

Radiation-use efficiency of a forest exposed to elevated concentrations of atmospheric carbon dioxide

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Summary We compared radiation-use efficiency of growth (ϵ), defined as rate of biomass accumulation per unit of absorbed photosynthetically active radiation, of forest plots exposed to ambient ($\sim 360 \mu\text{l l}^{-1}$) or elevated ($\sim 560 \mu\text{l l}^{-1}$) atmospheric CO_2 concentration ($[\text{CO}_2]$). Large plots (30-m diameter) in a loblolly pine (*Pinus taeda* L.) plantation, which contained several hardwood species in the understory, were fumigated with a free-air CO_2 enrichment system. Biomass accumulation of the dominant loblolly pines was calculated from monthly measurements of tree growth and site-specific allometric equations. Depending on the species, leaf area index (L^*) was estimated by three methods: optical, allometric and litterfall. Based on the relationship between tree height and diameter during the first 3 years of exposure, we conclude that elevated $[\text{CO}_2]$ did not alter the pattern of aboveground biomass allocation in loblolly pine. There was considerable variation in L^* estimates by the different methods; total L^* was 18–42% lower when estimated by the optical method compared with estimates from allometric calculations, and this discrepancy was reduced when optical measurements were corrected for the non-random distribution of loblolly pine foliage. The allometric + litterfall approach revealed a seasonal maximum total L^* of 6.2–7.1 with about 1/3 of the total from hardwood foliage. Elevated $[\text{CO}_2]$ had only a slight effect on L^* in the first 3 years of this study. Mean ϵ (\pm SD), calculated for loblolly pine only, was 0.49 ± 0.05 and $0.62 \pm 0.04 \text{ g MJ}^{-1}$ for trees in the ambient and elevated $[\text{CO}_2]$ plots, respectively. The 27% increase in ϵ in response to CO_2 enrichment was caused primarily by the stimulation of biomass increment, as there was only a small effect of elevated $[\text{CO}_2]$ on L^* during the initial years of fumigation. Long-term increases in atmospheric $[\text{CO}_2]$ can increase ϵ in closed-canopy forests but the absolute magnitude and duration of this increase remain uncertain.

Keywords: absorbed photosynthetically active radiation, biomass increment, free-air CO_2 enrichment, leaf area index, loblolly pine, *Pinus taeda*.

Introduction

Radiation-use efficiency (ϵ), a concept employed initially in crops research, is the quotient of cumulative biomass to ab-

sorbed radiation (Monteith 1972, 1977). Radiation-use efficiency models have been widely used to estimate productivity over large spatial scales (Gower et al. 1999). For example, Field et al. (1998) employed a model based on the conversion efficiency of solar radiation to biomass, combined with spatially resolved estimates of absorbed radiation, to calculate net primary production (NPP) of terrestrial and ocean ecosystems. Photosynthetically active radiation (PAR, 400–700 nm) absorbed by plant canopies can be estimated from satellite-derived measurements of leaf cover and solar radiation. However, estimating ϵ is problematic. Environmental variables that affect photosynthesis and its balance with respiration (e.g., temperature, soil water, humidity and atmospheric CO_2) also affect ϵ (Linder 1985, Joel et al. 1997). The potential effects of suboptimal environmental conditions on ϵ have been incorporated in some models (Potter et al. 1993, Field et al. 1998) but not others (Heinmann and Keeling 1989). To improve estimates of ϵ and obtain information about its response to environmental variables, we have determined the direct effect of elevated atmospheric CO_2 concentration ($[\text{CO}_2]$) on ϵ for a forest ecosystem.

The theoretical maximum value for ϵ is 2.5 g MJ^{-1} when calculated per total radiation absorbed or 5.0 g MJ^{-1} when calculated per absorbed PAR (Russell et al. 1989). For well-tended C_3 crops ϵ is approximately 1.5 g MJ^{-1} (total radiation; Saldarriaga and Luxmoore 1991). Conifers tend to have relatively low ϵ values, but for rapidly growing woody taxa, such as *Salix* and *Populus*, ϵ can approach values reported for crops (Cannell et al. 1987, 1988). Broad species comparisons are difficult, however, because of the myriad of methods used to express ϵ in the literature; for example, biomass accumulation has been reported as aboveground or total biomass, and radiation has been reported as absorbed or intercepted, or PAR or global.

