Effects of CO₂ enrichment on the photosynthetic light response of sun and shade leaves of canopy sweetgum trees (Liquidambar styraciflua) in a forest ecosystem

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Received October 28, 1998

Summary  To investigate whether sun and shade leaves respond differently to CO₂ enrichment, we examined photosynthetic light response of sun and shade leaves in canopy sweetgum (Liquidambar styraciflua L.) trees growing at ambient and elevated (ambient + 200 µl l⁻¹) atmospheric CO₂ in the Brookhaven National Laboratory/Duke University Free Air CO₂ Enrichment (FACE) experiment. The sweetgum trees were naturally established in a 15-year-old forest dominated by loblolly pine (Pinus taeda L.). Measurements were made in early June and late August 1997 during the first full year of CO₂ fumigation in the Duke Forest FACE experiment. Sun leaves had a 68% greater leaf mass per unit area, 63% more leaf N per unit leaf area, 27% more chlorophyll per unit leaf area and 77% greater light-saturated photosynthetic rates than shade leaves. Elevated CO₂ strongly stimulated light-saturated photosynthesis of sun and shade leaves in June and August; however, the relative photosynthetic enhancement by elevated CO₂ for sun leaves was more than double the relative enhancement of shade leaves. Elevated CO₂ stimulated apparent quantum yield by 30%, but there was no interaction between CO₂ and leaf position. Daytime leaf-level carbon gain extrapolated from photosynthetic light response curves indicated that sun leaves were enhanced 98% by elevated CO₂, whereas shade leaves were enhanced 41%. Elevated CO₂ did not significantly affect leaf N per unit area in sun or shade leaves during either measurement period. Thus, the greater CO₂ enhancement of light-saturated photosynthesis in sun leaves than in shade leaves was probably a result of a greater amount of nitrogen per unit leaf area in sun leaves. A full understanding of the effects of increasing atmospheric CO₂ concentrations on forest ecosystems must take account of the complex nature of the light environment through the canopy and how light interacts with CO₂ to affect photosynthesis.

Keywords: elevated CO₂, FACE, Free Air Carbon Dioxide Enrichment, nitrogen, quantum yield, shade leaves, sun leaves.

Introduction

Numerous greenhouse, growth chamber and open-top chamber studies have shown that elevated atmospheric CO₂ enhances photosynthesis and plant biomass production compared to that of plants grown at ambient CO₂ concentrations (Cure and Acock 1986, Eamus and Jarvis 1989, Poorter 1993, Ceulemans and Mousseau 1994, Gunderson and Wullschleger 1994, Curtis 1996). Ceulemans and Mousseau (1994) reviewed many studies and found that a doubling of atmospheric CO₂ increased leaf-level photosynthesis by approximately 40% for conifers and 61% for deciduous trees. However, studies of the effects of elevated CO₂ on tree species are often conducted with seedlings or small saplings grown in controlled environments with non-limiting amounts of water and nutrients. As a consequence, many of these studies do not reflect the complex nature of trees growing in a forest ecosystem. If elevated CO₂ stimulates leaf area production and produces denser forest canopies, a greater percentage of foliage will be shaded and the role of the shaded branches will increase in importance with respect to whole-tree carbon balance. Thus, an understanding of the photosynthetic responses of sun and shade leaves growing in a natural canopy is critical to predictions of the effects of increasing atmospheric CO₂ on forest ecosystems.

Most studies on the effects of elevated CO₂ on plants have used relatively high irradiances, so that CO₂ supply and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity are the main limitations on C₃ photosynthesis (Bowes 1993). In a natural forest ecosystem, much of the photosynthesis in a canopy takes place in reduced light because of shading. Local light environments affect developmental, morphological and physiological attributes of individual leaves such as leaf thickness, nitrogen per unit area, chlorophyll per unit area, and net photosynthesis (Boardman 1977, Björkman 1981, McClendon and McMullen 1982, Hirose and Werger 1987, Ellsworth and Reich 1993). Pearcy and Björkman (1983) suggested that elevated CO₂ would improve carbon balance in light-limited as well as high-light environments through the CO₂ enhancement of quantum yield. The present CO₂:O₂ ratio of the air constrains photosynthesis by 30–40%, because of O₂ inhibition of carboxylation and associated photorespiration (Bowes 1993). As CO₂ concentrations increase, quantum yield is increased because the ratio of carboxylation to oxygenation by Rubisco increases and photosorption decreases. Several studies have shown that CO₂ enrichment enhances photosyn-
thesis and growth under limiting irradiance conditions, and in some cases the relative enhancement was greater at low irradiance than at high irradiances (Sionit et al. 1982, Cure and Acoc 1986, Allen 1990, Long and Drake 1991, Gifford 1992). Very few studies have examined the effect of CO2 enrichment on photosynthesis in leaves shaded by a natural forest canopy (Osborne et al. 1997, Winter and Virgo 1998).

