level linear contrasts (based on the *t*-statistic) were used to test for the treatment effect in each year of the experiment.

$mBAI$ ($cm^2 m^{-1}$) was analyzed by year using the same model described previously for annual BAI except that month was substituted for year as the time interval.

The relationships of annual BAI and the log ratio of the response ratio ($\ln[BAI_{ele}/BAI_{amb}]$) to average and cumulative temperature, rainfall, cumulative soil moisture, PAR and vapor pressure deficit (VPD) were tested using one- and two-factor regression analysis (Proc Reg). Temperature and rainfall were available for the entire 8 years of the experiment and all other environmental variables were available from 1998 onwards. Unless otherwise stated, all data are presented as least square means estimated by generalized least squares within a mixed model. Error bars are 1 SE of the difference between least squared means of the treatment and control.

Results

The median duration of BA growth during the year was 162 days starting on day 81 (March 21; Table 1), and average BA was 90% of the annual maximum by day 233 (August 22; Table 1). The start of BA growth varied among years but not between ambient and elevated CO_2 treatments (Tables 1 and 2). The start of growth each year occurred when the minimum temperature was above freezing (Fig. 2), and interannual variance in the start of growth was closely related to the date of the last frost ($P < 0.05$, $R^2 = 0.61$). No relationship between other environmental variables and the timing of the end of growth was found.

Monthly BAI was not always significantly enhanced by elevated CO_2 during the growing season (Fig. 2). In some years (e.g. 1997 and 2003) the stimulation was most pronounced early in the growing season, while in 2002 the effect of elevated CO_2 was greatest later in the season (Fig. 2); the growth enhancement in the remain-

Table 1 The start, end and length of the active growth period for *Pinus taeda* growing under ambient and elevated CO_2 modeled from the change in basal area over time (Fig. 1)

Year	Start of growth (day of year) Ambient	Start of growth (day of year) Elevated	End of growth (day of year) Ambient	End of growth (day of year) Elevated	Period of active growth (days) Ambient	Period of active growth (days) Elevated
1997	82 (3)	80 (3)	252 (9)	253 (9)	173 (10)	173 (10)
1998	74 (4)	74 (4)	239 (9)	235 (9)	164 (10)	160 (10)
1999	81 (4)	80 (4)	245 (9)	255 (9)	163 (10)	175 (10)
2000	69 (3)	69 (3)	230 (9)	231 (9)	162 (10)	163 (10)
2001	99 (3)	94 (3)	204 (9)	214 (9)	107 (10)	122 (10)
2002	97 (4)	93 (4)	276 (9)	272 (9)	164 (12)	171 (12)
2003	90 (4)	91 (4)	199 (9)	199 (9)	108 (11)	108 (11)
2004	89 (4)	91 (4)	214 (9)	214 (9)	126 (11)	127 (11)

Least square means (± 1 SE) are reported and treatment differences were estimated using linear contrast statements within a mixed model ANOVA; there were no significant differences in any year (Table 2).

Table 2 Factors contributing to variation in the start of growth, the end of growth, and the length of the active growth period for *Pinus taeda* growing under ambient and elevated CO_2 estimated by a mixed model ANOVA

Source	Start of growth			End of growth			Season length		
	df	F value	P value	df	F value	P value	df	F value	P value
Block	2_2	0.92	0.5205	2_2	2.09	0.324	2_2	0.31	0.7638
Year	7_{28}	33.4	<0.0001	7_{28}	32.56	<0.0001	7_{28}	30.35	<0.0001
Treatment	1_2	0.19	0.7083	1_2	0.49	0.5551	1_2	0.65	0.5034
Year × treatment	7_{28}	0.42	0.8826	7_{28}	0.5	0.8264	7_{28}	0.51	0.8223