Both the rate of biomass accumulation (numerator) and the amount of absorbed radiation (denominator) affect ϵ and are potentially responsive to projected changes in atmospheric $[\text{CO}_2]$. Human activity is driving an unprecedented increase in atmospheric $[\text{CO}_2]$, from about $280 \mu\text{l l}^{-1}$ before the Industrial Revolution to $360 \mu\text{l l}^{-1}$ today; the concentration is projected to exceed $550 \mu\text{l l}^{-1}$ by 2050 (IPCC 1996). The rate of photosynthesis for trees is limited by current atmospheric $[\text{CO}_2]$

(Sharkey 1985, Gunderson and Wullschleger 1994) and a doubling of $[\text{CO}_2]$ causes an average 54% increase in photosynthetic rate and a 31% increase in growth rate of woody plants (Curtis 1996, Curtis and Wang 1998). Thus, elevated $[\text{CO}_2]$ can potentially increase ϵ by increasing its numerator.

Leaf area index (L^*) is the main factor controlling light absorption by plant canopies and the denominator of ϵ . Unfortunately, our understanding of the potential effects of elevated $[\text{CO}_2]$ on canopy development and L^* is incomplete. By influencing the rate of leaf expansion or canopy depth (Long 1991, Eamus 1996), elevated $[\text{CO}_2]$ can potentially increase L^* , thereby countering its stimulation of ϵ through enhanced growth rates. Although elevated $[\text{CO}_2]$ accelerated the initial accumulation of leaf area by herbaceous canopies (Campbell et al. 1990, Arnone and Körner 1993, Hartz-Rubin and DeLucia 2001), these species attained the same maximum L^* . In contrast, the stimulation of L^* for small beech trees persisted into the second year (Overdieck 1993). Currently, there is no consensus for the magnitude or direction of the response of L^* to projected increases in atmospheric $[\text{CO}_2]$. Furthermore, L^* in conifer forests is difficult to estimate by optical methods, because the spatial distribution of foliage elements violates some of the assumptions of these methods (Stenberg 1996, Gower et al. 1999).

The objective of this research was to quantify the effect of elevated $[\text{CO}_2]$ on ϵ and its components (biomass increment and L^*) for a forest ecosystem. In addition, three methods for estimating L^* were compared. Forest plots were exposed to elevated $[\text{CO}_2]$ for 3 years with free-air CO_2 enrichment (FACE) technology. This technology permits precise control of atmospheric $[\text{CO}_2]$ in forest plots without substantially altering other environmental and ecological variables.

Materials and methods

Field site and the experimental treatment

In 1996, six 30-m diameter FACE plots were installed in a 13-year-old loblolly pine (*Pinus taeda* L.) plantation in the Piedmont region of North Carolina (35°97' N 79°09' W; DeLucia et al. 1999, Hendrey et al. 1999). The clay-rich ultic Alfisols in this region are of the Enon series and are low in available nitrogen and phosphorus. Each plot circumscribed approximately 100 loblolly pine trees. The density of loblolly pine trees was 1733 stems ha^{-1} , and the forest had not yet initiated rapid self-thinning (Peet and Christensen 1987). Silvicultural practices have not been applied and several hardwood species, including sweetgum (*Liquidambar styraciflua* L.), red maple (*Acer rubrum* L.), redbud (*Cercis canadensis* L.) and dogwood (*Cornus florida* L.), have established in the forest understory. Loblolly pine, however, was dominant, representing more than 90% of the total basal area in this forest.

Each FACE plot consisted of a large circular plenum that delivered air to an array of 32 vertical pipes (Hendrey et al. 1999). The pipes extended from the forest floor through the 14-m tall forest canopy and contained adjustable ports at 50-cm intervals. These ports were regulated to control atmo-

spheric $[\text{CO}_2]$ through the entire volume of forest. Pure CO_2 was injected into the air stream supplying the three CO_2 -enriched plots to increase the atmospheric $[\text{CO}_2]$ by 200 $\mu\text{l l}^{-1}$, to approximately 560 $\mu\text{l l}^{-1}$. Each experimental plot was paired with a fully instrumented control plot that received air without added CO_2 and operated at the ambient $[\text{CO}_2]$ of approximately 360 $\mu\text{l l}^{-1}$.

The forest was fumigated for about 80% of the total time during this 3 year experiment. Fumigation, day and night, was terminated when maximum daily air temperature was below 5 °C and intermittently to accommodate ancillary measurements and maintenance of the system. The FACE system provided reliable control of atmospheric $[\text{CO}_2]$ for approximately 99% of the fumigation period.

Biomass increment and leaf area index

Diameter increment of trees in the elevated and ambient $[\text{CO}_2]$ plots was measured monthly with dendrometer bands installed on 30–40 canopy loblolly pine trees in each plot as described in Naidu and DeLucia (1999) and DeLucia et al. (1999). Allometric regressions, constructed by destructively harvesting trees at this site before initiation of the CO_2 treatments in 1996, were used to estimate biomass from diameter (Naidu et al. 1998). The form of the equation was: $\log(\text{mass}) = b_1 \log(\text{diameter}) + b_2$, and different equations were applied to dominant and suppressed trees in each plot. The coefficients relating total biomass (bole, foliage, branch and coarse woody roots) to diameter (1.45 m height) were $b_1 = 2.464$ and $b_2 = 1.830$ for dominant trees, and $b_1 = 2.250$ and $b_2 = 2.082$ for suppressed trees.