The Brookhaven National Laboratory/Duke University Free Air CO2 Enrichment (FACE) experiment in North Carolina permits direct study of the effects of elevated CO2 on large trees under natural field conditions. This experiment is being conducted in a piedmont forest dominated by loblolly pine trees (Pinus taeda L.) with sweetgum trees (Liquidambar sityrificlua L.) as the dominant deciduous tree species. Sweetgum is an early successional tree species that commonly invades broumesdge (Andropogon virginicus L.) fields in the piedmont of North Carolina during secondary succession (Oosting 1942). Although an early successional tree species, sweetgum leaves have the ability to acclimate to shaded conditions (Zimmerman and Brown 1971, Harley et al. 1996). Sun leaves and shade leaves of sweetgum differ morphologically and physiologically with photosynthesis and stomatal conductance as much as three times greater in sun leaves than in shade leaves (Harley et al. 1996). In addition, elevated CO2 has been shown to stimulate photosynthesis and biomass production of sweetgum seedlings under a variety of environmental conditions (Rogers 1983, Tolley and Strain 1984, Sionit et al. 1985, Groninger et al. 1995, 1996, Tschaplinski et al. 1995).

The objective of our study was to determine whether sun and shade leaves of canopy sweetgum trees in the Duke FACE experiment respond differentially to CO2 enrichment. We tested the hypothesis that CO2 enrichment will stimulate photosynthesis in sun and shade leaves in a manner that increases their daily carbon balance. We predicted that sun leaves would have the greatest absolute enhancement in response to CO2 enrichment, because sun leaves have a greater photosynthetic capacity. Shade leaves, however, would have the greatest relative enhancement of net photosynthesis by elevated CO2, because of very low net assimilation in the understory and a stimulation of quantum yield. Photosynthetic light responses and leaf characteristics were measured twice during the first full growing season of the Duke FACE experiment on sun and shade leaves of canopy sweetgum trees exposed to either elevated or ambient CO2. To place the sun and shade leaf responses in the context of a natural light environment, a simulation of leaf-level daily carbon gain was constructed.

Materials and methods

Brookhaven National Laboratory/Duke University Free-Air CO2 Enrichment (FACE) experiment

The Duke University FACE experiment in the Blackwood division of the Duke Forest (35°97′ N, 79°09′ W) was established to examine responses of an intact forest ecosystem to elevated concentrations of atmospheric CO2. The forest is dominated by loblolly pine (1733 stems ha−1) with significant numbers of sweetgum (Liquidambar styrificlua, 620 stems ha−1) and yellow poplar (Liriodendron tulipifera L., 68 stems ha−1) as secondary associates. The loblolly pine trees in the plantation have exhibited remarkably uniform growth, with a median height of 14 m, a mean diameter of about 15 cm and a leaf area index of about 3.5 (Katul et al. 1997). The forest has not yet initiated self thinning. The clay-rich Alfisols are of the Enon series, a soil with low nitrogen and phosphorus availability that is typical of many upland areas in Southeastern USA. This section of the Duke forest was farmed a century ago, and the current plantation was established in 1983 after the regenerating forest was clear-cut in 1979.

The FACE system increases atmospheric CO2 concentrations in 30-m diameter experimental circular plots (or rings) nested within this continuous loblolly pine forest. Each FACE ring consists of a large circular plenum that delivers air to an array of 32 vertical pipes. The pipes extend from the forest floor through the 14-m tall forest canopy and contain adjustable ports at 50-cm intervals. These ports are tuned to control atmospheric CO2 concentration through the entire forest volume. Fumigation with CO2 in three experimental rings (ambient + 200 ± 84 µl l−1 or approximately 560 µl l−1) began in August 1996. Three control rings (approximately 366 µl l−1) receive the same volume of air to replicate any micrometeorological effects on the forest that occur during the operation of the FACE facility. To control for topographic variation (>5 m) and potential gradients in site fertility between rings, the three control and three elevated-CO2 rings were arranged in complete block design (three pairs).