The year effect included each calendar year from 1997 to 2004. The treatment was either elevated or ambient CO_2. The denominator degrees of freedom are shown as a subscript beside the numerator degrees of freedom (df), F-statistic and probability (P) values are shown for each factor in the model.
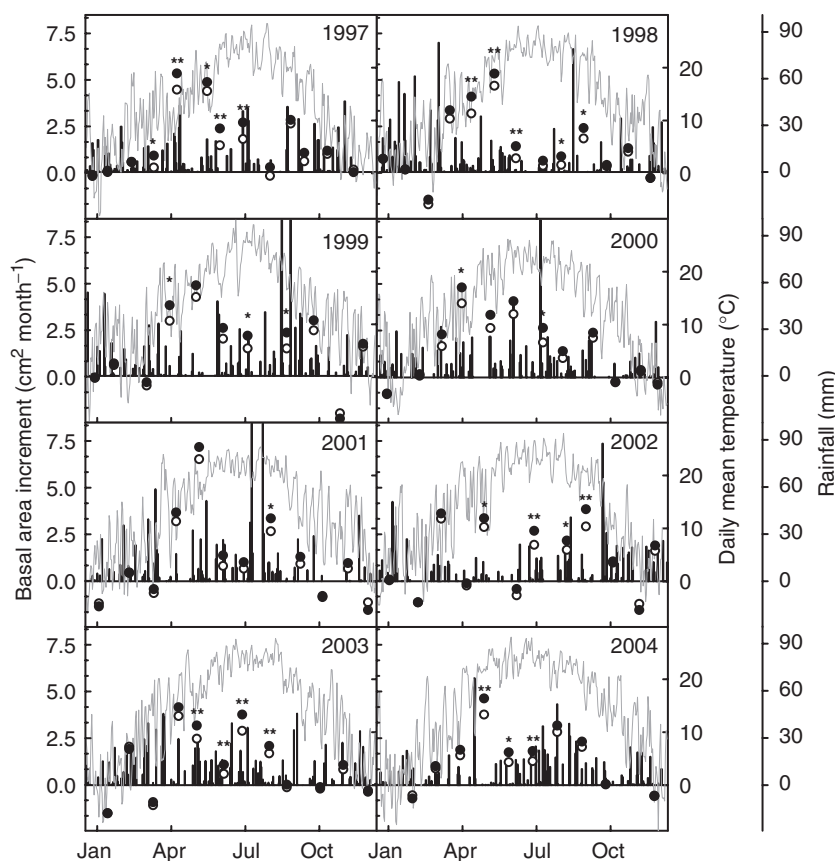

Fig. 2 Mean monthly basal area increment ($cm^2\,month^{-1}$), mean daily temperature (grey line; °C) and daily rainfall (black bars; mm) for each year of the experiment. Basal area increment of *Pinus taeda* exposed to ambient CO_2 is represented by ' ∘ ' and elevated CO_2 is shown by ' • '. Symbols for monthly *BAI* represent least square means from three independent replicate forest plots. Treatment differences at $P<0.1$ and $P<0.05$, indicated by '*' and '**', respectively, were estimated using upper level linear contrast statements within a repeated measures mixed model ANOVA conducted within each year 1997 to 2004.

ing years was more evenly distributed throughout the growing season.

Annual *BAI* varied among years and was on average higher in trees exposed to elevated CO_2 (Table 1; Fig. 3a). There was a significant stimulation of annual *BAI* in each year of the experiment that varied between 13.2%

and 27.4% (Fig. 3). Although a significant crown class by treatment interaction could not be resolved (Table 3), it appeared that the relative stimulation was greater for emergent (19%) and dominant trees (24.5%) than for the subcanopy individuals (11.4%; Fig. 4), suggesting that the smaller suppressed trees may not have been able to
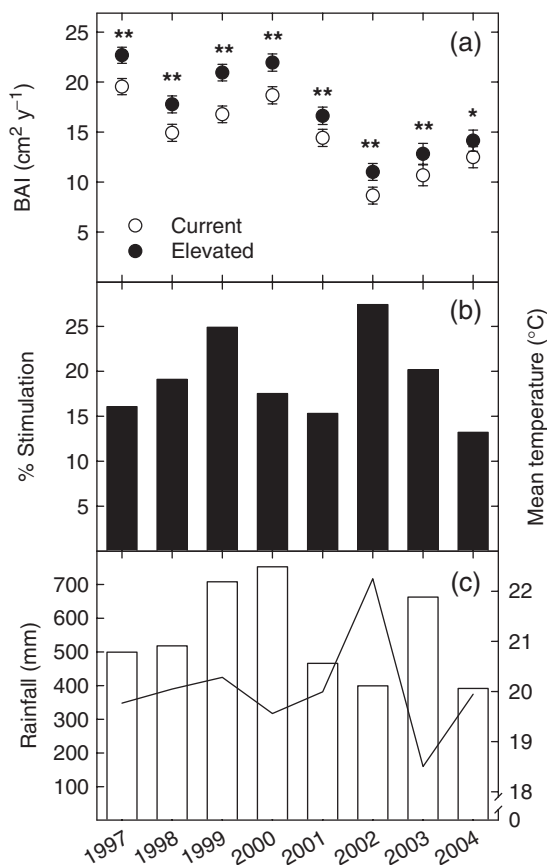
Fig. 3 The basal area increment (*BAI*) for *Pinus taeda* trees exposed to ambient CO_2 ' ○ ' and elevated CO_2 ' ● ' (a) and the percentage stimulation in *BAI* caused by elevated CO_2 (b) and the variation in total rainfall (open bars; mm) and mean temperature (black line; °C) during the active growth period (c). Symbols in panel a are least square means from three independent replicate forest plots. Error bars represent ± 1 standard error of the difference between LSmeans. Treatment differences at $P < 0.1$ and $P < 0.05$, indicated by '*' and '**', respectively, were estimated using upper level linear contrast statements within a repeated measures mixed model ANOVA (Table 1).