The diameters of all trees in each plot were measured, and the growth rates of the dendrometer trees were applied to all trees in each of the three ambient and elevated $[\text{CO}_2]$ plots to calculate the mean cumulative total biomass monthly from 1997 through 1999. Radiation-use efficiency (ϵ) was calculated as the slope of the cumulative total biomass versus cumulative absorbed radiation by the canopy. To facilitate comparisons with the literature, ϵ was also calculated for aboveground biomass only. Root mass was subtracted from total mass; the coefficients relating root biomass to diameter for dominant trees were $b_1 = 0.811$ and $b_2 = 0.007$, and for suppressed trees $b_1 = 0.890$ and $b_2 = -0.369$.

We assumed these allometric regressions were unaffected by the treatment over the 3 years of the experiment. A direct test of this assumption was impractical because it would have necessitated destructive harvests of our experimental trees. The relationship between tree height and diameter was measured on the banded trees in the control and experimental plots in 1996, 1997 and 1998, to provide an indirect test of this assumption.

Three methods were used to estimate L^* for each plot: (1) optical estimates derived from measurements of the canopy gap fraction; (2) allometric scaling; and (3) for the hardwoods, measurements of litterfall. The LAI-2000 (Li-Cor, Lincoln, NE) was used to measure the spatial distribution of light transmitted through the canopy and to calculate total L^* (total projected leaf area above 1 m) as described by Norman and Wells

(1983) and Li-Cor (1991). Measurements were made with matched instruments—one was mounted above the canopy and the other was used to measure transmitted light beneath the canopy. The input optics of both instruments were masked so they captured light from only a quarter of the hemisphere. By restricting the view of optical sensor and directing it toward the center of the plot, the influence of the surrounding forest on estimates of L^* within the experimental plots was minimized. The potential influence of the surrounding forest was further reduced by recalculating L^* without using low-angle light received by the sensor. Measurements were made below the canopy “looking” inward from the perimeter of each circular plot at the four cardinal points. Reported values are the means of these four measurements. Optical measurements of L^* were made in September each year when values were near their maximum.

To quantify L^* by allometric scaling, we used estimates of foliage mass, derived from the destructive harvests described by Naidu et al. (1998), with annual measurements of specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$). Following the same form of the equation used to calculate tree mass, the needle mass was calculated from diameter using $b_1 = 1.567$ and $b_2 = 1.927$ for dominant trees, and $b_1 = 1.198$ and $b_2 = 2.072$ for suppressed trees. Needles from each living cohort were harvested from each plot in September of 1997, 1998 and 1999. Using an electric lift, sun needles, from the top of the canopy, and shade needles were harvested from three to four trees in each of four locations per plot. A total of 1536 fascicles were harvested across all years, positions and treatments. Projected needle surface area was estimated with a geometric model (Naidu et al. 1998) and the samples were dried at 70 °C to constant mass and weighed. The value of L^* was calculated by dividing the estimate of needle mass per plot by a weighted SLA. The SLA values used to calculate L^* were weighted by needle age (50% new foliage and 50% old foliage) and canopy position (25% top, 50% middle and 25% bottom).

Leaf area index for hardwoods was calculated by multiplying total leaf mass of litter by a weighted mid-season value for SLA. Litter and SLA values are from Finzi et al. (2001). The SLA (one-sided) for the understory species red maple, sweetgum, redbud and dogwood were measured in July 1998. These values were weighted by the relative basal area of each species in each plot to create a mean value for hardwoods and this mean value was multiplied by litter dry mass to calculate total leaf area. The weighted values for hardwood SLA in the ambient and elevated [CO₂] plots (\pm SD) were 233.0 ± 37.2 and $186.0 \pm 48.6 \text{ cm}^2 \text{g}^{-1}$, respectively, and the differences between these values were not statistically different ($P = 0.33$, paired t -test).

Leaf area index of the loblolly pines varied by about 44% over a year with a maximum in August and a minimum in January (D. Ellsworth, University of Michigan, unpublished data). Monthly L^* was calculated by multiplying the fractional L^* for that month (reported by Luo et al. 2001) by the September value reported in Table 1.