Gas exchange and leaf chemistry

Measurements were made twice during the first growing season (1997) of the experiment. In June, mean maximum temperature was 27 °C and mean minimum temperature was 16 °C (Figure 1). Rainfall was 9.86 cm in June and soil water content averaged 23.3% across the three control rings and 26.2% across the experimental rings (K. Schäfer, Duke University, unpublished data). The second measurement period was in August, at which time mean maximum temperature was 31°C and mean minimum temperature was 19 °C. In August, there was 3.26 cm of rainfall and soil water content averaged 15.5% across the three control rings and 16.1% across the experimental rings (Schäfer, unpublished data).

Two sweetgum trees approximately 7–11 m in height were selected in each FACE ring based on the proximity of trees to areas accessible from portable hydraulic lifts. All trees in this study had leaves exposed to full sunlight at the top of the canopy and deep shade at the bottom of the canopy. Photosynthetic light response curves were measured at growth CO2 concentrations on two sun and two shade leaves from each tree with an open flow infrared gas analyzer with an attached red LED light source (LI-6400, Li-Cor, Inc., Lincoln, NE). Measurements began with approximately 5 minutes of saturating light (1500 µmol m−2 s−1) followed by nine incremental reductions until the irradiance was 10 µmol m−2 s−1. Use of decreasing light rather than increasing light reduces the equilibrium time required for stomatal opening and photosyn-
thletic induction (Kubiske and Pregitzer 1996). Preliminary trials indicated that photosynthetic rates reached steady state within 2 minutes following each incremental decrease in light. Measurements were made on fully expanded leaves that were at least 2–3 weeks old. Leaf age was determined by a concurrent study of sweetgum leaf demography (Herrick, unpublished data). Gas exchange measurements were restricted to the hours between 1000 and 1500 h on sunny days to minimize diurnal effects on photosynthesis. Leaf temperatures averaged 28.12 ± 0.67 °C in June and 31.23 ± 0.58 °C in August. Within each measurement period, leaf temperatures were not significantly different between the CO₂ treatments or the leaf positions. Trees in one blocked pair of rings were measured each day so that slight differences in daily weather conditions could be included in the block effect in the analysis of variance. All Measurements made in June and August were analyzed separately. Two leaves were measured in June on each tree at both canopy positions. The June data were subjected to analysis of variance (ANOVA) with CO₂ treatment, leaf position and blocked ring pair as main effects and CO₂ treatment by ring pair interaction (JMP, SAS Institute, Cary, NC). Only one leaf was measured in August on each tree at both canopy positions. Sun and shade leaf measurements were averaged for each ring. Data from August were limited to the response of photosynthetic rate to light and ignore any possible changes in stomatal conductance to elevated CO₂ and photosynthetic induction response to sun-flecks or diurnal effects. The relative CO₂ enhancement of sun and shade leaf carbon gain was compared.

**Data analysis**

Measurements made in June and August were analyzed separately. Two leaves were measured in June on each tree at both canopy positions. The June data were subjected to analysis of variance (ANOVA) with CO₂ treatment, leaf position and blocked ring pair as main effects and tree nested within the CO₂ treatment by ring pair interaction (JMP, SAS Institute, Cary, NC). Only one leaf was measured in August on each tree at both canopy positions. Sun and shade leaf measurements were averaged for each ring. Data from August were analyzed by an ANOVA model with CO₂ treatment, leaf position and blocked ring pair as main effects and CO₂ treatment by leaf position and CO₂ treatment by ring pair as interactions (JMP, SAS Institute). Post hoc comparison of parameter means was performed with the Tukey-Kramer HSD test (JMP, SAS Institute). Parameters were considered significantly different when P < 0.05.

**Results**

**Photosynthetic light response**

Photosynthetic light response curves are shown in Figure 2. Light-saturated net photosynthesis (A.sat) was greater in sun

\[ A + R_d = \frac{4I_3}{\Phi_4 + A_{sat}} - \frac{4I_3 A_{sat} C}{2C} \]
leaves than in shade leaves during June \((P < 0.0001)\) and August \((P < 0.001)\) (Figure 3a). Elevated \(\text{CO}_2\) resulted in higher rates of \(A_{\text{sat}}\) in June \((P < 0.001)\) and August \((P < 0.001)\) (Figure 3a). The enhancement of \(A_{\text{sat}}\) by \(\text{CO}_2\) enrichment was significantly greater for sun leaves than for shade leaves \((\text{CO}_2 \times \text{leaf position}, P < 0.01, \text{Figure 3a})\). In June, elevated \(\text{CO}_2\) enhanced \(A_{\text{sat}}\) by 92\% in sun leaves and by 54\% in shade leaves. During August, \(\text{CO}_2\) enhancement of \(A_{\text{sat}}\) was 166\% and 68\% in sun and shade leaves, respectively. There were no blocked ring pair effects on any of the gas exchange parameters measured.