Table 3 Factors contributing to variation in annual basal area increment (*BAI*; $cm^2 \, yr^{-1}$) for *P. taeda* growing under ambient and elevated CO_2 estimated by a mixed model ANCOVA

Source	*BAI* df	*F* value	*P* value
Block	$2_{3.8}$	1.16	0.3966
Year	7_{36}	2.14	0.0638
Covariate × year	8_{552}	164.16	<0.0001
Treatment	$1_{2.3}$	18.48	0.0353
Year × treatment	7_{18}	1.29	0.3099
Crown class	$2_{20.1}$	0.53	0.5983
Crown class × year	$14_{35.4}$	0.53	0.8844
Crown class × treatment	$2_{11.4}$	1.15	0.3503
Year × crown class × treatment	14_{822}	1.80	0.0351

The year effect included each calendar year from 1997 to 2004. The covariate in the *BAI* model was the pretreatment basal area increment of each tree. Crown class represents whether the trees were suppressed, dominant or emergent from the canopy, and the treatment was either elevated or ambient CO_2. The numerator and denominator degrees of freedom (df), *F*-statistic and probability (*P*) value are shown for each factor in the model. Denominator degrees of freedom are shown as a subscript to the numerator denominator degrees of freedom and were calculated using the Kenward–Rogers approximation.

take full advantage of the extra CO_2 provided by the treatment. Disproportionate damage to dominant and emergent trees in the ambient plots caused by the ice storm in 2002 (McCarthy *et al.*, in press) contributed to the significant three-way interaction between the CO_2 treatment, crown class, and year (Table 3).

Temperature, rainfall, incident irradiance and soil moisture during the period of active growth varied from year to year (data not shown). Growth was positively correlated with seasonal ($R^2 = 0.46$, $P < 0.05$) but not annual rainfall. With the exception of 2002 when low water availability limited growth during the summer months (Fig. 2), the average *BAI* of trees in both treatments was positively correlated with the length of the active growing period ($R^2 = 0.56$, $P < 0.05$), cumula-

tive photosynthetic active radiation ($R^2 = 0.52$, $P < 0.05$), and cumulative temperature ($R^2 = 0.55$, $P < 0.05$), and less strongly with soil moisture ($R^2 = 0.35$, $P < 0.05$). However, many of these environmental variables were correlated with one another. The relative stimulation of *BAI* by elevated CO_2 from 1997 to 2004 was related to temperature and rainfall during the active growth period ($\ln[BAI_{ele}/BAI_{amb}] = 0.03564 \times$ [mean temperature] $+ 0.00018 \times$ [rainfall] -0.64; $R^2 = 0.64$, $P = 0.07$). When the 2003 was omitted, because it followed an extreme drought and a severe ice storm, the combination of temperature and rainfall accounted for 93% of the variation in the relative stimulation ($\ln[BAI_{ele}/BAI_{amb}] = 0.0513 \times$ [mean temperature] $+ 0.00018 \times$ [rainfall] -0.96; $R^2 = 0.93$, $P < 0.01$). Similarly, the relative growth enhancement was related to VPD integrated during the active growth period ($\ln[BAI_{ele}/BAI_{amb}] = 0.0013 \times$ [cumulative VPD] $+ 0.0279$; $R^2 = 0.87$, $P < 0.01$, 2003 omitted). For 2003, the stimulation predicted by either of these simple regression models was substantially lower than that observed.

Discussion

Exposure to elevated CO_2 caused a sustained increase in *BAI* over the first 8 years of the experiment, but the
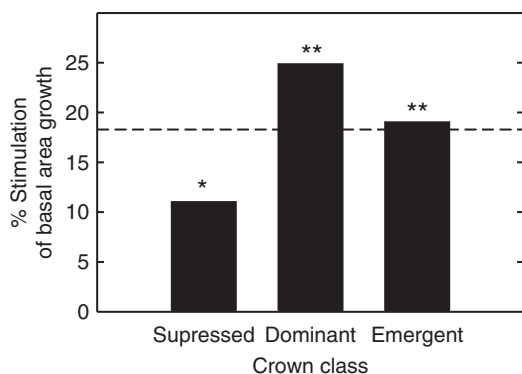
Fig. 4 The relative stimulation of basal area increment in *Pinus taeda* trees with suppressed, dominant, or emergent crowns caused by exposure to elevated CO_2 for 8 years. The mean response of all trees is shown by the dashed line. Individual crowns were classified as either emergent, co-dominant or suppressed based on their position relative to the average canopy height in each plot (Naidu *et al.*, 1998). Each bar represents the mean effect comparing trees in each crown class from three ambient and three elevated CO_2 forest plots. Treatment differences at $P < 0.1$ and $P < 0.05$, indicated by '*' and '**', respectively, were estimated using upper level linear contrast statements within a repeated measures mixed model ANOVA.