Table 1. Least-squares mean values for specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) for loblolly pine needles collected from the top, middle or bottom of the forest canopy of trees grown in ambient (Amb; $\sim 360 \mu\text{l l}^{-1}$) or elevated (Elev; $\sim 560 \mu\text{l l}^{-1}$) atmospheric [CO₂]. New needles were those that developed during the current year and old needles were those that developed during the previous summer. Weighted values (by age and canopy position) were those used to calculate canopy leaf area index from needle mass (see Materials and methods). The standard error for all values was either 1.4 or 1.5.

Canopy	Needle age	1997		1998		1999	
		Amb	Elev	Amb	Elev	Amb	Elev
Top	New	38.9	37.0	35.0	34.0	39.0	35.4
	Old	33.9	30.1	31.8	28.9	30.7	29.1
Middle	New	44.7	40.8	41.6	39.9	43.7	38.2
	Old	37.5	35.5	33.9	34.5	35.5	32.7
Bottom	New	53.0	48.3	48.6	48.2	51.4	52.6
	Old	43.6	40.9	38.5	38.8	42.1	39.7
Weighted		41.6	38.6	38.1	37.3	40.2	37.3

Absorbed irradiance

Photosynthetically active radiation (PAR; 400–700 nm) incident on the forest canopy was measured with a cosine-corrected quantum sensor (LI-190SA, Li-Cor) at 1-s intervals and summed to produce monthly totals. Quanta were converted to energy (MJ) by assuming 1 W m^{-2} (PAR) equals $4.6 \mu\text{mol (photons)} \text{ m}^{-2} \text{ s}^{-1}$ (McCartney 1978). This value is appropriate for full sun conditions but would be slightly less for a completely diffuse sky. The PAR absorbed by the pine canopy (APAR) in each plot was calculated as:

$$\text{APAR} = (\varphi_a - \varphi_{\text{cr}})(1 - \exp(-kL^*)), \quad (1)$$

where φ_a and φ_{cr} are irradiance incident on and reflected from the canopy, respectively and k is the canopy extinction coefficient. For values of L^* above about 3, reflected PAR can be estimated following Ross (1981) as:

$$\varphi_{\text{cr}} = 0.5\varphi_{\text{nr}}, \quad (2)$$

where φ_{nr} is needle reflectance. Total reflectance (400–700 nm) from 1-year-old loblolly pine needles was 11.1% and did not vary between the CO₂ treatments (E.H. DeLucia, unpublished data).

McCrary and Jokela (1998) reported k values of 0.28–0.38 for 5-year-old loblolly pine stands. The extinction coefficient may increase with stand age, and we therefore chose to use a value of 0.5. This value represents the average for large-stature canopies of several different pine species, which varied between 0.40 and 0.62 (Jarvis and Leverenz 1983, Chen et al. 1997). For a canopy with an L^* of 6, varying k by 0.2 above and below 0.5 would change APAR by about 4 and 12%, respectively.

Statistical analyses

The relationship between tree height and diameter and between plot biomass increment and absorbed PAR were fit with

linear or log-linear regressions. The regressions were compared with an analysis of covariance. If the interaction term (slopes) was not significant ($P > 0.05$), this term was dropped from the model to test for differences in the intercepts (SYSTAT Version 7.0, SPSS, Chicago, IL).

Treatment, time and position effects on SLA were analyzed with a split-split-split-plot design. In the model, year was held as the whole-plot fixed effect with the random-effect block as units. Block was the block for the fixed split-plot treatment, CO_2 concentration. Within this treatment, arm and tree together were random blocks for the fixed split-split-plot treatment, height. Within height the fixed split-split-split-plot treatment was needle age.

Temporal and treatment effects on needle mass and L^* were analyzed with a repeat-measures ANOVA (SYSTAT Version 7.0, SPSS); data were transformed as necessary to meet assumptions of normality and were analyzed in a blocked design, where the blocks were established before initiation of the experiment in 1996.

Results and discussion

Substantial stimulation of photosynthesis, as reported by Myers et al. (1999) and Ellsworth (2000), contributed to the increase in biomass production for the dominant loblolly pines during the first 3 years of exposure to elevated atmospheric $[\text{CO}_2]$. Because the elevated $[\text{CO}_2]$ treatment had only a small effect on L^* , we conclude that most of the increase in ϵ was caused by the large stimulation in biomass increment. However, this conclusion, discussed below, is predicated on the assumption that exposure to elevated $[\text{CO}_2]$ did not alter the allometric equations relating tree diameter to biomass.

Consistent with theoretical predictions (West et al. 1997), the relationship between tree height and diameter was nonlinear (Figure 1); smaller diameter trees were comparatively taller than larger diameter trees. In most years, the diameter–height relationship was effectively linearized by a log–log transformation. A statistical test for the homogeneity of slopes (ANCOVA), applied to the log-transformed data for trees in the ambient and elevated $[\text{CO}_2]$ plots, indicated that there was no statistical difference in the relationship between tree height and diameter before initiation of the treatment, or after 3 years of exposure to elevated $[\text{CO}_2]$.