Apparent quantum yield, calculated from the initial slope of the light response curves, was slightly lower in shade leaves than in sun leaves during June \((P = 0.0569)\). During August, sun leaves had a higher quantum yield than shade leaves \((P < 0.05)\). Elevated \(\text{CO}_2\) increased apparent quantum yield in sun leaves \((P < 0.01)\) and shade leaves \((P < 0.01)\) during both measurement periods, but there was no interaction between \(\text{CO}_2\) and leaf position (Figure 3b). In June, quantum yield was enhanced by 29\% in sun leaves and by 40\% in shade leaves. In August, apparent quantum yield was enhanced by approximately 25\% in both sun and shade leaves (Figure 3b).

Shade leaves had a lower light compensation point \((\Gamma)\) and dark respiration rate \((R_d)\) than sun leaves in June \((P < 0.01)\) and August \((P < 0.01)\) (Figures 3c and 3d). Elevated \(\text{CO}_2\) had no significant effect on \(\Gamma\) or \(R_d\), as estimated from the photosynthetic light response curves (Figures 3c and 3d). There were no interactions between \(\text{CO}_2\) and leaf position for \(\Gamma\) or \(R_d\).

Leaf chemistry

Sun and shade leaves did not differ in N concentration on a dry mass basis (Table 1). However, sun leaves had greater N per unit area than shade leaves \((P < 0.01)\), because leaf mass per unit area \((\text{LMA})\) was 68\% greater in sun leaves than in shade leaves in June and August \((P < 0.01)\). Leaf N per unit area was 67 and 61\% greater in sun leaves than in shade leaves in June and August, respectively. Neither leaf N per unit mass nor leaf N per unit area was significantly affected by \(\text{CO}_2\) enrichment, although there was evidence of a trend for \(\text{CO}_2\)-induced reduction in N per unit mass in June \((P = 0.0762)\) and August \((P = 0.0532)\). There were no significant ring pair effects, or interactions between ring pair, \(\text{CO}_2\) and leaf position, on leaf N per unit mass or per unit area. During June, there was a significant \(\text{CO}_2 \times \text{leaf position}\) interaction on \(\text{LMA}\) because elevated \(\text{CO}_2\) increased \(\text{LMA}\) in sun leaves, but not in shade leaves \((P < 0.0001)\). However, in August, there were no effects of \(\text{CO}_2\) and no interactions of \(\text{CO}_2\), leaf position or ring pair on \(\text{LMA}\).

Shade leaves had more chlorophyll on a dry mass basis than sun leaves \((P < 0.05; \text{Table 1})\). In contrast, chlorophyll expressed on a leaf area basis was 35\% greater in sun leaves than...
shade leaves in June \((P < 0.05)\) and, in August, sun leaves had 18\% more chlorophyll per unit leaf area than shade leaves \((P < 0.05, \text{Table 1})\). Elevated CO\(_2\) reduced leaf chlorophyll per unit dry mass in June \((P < 0.05)\). In August, there was no significant effect of CO\(_2\) on leaf chlorophyll per unit dry mass \((P = 0.0766)\). Chlorophyll per unit leaf area was not affected by CO\(_2\) enrichment. There were no significant effects of ring pair, or interactions between CO\(_2\), leaf position, and ring pair, on leaf chlorophyll per unit dry mass or per unit leaf area.