relative stimulation was modulated by year-to-year variation in weather and in the timing of growth. The effect of elevated CO_2 on *BA* growth rate was most apparent for dominant and emergent trees and least for suppressed trees. There was no evidence of a decline in the relative enhancement of tree growth by elevated CO_2 as might be expected if soil nutrients were becoming progressively more limiting, although the average enhancement (18.7%) was lower than previously reported for this *P. taeda* forest (24–26%; DeLucia *et al.*, 1999; Naidu & DeLucia, 1999; Hamilton *et al.*, 2002). This lower estimate of the percentage stimulation in basal area growth caused by CO_2 in part stems from using pretreatment tree growth rate as a covariate in the statistical analysis. Small differences in pretreatment growth rates contributed to a bias in earlier estimates of the percentage stimulation. There was no detectable effect of elevated CO_2 on either the onset or cessation of diameter growth in *P. taeda*. The growth rate of trees in each year of the experiment was stimulated by exposure to high CO_2, and this stimulation in growth rate, rather than differences in the duration of growth, contributed to the greater productivity in this forest under elevated CO_2 (Finzi *et al.*, 2006).

BA growth started after temperatures consistently were above freezing (Fig. 2) and the timing of growth was not affected by the CO_2 treatment (Table 2). While basal area growth ceased in the winter (Figs 1 and 2), *P. taeda* needles are physiologically active throughout

the year (Hymus *et al.*, 1999). We might expect photosynthetic enhancements during the winter to provide more carbohydrate to pines in elevated CO_2 and perhaps allow them to commence growth earlier, during slightly colder conditions. Although photosynthesis is much lower in the winter months (Hymus *et al.*, 1999), carbon gain in loblolly pine is sufficient to offset autotrophic respiration and maintain a positive or near zero carbon balance (Baldocchi *et al.*, 2001).

The absence of an effect of elevated CO_2 on the onset of growth (Table 1; Fig. 2) can probably be explained by two main reasons. First, the photosynthetic enhancement by elevated CO_2 increases strongly with temperature (Long, 1991; Teskey, 1995; Lewis *et al.*, 1996; Myers *et al.*, 1999; Sigurdsson *et al.*, 2002) and its effect on carbon gain is small during the cold winter months. Second, the rate of electron transport is inhibited by elevated CO_2 during the colder winter months, probably because of reduced translocation of assimilates (Hymus *et al.*, 1999). Thus, elevated CO_2 induces photoinhibition in pine needles during winter and may lead to greater frost damage (Hymus *et al.*, 1999), as seen in other evergreen species (Lutze *et al.*, 1998). Given this potentially damaging effect of elevated CO_2, it is perhaps surprising that trees do not commence growth slightly later than their ambient grown counterparts.

Although leaf area duration in crops and other tree species may be extended (Li *et al.*, 2000; Tricker *et al.*, 2005; Dermody *et al.*, 2006), exposure to elevated CO_2 did not cause a shift in the timing of either peak leaf area index or peak litterfall in this forest (H. R. McCarthy, personal communication), and we found no detectable effect of the treatment on when basal area growth ceased (Fig. 2; Table 2). The cessation of stem growth in trees is not coincident with canopy senescence; diameter growth in deciduous trees often stops in midsummer, well before leaf drop (Hanson & Weltzin, 2000; Hanson *et al.*, 2001), and in evergreen species diameter growth and needle fall are decoupled entirely. While stem growth starts in the spring and stops in late summer (Fig. 2; Table 2) the typical lifespan of a *P. taeda* needle in the Piedmont region of North Carolina is 19 months (Zhang & Allen, 1996; Finzi *et al.*, 2001) and needles remain physiologically active through the winter (Hymus *et al.*, 1999; Baldocchi *et al.*, 2001). Because species like *P. taeda* retain their needles over the winter and drop them only after a new cohort of needles is ready to sustain carbon uptake, the end of the active growth period in evergreen plants is unlikely to be altered by elevated CO_2.