In loblolly pine, the pattern of biomass allocation is responsive to irrigation and fertilization with mineral nutrients, though the effects are small (King et al. 1999). Studies that have included ontogenetic changes in their analysis typically have not shown an effect of elevated $[\text{CO}_2]$ on the pattern of biomass allocation (Curtis 1996). During the first 3 years of this study, there was no indication that elevated $[\text{CO}_2]$ changed the aboveground allometry of the loblolly pine trees. However, we cannot exclude the possibility that elevated $[\text{CO}_2]$ altered the taper of tree boles (Norby et al. 2001) and it was demonstrated recently that trees in the elevated $[\text{CO}_2]$ plots were investing more of their aboveground carbon in cone production (LaDeau and Clark 2001). Although the increase in al-

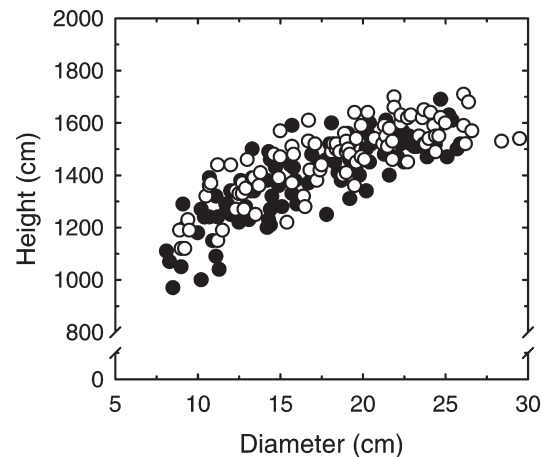


Figure 1. Relationship between height and diameter for loblolly pine trees growing in ambient ($\sim 360 \mu\text{l l}^{-1}$; ●) and elevated ($\sim 560 \mu\text{l l}^{-1}$; ○) atmospheric $[\text{CO}_2]$. Diameter was measured at 1.35 m above ground. Measurements were made shortly after the initiation of the CO_2 treatment, in 1996, and again in 1997 and 1999; the data presented are from 1999. The data were fit with the following equation: $\log(\text{height}) = \text{constant} + \text{slope coefficient} \times \log(\text{diameter})$. In 1999, the constant and slope coefficient for trees in ambient $[\text{CO}_2]$ were 2.767 and 0.103, respectively and the corresponding values for trees in elevated $[\text{CO}_2]$ they were 2.834 and 0.265. An ANCOVA applied to log–log transformed data indicated no effect of the CO_2 treatment on the height–diameter relationship in any of the 3 years (treatment \times $\log(\text{diameter})$; $P > 0.05$).

location to reproduction was too small to alter our results, it may portend larger changes in allocation as the canopy continues to close and the collective root system in this forest more fully explores the soil.

Specific leaf area is an important ecosystem attribute used to extrapolate many tissue-specific variables (e.g., foliage respiration and nitrogen content) to the level of the whole canopy. We used measured values of SLA to convert allometrically derived estimates of foliage mass per unit ground area to L^* . As noted by Hollinger (1989) and Ellsworth and Reich (1994), SLA varies systematically within the canopy. In our study (Table 1), SLA increased with depth in the canopy (33.5 top, 38.2 middle and $45.6 \text{ cm}^2 \text{ g}^{-1}$ bottom; $P < 0.05$), and was substantially greater for needles formed during the current growing season ($42.6 \text{ cm}^2 \text{ g}^{-1}$) than for needles formed during the previous season ($35.6 \text{ cm}^2 \text{ g}^{-1}$); these older needles were approaching senescence at approximately 19 months old. Although inconsistent, there was also statistically significant variation in SLA among years. There was a trend of lower SLA ($\sim 4\%$) for loblolly pines grown in elevated $[\text{CO}_2]$ than in ambient $[\text{CO}_2]$ (38.4 versus $39.8 \text{ cm}^2 \text{ g}^{-1}$); this trend was most evident in the upper canopy.

A decrease in SLA is a characteristic feature of leaves grown in elevated $[\text{CO}_2]$ (Curtis 1996). A portion of this decrease is associated with the accumulation of starch (DeLucia et al. 1985). An increase in leaf thickness caused by elongation of palisade cells, or in some cases, by the formation of additional cell layers, also contributes to the observed decrease in

SLA. Thomas and Harvey (1983) reported increases in leaf thickness of more than 20% for plants grown at twice ambient [CO₂]. Although not intended as a phylogenetic survey, these increases were greatest for the two dicotyledonous species studied and least for the gymnosperm and monocotyledonous species. In many cases, lower SLA contributes to a dilution of leaf nitrogen and reduces total leaf area for a given investment in biomass for plants grown in elevated [CO₂].