**Modeled diurnal net photosynthesis**

The light environment of sun and shade leaves varied greatly on a daily basis (Figure 4). Photosynthetic photon flux density (PPFD), measured on June 29, 1997 at the top of a tree (approximately 8 m high), where sun leaves developed, and at the bottom of the same tree (approximately 3 m high), where shade leaves developed, is shown in Figure 4. These data were chosen because they represent a typical day during the mid-growing season with intermittent cloud cover. The irradiance data were used to estimate daytime photosynthetic rate \((A')\) and provide a theoretical indication of the effects of elevated CO\(_2\) on daily carbon gain of sun and shade leaves. Modeled results of leaf C gain for sun leaves and shade leaves for the June measurement period are shown in Figure 5. Daytime integrated net photosynthesis was strongly enhanced by elevated CO\(_2\) in sun leaves \((P < 0.0001)\), whereas there was only a small treatment effect in shade leaves (Figure 6). Sun leaves had a higher daytime integrated carbon gain than shade leaves \((P < 0.0001)\). Elevated CO\(_2\) stimulated daytime carbon uptake much more in sun leaves than in shade leaves \((CO_2 \times \text{leaf position}, \ P < 0.0001)\). During June, CO\(_2\) enrichment enhanced daytime carbon uptake of sun and shade leaves by 79 and 49\%, respectively. The same irradiance data were also used to model daytime carbon gain for the sweetgum leaves measured in August. In August, elevated CO\(_2\) enhanced daytime carbon gain by 120\% in sun leaves \((P < 0.0001)\) and 33\% in shade leaves \((P < 0.0001)\) (data not shown).

![Image](https://academic.oup.com/treephys/article-abstract/19/12/779/1658335)

**Figure 4.** Representative light microenvironment on a sunny day (June 29, 1997) at the sun and shade canopy positions. The dark period at 1700 h was caused by cloud cover.

**Discussion**

Elevated CO\(_2\) may stimulate leaf area production (Tolley and Strain 1984a, Sionit et al. 1985), producing denser forest canopies. As a result, a greater proportion of canopy foliage will be shaded and the role of shaded branches in whole-tree carbon balance will increase in importance. We hypothesized that elevated CO\(_2\) would enhance photosynthetic rates of both sun and shade leaves of sweetgum trees growing in the canopy of the Duke Forest FACE experiment. During the first full year of fumigation with CO\(_2\) at the FACE experiment, we found that light-saturated net photosynthetic rates \((A_{sat})\) of canopy sweetgum sun and shade leaves were strongly stimulated by CO\(_2\) enrichment. We had predicted, however, that shade leaves would show a greater relative response to CO\(_2\) enrichment than sun leaves because of the generally low photosynthetic rates of shade leaves and subsequent stimulation of quantum yield by high CO\(_2\) concentrations. In contrast to our predictions, the relative photosynthetic enhancement by elevated CO\(_2\) was greater in sun leaves than in shade leaves. The elevated CO\(_2\)-
induced stimulation of $A_{sat}$ in sun leaves was 92% in June and 166% in August. In contrast, elevated CO$_2$ enhanced $A_{sat}$ of shade leaves by 54% in June and by 68% in August (Figure 3a).

Many studies have suggested that shade leaves respond to atmospheric CO$_2$ enrichment to a greater extent than sun leaves as a result of increased quantum yields (Mortensen and Moe 1983, Lasko et al. 1984, Spalding and Portis 1985, Kirchbaum and Farquhar 1987, Idso et al. 1994, Kubiske and Pregitzer 1996). A small increase in quantum yield may increase daily carbon gain under low light conditions (Pearcy and Björkman 1983). In our study, elevated CO$_2$ increased apparent quantum yields of sun and shade leaves, but there was no difference in the amount of CO$_2$ stimulation between the two leaf types (Figure 3b). In addition, in June, we found no significant differences between apparent quantum yield of sun and shade leaves, a result that is consistent with studies of shade-intolerant species (Kubiske and Pregitzer 1996), including sweetgum trees (Teskey and Shrestha 1985). During August, however, sun leaves had a greater apparent quantum yield than shade leaves.

Sun leaves of canopy sweetgum trees had a 68% greater leaf mass per unit area, 63% more N per unit leaf area and 27% more chlorophyll per unit leaf area than shade leaves (Table 1). Because the light-saturated portion of a light response curve ($A_{sat}$) is limited by Rubisco activity (Stitt 1991), we believe that the differential response of $A_{sat}$ to CO$_2$ enrichment between the two leaf types was driven by greater amounts of N per unit leaf area in sun leaves than in shade leaves. A reduction in leaf N concentration has been observed in many CO$_2$ enrichment studies (Wong 1979, Norby et al. 1986, Williams et al. 1986). During the first year of the FACE experiment, however, we found no significant reductions in leaf nitrogen in response to CO$_2$ enrichment (Table 1). Several studies have reported leaf N concentrations of approximately 15.1 mg g$^{-1}$ in forest-grown sweetgum trees (Blinn and Buckner 1989). We found leaf N concentrations that were greater than this value during both measurement periods suggesting that the sweetgum trees in the Duke Forest FACE experiment were not N limited (Table 1). However, these results are from the first year of a long-term study, and it may take longer for CO$_2$-induced reductions in leaf N to become apparent in forest-grown trees.