The availability of water is an important determinant of plant growth and productivity (Kozlowski *et al.*, 1991; Arneth *et al.*, 1998; Eamus, 2003). However, at a given location interannual variation in *NPP* seldom is

strongly correlated with annual rainfall (Knapp & Smith, 2001; Eamus, 2003; Weltzin *et al.*, 2003), instead the timing of rainfall events is more important (Hanson & Weltzin, 2000). There was no correlation between annual precipitation or soil moisture and *BAI* in this study. During winter dormancy growth is uncoupled from rainfall as transpiration is low and more water is lost by evaporation and run-off than used for growth. Even by limiting the analysis to the period of active diameter growth, no clear correlation between *BAI* and rainfall or soil moisture was observed in ambient and elevated plots. However, if data for 2003 were omitted, *BAI* was positively correlated with rainfall ($R^2 = 0.46$, $P < 0.01$). There was a severe drought in 2002 (the Palmer Drought Severity Index during the growing season was -3.7) that caused unusually high litterfall (Finzi *et al.*, 2006) and may have increased the mortality of fine roots. In addition, an ice storm in the winter of 2002 caused widespread needle loss and damage to leaders and branches and this was more severe in ambient plots (McCarthy *et al.*, in press). These two severe disturbances may have suppressed growth rates in 2003 even though rainfall was abundant.

In many species a reduction in stomatal conductance and lower rates of transpiration contribute to a greater relative stimulation of growth by elevated CO_2 under dry conditions (Drake *et al.*, 1997; Curtis & Wang, 1998). In this study, elevated CO_2 had no effect on the relationship between tree growth and rainfall or soil moisture. Stomatal conductance and transpiration in *P. taeda* are unresponsive to elevated CO_2 (Teskey, 1995; Pataki *et al.*, 1998; Ellsworth, 1999; Schäfer *et al.*, 2002) so for this species it is not likely to have a disproportionate effect on growth during times of low rainfall.

Enhanced photosynthesis is the primary mechanism leading to increased growth rates for *P. taeda* exposed to elevated CO_2. Photosynthesis in *P. taeda* was enhanced by an average of 60% from 1998 to 2002 (Crous & Ellsworth, 2004). Physiological theory (Long, 1991) and empirical observations (Teskey, 1995; Lewis *et al.*, 1996; Myers *et al.*, 1999; Sigurdsson *et al.*, 2002) indicate that exposure to elevated CO_2 disproportionately stimulates carbon gain at high temperatures. Increased temperature reduces the solubility of CO_2 in water and also reduces the specificity of the primary carboxylating enzyme (ribulose-1,5-bisphosphate carboxylase-oxygenase) for CO_2 (Jordan & Ogren, 1984) leading to increased photorespiration and less carbon gain. Photorespiration increases more rapidly than photosynthesis in *P. taeda* from 25 to 35 °C (Samuelson & Teskey, 1991), a similar range of temperatures experienced during the middle of the growing season throughout this experiment (the average July temperature was 24.5 °C and the average maximum July temperature was 30.3 °C). As

such the suppression of photorespiration by elevated CO_2 becomes more important as temperature increases.

The growth stimulation by elevated CO_2 appeared to track mean temperature during the active growth period for the first 6 years of the experiment (Fig. 3). However, the variation in temperature (± 4 °C) was insufficient to explain such large differences in the stimulation of growth ($\pm 14\%$). Typically, percent increases in growth caused by elevated CO_2 are less than the observed increase in photosynthesis (Ainsworth & Long, 2005). Based on Long (1991) an increase in mean temperature from 19.5 to 22.5 °C should increase the stimulation of net photosynthesis by approximately 8%. A multiple linear regression including temperature and rainfall during the active growth period explained most of the variation in the stimulation of growth from 1997 to 2004 ($R^2 = 0.64$, $P = 0.07$). If the data for 2003 were omitted because this year followed an extreme drought and an ice storm the regression explained considerably more of the variation in growth rate ($R^2 = 0.93$, $P < 0.01$).

Because stomatal conductance does not respond to elevated CO_2 (Ellsworth, 1999) the ratio of intracellular leaf [CO_2] to that in ambient air should decline with increasing VPD in trees regardless of the concentration of CO_2 in the atmosphere. In addition, only slight differences in the average maximum rate of carboxylation are caused by the treatment (Crous & Ellsworth, 2004). Consequently, when VPD is high and stomatal conductance is low, a greater relative stimulation of net photosynthesis is observed compared with moist cool conditions when conductance is high (Ellsworth, 1999). We found that with the exception of 2003 the relative stimulation of growth was positively related to VPD integrated across the period of active growth in each year ($R^2 = 0.87$, $P < 0.05$), which is consistent with the expected stimulation in photosynthesis.

The relative stimulation of growth in 2003 was higher than we would predict from physiological theory driven by any combination of environmental variables. This may be because canopy removal by the ice storm in the winter of 2002 was less severe in the elevated plots than in the ambient plots. It is important to note that several of the environmental variables were correlated and as such we cannot conclude that any one factor accounted for the interannual variation in the CO_2 effect. We have highlighted those variables that have a well-established physiological effect on photosynthesis and so are more likely to alter the treatment effect from year to year. It appears that the interannual variation in relative growth enhancement caused by elevated CO_2 can be explained from physiological principles.