Estimates of L^* varied considerably with measurement technique (Table 2); values derived from optical measurements were consistently lower than estimates derived from allometric regressions and litter collections. For example, in September 1998, mean L^* estimated optically for trees in the ambient [CO₂] plots was 4.6 compared with 6.7 when estimated by combining data from the allometric regressions with litterfall.

Estimation of L^* by optical methods relies on the assumption that leaves are infinitely thin, planar and randomly distributed in space (Norman and Wells 1983). The violation of this last assumption by the highly clumped needles of many conifer species presents the greatest limitation of this method, and optical estimates often underestimate L^* in conifer stands. Incorporating a clumping factor greatly reduces the bias in estimating L^* by optical methods (Stenberg et al. 1994, Chen et al. 1997). Another source of error when using optical methods to estimate L^* in conifer stands is the inclusion of stem and branch area. In boreal forests this error is relatively small (Chen et al. 1997), but it may be significant for young loblolly pine stands (Sampson and Allen 1995).

When appropriate shoot- and stand-level clumping factors were used, the error in our estimates of L^* caused by the non-random distribution of foliage was reduced considerably.

By correcting the fraction of total L^* attributed to loblolly pine (0.62, Table 2) with clumping factors derived for ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and assuming that 16% of the total area was stems and branches (Law et al. 2001a, 2001b), the new value of 6.2 compared favorably with the estimate of 6.6 derived from allometric equations (averaged across treatments and years). Applying the correction derived by Stenberg (1996) for Scots pine (*Pinus sylvestris* L.) to our forest produced an L^* value of 6.1.

In our loblolly pine forest, successional hardwood species in the understory contributed almost one third of total L^* . The combination of hardwood and conifer foliage created a complex canopy where a combination of different methods for estimating L^* may be appropriate. Allometric or corrected-optical measurements can be applied to the conifer overstory, whereas litterfall may provide the most direct estimate of L^* for the understory hardwoods.

There was a consistent increase in L^* over the 3-year measurement period. Averaged across treatments, the allometric estimates of L^* for the loblolly pines increased from 4.0 in 1997 to 4.3 in 1999 ($P = 0.09$), and there was a ~9% increase in hardwood L^* over this period. Total L^* measured optically increased by 25% ($P = 0.12$), and L^* estimated by combining allometric values with litter increased by 7% ($P = 0.051$) over the same period. These rather small temporal changes suggest that this stand is near its maximum L^* , at least for the loblolly pines. The contribution of the hardwoods will increase with time as they become a more dominant component of this forest and this may cause a subsequent increase in L^* .

Elevated [CO₂] caused only a small increase in L^* during the first 3 years of the experiment. There was no statistically significant main effect of CO₂ on L^* , however, the marginally

Table 2. Maximum leaf area index (L^*) and leaf mass (g m^{-2}) for a 15-year old loblolly pine forest exposed to ambient (Amb) or elevated (Elev) atmospheric [CO₂]. Each value is the mean (± 1 SD) of the three ambient or three elevated [CO₂] plots. Measurements were made each September from 1997 through 1999. The L^* for the pine canopy was estimated with an allometric regression of leaf mass as a function of stem diameter (Allometric). The L^* for the hardwoods was estimated from litter mass (Litter)¹. Total L^* was estimated optically (Optical) or by summing (Summing) the independent estimates of L^* (Allometric) for pine and hardwoods. Results of a repeat-measures ANOVA are shown in the last column, where d indicates a significant effect of date ($P < 0.05$) and $d \times t$ indicates a significant date by CO₂ treatment interaction. There was no main effect of the CO₂ treatment for any variable. An asterisk indicates marginal significance ($P < 0.1$).

Species	Method	CO ₂	1997	1998	1999	
Pine	Allometric	Amb	4.2 (0.5)	4.0 (0.5)	4.5 (0.6)	d
		Elev	3.7 (0.5)	3.8 (0.7)	4.1 (0.7)	$d \times t^*$
	Needle mass	Amb	1014 (230)	1054 (232)	1105 (234)	$d \times t^*$
		Elev	959 (257)	1008 (263)	1068 (272)	
Hardwood	Litter	Amb	2.4 (0.4)	2.6 (0.6)	2.6 (0.5)	d
		Elev	2.0 (0.3)	2.2 (0.3)	2.1 (0.3)	
	Litter mass	Amb	104.1 (16.1)	112.2 (21.6)	112.4 (19.2)	d^*
		Elev	119.9 (38.1)	130.6 (38.9)	126.3 (38.6)	
Total	Optical	Amb	3.9 (0.4)	4.6 (0.4)	4.9 (0.3)	d
		Elev	4.3 (0.4)	4.5 (0.3)	5.1 (0.3)	
	Summing	Amb	6.7 (0.3)	6.7 (0.2)	7.1 (0.4)	d^*
		Elev	5.7 (0.3)	6.0 (0.4)	6.2 (0.4)	

¹ Litter data are from Finzi et al. (2001).

significant date \times treatment interaction term ($P < 0.1$; Table 2) suggests that the allometrically derived L^* increased more rapidly in trees in elevated $[\text{CO}_2]$ than in ambient $[\text{CO}_2]$. It has been hypothesized that elevated $[\text{CO}_2]$ will cause an increase in L^* by stimulating carbon gain of shaded foliage deep in the canopy, thereby increasing its longevity (Long 1991, Long and Drake 1991, Eamus 1996). Loblolly pine is intolerant of shade and rapidly self prunes lower branches. The substantial increase in loblolly pine litter in response to elevated $[\text{CO}_2]$ (Finzi et al. 2001), suggests that loblolly pine primarily responded to elevated $[\text{CO}_2]$ by increasing leaf turnover rather than by promoting the retention of shade foliage.

Environmental conditions were similar between years (Figure 2). Annually integrated PAR incident on the forest canopy varied between 2314 and 2398 MJ for 1997 to 1999 and the mean annual temperature for these years was between 14.3 and 16.3 °C. Elevated $[\text{CO}_2]$ stimulated the basal area increment of loblolly pine by ~25% in 1997 and 1998 (DeLucia et al. 1999), and this stimulation has been sustained through 2001 (Hamilton et al. 2002).

The increase in basal area increment and the corresponding increase in both aboveground and total biomass (aboveground + belowground) caused a ~27% increase in ϵ in elevated $[\text{CO}_2]$ (Figure 3). Radiation-use efficiency was 0.49 ± 0.05 (SD) g MJ^{-1} for trees in ambient $[\text{CO}_2]$ and 0.62 ± 0.04 g MJ^{-1} for

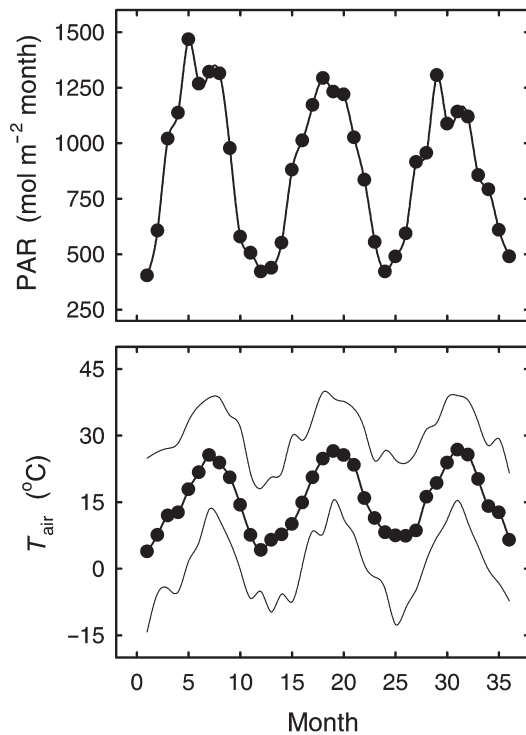


Figure 2. Mean monthly photosynthetically active radiation (PAR), and mean monthly minimum, maximum and mean air temperatures for the FACTS-1 research forest in Chapel Hill, North Carolina. Data are for January 1997 through December 1999, and the values are plotted at the end of each month. Total PAR per year was 2398, 2314 and 2314 MJ, for 1997, 1998 and 1999, respectively.

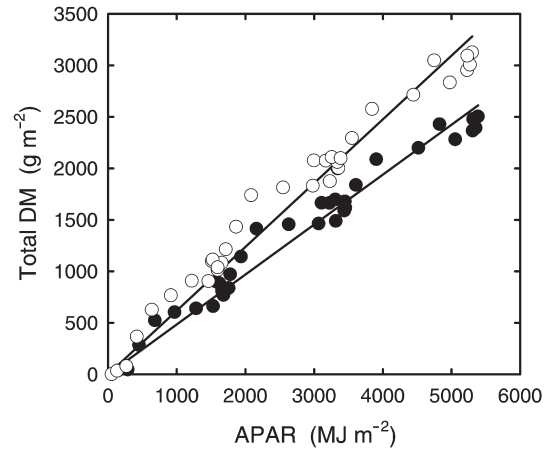


Figure 3. Cumulative total biomass (Total DM; aboveground dry mass + belowground dry mass) for loblolly pine as a function of cumulative absorbed photosynthetically active radiation (APAR) for plots exposed to ambient ($\sim 360 \mu\text{l l}^{-1}$, ●) and elevated ($\sim 560 \mu\text{l l}^{-1}$, ○) atmospheric $[\text{CO}_2]$. Radiation-use efficiency (ϵ) was calculated as the slope of the relationship between total dry mass and APAR, where APAR was calculated from pine L^* derived from allometric equations (see Materials and methods). The data were collected over 3 years and each value is the mean from either the three ambient or the three elevated $[\text{CO}_2]$ plots.