Elevated CO_2 caused a significant enhancement of *BAI* in each year (Fig. 3a) but dominant and emergent trees responded more strongly than suppressed trees

(Fig. 4). Competitively suppressed trees had limited access to light and nutrients because of their small size and subordinate canopy position. McDonald *et al.* (2002) also found that competitively suppressed *Populus tremuloides* Michx. trees responded less to elevated CO$_2$ than competitively advantaged trees. Because *P. taeda* trees grew more in elevated CO$_2$ and consequently used more nutrients (Finzi *et al.*, 2002) it is possible that the suppressed individuals would be more competitively disadvantaged in elevated CO$_2$ than in ambient CO$_2$.

The sustained enhancement of basal area growth seen in this forest is not common to all multiyear elevated CO$_2$ experiments. The initial stimulation in above ground stem growth diminished substantially in a *Liquidambar styraciflua* forest after 3 years of CO$_2$ exposure, as trees allocated new carbon to the production of fine roots (Norby *et al.*, 2004). Similarly, only a transient increase in stem growth was observed in 10 trees exposed to elevated CO$_2$ in an old growth European forest, despite significant enhancements in photosynthetic rate (Körner *et al.*, 2005). While the increase in *NPP* cause by elevated CO$_2$ in this *P. taeda* forest was driven by a combination of increased wood increment and aboveground litterfall (Hamilton *et al.*, 2002), increased productivity in the *L. styraciflua* forest was driven by greater allocation to fine roots in elevated CO$_2$ (Norby *et al.*, 2004; DeLucia *et al.*, 2005). Because of this difference in allocation the fate of additional carbon fixed by these two contrasting forest types will likely be very different. Although it is now clear that *NPP* of young actively growing forests is stimulated by elevated CO$_2$ (Norby *et al.*, 2005), questions still remain as to the long-term fate of extra carbon fixed annually, especially in complex forest ecosystems (Körner *et al.*, 2005).

Enhanced *NPP* reported previously for this *P. taeda* forest (DeLucia *et al.*, 1999, 2005; Hamilton *et al.*, 2002; Finzi *et al.*, 2006) was caused by an increase in growth rate rather than an increase in the duration of growth. Based on analyses up to 2002, trees grown in elevated CO$_2$ accumulate nitrogen in biomass at a faster rate than their ambient grown counterparts, and depending on future changes in ecosystem C : N ratio and net nitrogen mineralization rates, the CO$_2$ effect on growth and productivity may diminish in coming years (Finzi *et al.*, 2006). However, for the first 8 years of this experiment there has been a consistently positive effect of CO$_2$ on *P. taeda* growth. Much of the variation in the growth enhancement was explained by rainfall, temperature, and VPD during the active growth period. As there was no evidence that the growth stimulation abated with time, the putative N limitations to growth have not yet engaged.

References

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO$_2$ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO$_2$. *New Phytologist*, **165**, 351–371.

Arneth A, Kelliher FM, McSeveny TM *et al.* (1998) Net ecosystem productivity, net primary productivity and ecosystem carbon sequestration in a *Pinus radiata* plantation subject to soil water deficit. *Tree Physiology*, **18**, 785–793.

Baldocchi DD, Falge E, Gu L *et al.* (2001) FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor and energy flux densities. *Bulletin of the American Meteorological Society*, **82**, 2415–2435.

Calfapietra C, Gielen B, Galema ANJ *et al.* (2003) Free-air CO$_2$ enrichment (FACE) enhances biomass production in a short-rotation poplar plantation. *Tree Physiology*, **23**, 805–814.

Cramer W, Bondeau A, Woodward FI *et al.* (2001) Global response of terrestrial ecosystem structure and function to CO$_2$ and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.

Crous KY, Ellsworth DS (2004) Canopy position affects photosynthetic adjustments to long-term elevated CO$_2$ concentration (FACE) in a mature *Pinus taeda* L. fosest. *Tree Physiology*, **24**, 961–970.

Curtis PS, Wang XZ (1998) A meta-analysis of elevated CO$_2$ effects on woody plant mass, form, and physiology. *Oecologia*, **113**, 299–313.

Davey PA, Hunt S, Hymus GJ *et al.* (2004) Respiratory oxygen uptake is not decreased by an instantaneous elevation of [CO$_2$], but is increased by long-term growth in the field at elevated [CO$_2$]. *Plant Physiology*, **134**, 520–527.

DeLucia EH, Hamilton JG, Naidu SL *et al.* (1999) Net primary production of a forest ecosystem with experimental CO$_2$ enrichment. *Science*, **284**, 1177–1179.

DeLucia EH, Moore DJ, Norby RJ (2005) Contrasting responses of forest ecosystems to rising atmospheric CO$_2$: implications for the global C cycle. *Global Biogeochemical Cycles*, **19**, GB3006, doi:10.1029/2004GB002346.

Dermody O, Long SP, DeLucia EH (2006) How does elevated CO_2 or ozone affect LAI of soybean when applied independently? *New Phytologist*, **169**, 145–155.

Drake BG, GonzalezMeler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO_2? *Annual Review of Plant Physiology and Plant Molecular Biology*, **48**, 609–639.

Eamus D (2003) How does ecosystem water balance affect net primary productivity of woody ecosystems? *Functional Plant Biology*, **30**, 187–205.

Ellsworth DS (1999) CO_2 enrichment in a maturing pine forest: are CO_2 exchange and water status in the canopy affected? *Plant Cell and Environment*, **22**, 461–472.

Finzi AC, Allen AS, DeLucia EH *et al.* (2001) Forest litter production, chemistry, and decomposition following two years of free-air CO_2 enrichment. *Ecology*, **82**, 470–484.

Finzi AC, DeLucia EH, Hamilton JG *et al.* (2002) The nitrogen budget of a pine forest under free air CO_2 enrichment. *Oecologia*, **132**, 567–578.

Finzi AC, Moore DJP, DeLucia EH *et al.* (2006) Progressive N Limitation in the Duke Forest FACE Experiment: a six year synthesis. *Ecology*, **87**, 15–25.

Hamilton JG, DeLucia EH, George K *et al.* (2002) Forest carbon balance under elevated CO_2. *Oecologia*, **131**, 250–260.

Hanson PJ, Todd DE, Amthor JS (2001) A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and throughfall. *Tree Physiology*, **21**, 345–358.

Hanson PJ, Weltzin JF (2000) Drought disturbance from climate change: response of United States forests. *Science of the Total Environment*, **262**, 205–220.

Hendrey GR, Ellsworth DS, Lewin KF *et al.* (1999) A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO_2. *Global Change Biology*, **5**, 293–309.

Hendrey GR, Kimball BA (1994) The Face Program. *Agricultural and Forest Meteorology*, **70**, 3–14.

Hungate BA, Dukes JS, Shaw MR *et al.* (2003) Nitrogen and climate change. *Science*, **302**, 1512–1513.

Hymus GJ, Ellsworth DS, Baker NR *et al.* (1999) Does free-air carbon dioxide enrichment affect photochemical energy use by evergreen trees in different seasons? A chlorophyll fluorescence study of mature Loblolly Pine. *Plant Physiology*, **120**, 1183–1191.

Jordan DB, Ogren WL (1984) The CO_2/O_2 specificity of ribulose 1,5-bisphosphate carboxylase oxygenase – dependence on ribulosebisphosphate concentration, pH and temperature. *Planta*, **161**, 308–313.

Keeland BD, Sharitz RR (1993) Accuracy of tree growth measurements using dendrometer bands. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **23**, 2454–2457.

Kenward MG, Roger JH (1997) Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics*, **53**, 983–997.

Knapp AK, Smith MD (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science*, **291**, 481–484.

Körner C, Asshoff R, Bignucolo O *et al.* (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. *Science*, **309**, 1360–1362.

Kozlowski TT, Kramer PJ, Pallary SG (1991) *The Phsyiological Ecology of Woody Plants*. Academic Press Inc., San Diego, CA, USA.

Lenton TM, Huntingford C (2003) Global terrestrial carbon storage and uncertainties in its temperature sensitivity examined with a simple model. *Global Change Biology*, **9**, 1333–1352.

Lewis JD, Tissue DT, Strain BR (1996) Seasonal response of photosynthesis to elevated CO_2 in loblolly pine (*Pinus taeda* L.) over two growing seasons. *Global Change Biology*, **2**, 103–114.

Littell RC, Stroup WW, Freund RJ (2002) *SAS for Linear Models*, 4th Edn. SAS Publishing, Wiley-Interscience.

Li JH, Dijkstra P, Hymus GJ *et al.* (2000) Leaf scenescence of *Quercus myrtifolia* as affected by long-term CO_2 enrichment in its native environment. *Global Change Biology*, **6**, 727–734.

Long SP (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations – has its importance been underestimated? *Plant Cell and Environment*, **14**, 729–739.

Luo YQ, Reynolds JF (1999) Validity of extrapolating field CO_2 experiments to predict carbon sequestration in natural ecosystems. *Ecology*, **80**, 1568–1583.