trees in elevated $[\text{CO}_2]$. On a total biomass basis, these values are comparable with the global average of 0.62 ± 0.29 g MJ^{-1} for temperate evergreen forests reported by Gower et al. (1999). When calculated for aboveground biomass only, the values of ϵ were 0.44 ± 0.05 and 0.56 ± 0.03 g MJ^{-1} for trees exposed to ambient and elevated $[\text{CO}_2]$, respectively (data not shown). Because elevated $[\text{CO}_2]$ had little effect on L^* and thus APAR during this first 3 years of the experiment (ambient = 5811 MJ m^{-2} , elevated 5637 MJ m^{-2} ; APAR), the increase in ϵ was driven by the stimulation of biomass accumulation.

Use of allometric regressions with measurements of the change in tree diameter to calculate biomass increment introduced two errors in our estimate of ϵ . First, the allometric equations were generated for trees carrying the maximum annual foliage biomass (Naidu et al. 1998); these equations therefore overestimated biomass during the winter and early in the season as the new cohort of foliage emerged. Maximum foliage biomass is about 10% of the total biomass in this forest (Hamilton et al. 2002) so this error is small. Second, the estimate of ϵ was based on biomass increment and did not include other components of net primary production (NPP), such as litterfall, fine root production, and C losses as dissolved organic carbon (DOC) and by herbivory. Though fine root production, herbivory and losses of carbon as DOC are small in this forest (≤ 44 $\text{g C m}^{-2} \text{ year}^{-1}$ in 1999; Hamilton et al. 2002), litterfall can be substantial. During 1999, litterfall was 358 g C m^{-2} compared to an annual increment of wood and foliage of 465 g C m^{-2} (Finzi et al. 2001, Hamilton et al. 2002). When calculated based on NPP (1439 $\text{gDM m}^{-2} \text{ year}^{-1}$ in ambient plots; 1831 $\text{gDM m}^{-2} \text{ year}^{-1}$ in elevated plots) and APAR (1791 MJ m^{-2} in ambient plots; 1737 MJ m^{-2} in elevated plots)

for 1999, the only year with a nearly complete C budget (Hamilton et al. 2002), the values of ϵ for the ambient and elevated plots increased to 0.80 and 1.05 MJ m⁻², respectively. Thus, the estimate of ϵ from cumulative biomass provides an underestimate of the value based on NPP.

The stimulation of biomass by elevated [CO₂] is quite variable for woody plants (Curtis and Wang 1996). Differences among experiments in plant age, stage of development and the pattern of biomass allocation contribute to these divergent results. Norby (1998) observed that expressing the growth response as a canopy productivity index (CPI), defined as the annual wood production per unit leaf area, greatly reduces this variation. The CPI values converged on 29% for species with biomass stimulations ranging from 18 to 180% in response to a doubling of [CO₂].

Forest ϵ is analogous to the CPI in that it relates the rate of biomass production to absorbed irradiance, which is in turn a function of L^* . If we assume that the stimulation in ϵ is linearly related to [CO₂], and we extrapolate the values we have reported for a +200 $\mu\text{l l}^{-1}$ CO₂ treatment to an atmospheric concentration of 700 $\mu\text{l l}^{-1}$, the median concentration for the studies reported by Norby (1998), the ~34% stimulation in ϵ we calculate for loblolly pine is similar to the 29 ± 7 (SD) stimulation in CPI. Once adjusted for differences in total leaf area, our results for loblolly pine support the assertion that at least the initial response to elevated [CO₂] is similar among tree species (Norby 1988).

Assuming a linear response, our results indicate that ϵ will increase by approximately 0.2% with an annual increase in atmospheric CO₂ of 1.5 $\mu\text{l l}^{-1}$. Though the effect of elevated [CO₂] on ϵ may be useful in modeling exercises, there is some evidence that the 27% stimulation represents a maximum response that will diminish as the forest acclimates to the step change in [CO₂] (Idso 1998). Preliminary evidence from a nearby prototype plot indicates that the growth response of loblolly pine was greatly diminished after 5 years of exposure to elevated [CO₂] (Oren et al. 2001). Increasing atmospheric [CO₂] will stimulate biomass accumulation and thus ϵ for closed-canopy forests, but the duration and absolute magnitude of this increase remains uncertain.

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