Luo YQ, Su B, Currie WS *et al.* (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience*, **54**, 731–739.

Lutze JL, Roden JS, Holly CJ *et al.* (1998) Elevated atmospheric [CO_2] promotes frost damage in evergreen tree seedlings. *Plant Cell and Environment*, **21**, 631–635.

McCarthy H, Oren R, Johnsen KH *et al.* (in press) Ice storm impacts on carbon sequestration under current and future CO_2 atmosphere. *Journal of Geophysical Research – Atmospheres*.

McDonald EP, Kruger EL, Riemenschneider DE *et al.* (2002) Competitive status influences tree-growth responses to elevated CO_2 and O-3 in aggrading aspen stands. *Functional Ecology*, **16**, 792–801.

Medlyn BE, McMurtrie RE, Dewar RC *et al.* (2000) Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO_2 concentration. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **30**, 873–888.

Myers DA, Thomas RB, Delucia EH (1999) Photosynthetic capacity of loblolly pine (*Pinus taeda* L.) trees during the first year of carbon dioxide enrichment in a forest ecosystem. *Plant Cell and Environment*, **22**, 473–481.

Naidu SL, DeLucia EH (1999) First-year growth response of trees in an intact forest exposed to elevated C_2. *Global Change Biology*, **5**, 609–613.

Naidu SL, DeLucia EH, Thomas RB (1998) Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **28**, 1116–1124.

Norby RJ, DeLucia EH, Gielen B *et al.* (2005) Forest response to elevated CO_2 is conserved across a broad range of pro-

ductivity. *Proceedings of the National Academy of Science*, **102**, 18052–18056.

Norby RJ, Hanson PJ, O'Neill EG *et al.* (2002) Net primary productivity of a CO$_2$-enriched deciduous forest and the implications for carbon storage. *Ecological Applications*, **12**, 1261–1266.

Norby RJ, Ledford J, Reilly CD *et al.* (2004) Fine-root production dominates response of a deciduous forest to atmospheric CO$_2$ enrichment. *Proceedings of the National Academy of Sciences*, **101**, 9689–9693.

Oren R, Ellsworth DS, Johnsen KH *et al.* (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO$_2$-enriched atmosphere. *Nature*, **411**, 469–472.

Pataki DE, Oren R, Tissue DT (1998) Elevated carbon dioxide does not affect average canopy stomatal conductance of *Pinus taeda* L. *Oecologia*, **117**, 47–52.

Reich PB, Grigal DF, Aber JD *et al.* (1997) Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology*, **78**, 335–347.

Samuelson LJ, Teskey RO (1991) Net photosynthesis and leaf conductance of loblolly-pine seedlings in 2-percent and 21-percent oxygen as influenced by irradiance, temperature and provenance. *Tree Physiology*, **8**, 205–211.

Schäfer KVR, Oren R, Ellsworth DS *et al.* (2003) Exposure to an enriched CO$_2$ atmosphere alters carbon assimilation and allocation in a pine forest ecosystem. *Global Change Biology*, **9**, 1378–1400.

Schäfer KVR, Oren R, Lai CT *et al.* (2002) Hydrologic balance in an intact temperate forest ecosystem under ambient and elevated atmospheric CO$_2$ concentration. *Global Change Biology*, **8**, 895–911.

Schlesinger WH (1997) *Biogeochemistry: An Analysis of Global Change*, 2nd Edn. Academic Press, NY, USA.

Sigurdsson BD, Roberntz P, Freeman M *et al.* (2002) Impact studies on Nordic forests: effects of elevated CO$_2$ and fertilization on gas exchange. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **32**, 779–788.

Strain BR, Bazzaz FA (1983) Terrestrial plant communities. In: *CO$_2$ and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide. American Association for the Advancement of Science Select Symposium 8*, Boulder, CO, USA (ed. Lemon ER), pp. 177–222. American Association for the Advancement of Science, Washington, DC.

Teskey RO (1995) A field study of the effects of elevated CO$_2$ on carbon assimilation, stomatal conductance and leaf and branch growth of *Pinus taeda* trees. *Plant Cell and Environment*, **18**, 565–573.

Tricker PJ, Calfapietra C, Kuzminsky E *et al.* (2005) Long-term acclimation of leaf production, development, longevity and quality following 3 yr exposure to free-air CO$_2$ enrichment during canopy closure in *Populus*. *New Phytologist*, **162**, 413–426.

Weltzin JF, Loik ME, Schwinning S *et al.* (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience*, **53**, 941–952.

Zhang S, Allen HL (1996) Foliar nutrient dynamics of 11-year-old loblolly pine (*Pinus taeda*) following nitrogen fertilization. *Canadian Journal of Forest Research*, **26**, 1426–1439.