The FACE experiment is a perturbation of an intact forest system, which means that, as the elevated CO$_2$ treatment stimulates biomass production, nutrient availability may decrease causing a new equilibrium to become established.

Even if one documents a CO$_2$-induced increase in $A_{sat}$ and quantum yield, it is not clear how changes in these parameters will affect leaf carbon gain. We know that the light environment is highly variable above and below the canopy because of periodic cloud cover and shading through the canopy (Figure 4). Pearcy (1988) reported that 30 to 60% of the daily carbon uptake of sun leaves was 92% in June and 166% in August. Between 1000 and 1500 h, PPFD averaged 130 µmol m$^{-2}$ s$^{-1}$ below the canopy and 729 µmol m$^{-2}$ s$^{-1}$ at the top of the sweetgum canopy. The enhancement of modeled C uptake during this time period was 81% in sun leaves and 45% in shade leaves. Although stimulation of modeled C uptake by elevated CO$_2$ was lower than stimulation of $A_{sat}$, there was still a strong enhancement. Between 900 and 1000 h, PPFD in the shaded average 39 µmol m$^{-2}$ s$^{-1}$ and modeled C uptake was enhanced 36% by elevated CO$_2$. In contrast, between 1450 and

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**Figure 5.** Daytime leaf photosynthetic rates ($A'$) interpolated from June photosynthetic light response curves (shown in Figure 2) and the diurnal light environment (shown in Figure 4) of sun and shade leaves of sweetgum trees grown at elevated CO$_2$ (dashed lines) and ambient CO$_2$ (solid lines).

**Figure 6.** Daytime integrated leaf carbon gain of sun and shade leaves of large sweetgum trees grown at ambient CO$_2$ or elevated CO$_2$. Values are means of three rings in each CO$_2$ treatment based on interpolated diurnal photosynthetic rates shown in Figure 5. Error bars represent ± 1 SE. Within a measurement period, values that are designated by the same letter are not different at the 0.05 level of significance.
1550 h, PPFD in the shade averaged 536 µmol m^{-2} s\(^{-1}\) and modeled C uptake was enhanced 51%. These modeled data indicate the importance of considering patches of high irradiance when predicting the response of shade leaves to elevated CO\(_2\). Kubiske and Pregitzer (1996) found similar results with red oak seedlings grown at elevated CO\(_2\) in shaded open-top chambers.

Previous studies of sweetgum seedlings and saplings have reported that elevated CO\(_2\) enhances photosynthesis by 0 to 71% (Rogers 1983, Tolley and Strain 1984a, 1984b, 1985, Sionit et al. 1985, Fetcher et al. 1988, Groninger et al. 1995, 1996, Tschaplinski et al. 1995). This range of response to CO\(_2\), which is lower than that observed in our study, reflects variability in tree age, CO\(_2\) treatments, duration of study, measurement techniques and experimental design. These factors make comparisons with our study difficult. We attribute the greater response to elevated CO\(_2\) in sun leaves of canopy sweetgum trees of the FACE experiment to several of interactive factors including high leaf nitrogen and high air temperatures. A third factor that may have had a strong influence on the photosynthetic response to elevated CO\(_2\) was the dry soil conditions resulting from low rainfall in August. Tolley and Strain (1985) found that elevated CO\(_2\) significantly moderated the effects of water stress on sweetgum seedlings. Young seedlings in elevated CO\(_2\) maintained high whole-plant assimilation rates during the soil drying cycle and, as a result, photosynthetic enhancement by CO\(_2\) increased throughout the drying cycle until the last day of the cycle when there was no photosynthetic enhancement (Tolley and Strain 1985). In contrast, Tschaplinski et al. (1995) found that severe drought significantly reduced the enhancement of leaf photosynthetic rates by elevated CO\(_2\). During August, at the FACE experiment, soil moisture was low and \(A_{\text{sat}}\) of sun leaves was enhanced by 166% by elevated CO\(_2\). This high enhancement resulted from lower \(A_{\text{sat}}\) in August than in June in leaves grown in ambient CO\(_2\) leaves, whereas \(A_{\text{sat}}\) of leaves grown in elevated CO\(_2\) did not differ between the two sample periods.

In summary, elevated CO\(_2\) significantly increased light-saturated photosynthetic rates, quantum yield and modeled daytime leaf carbon gain of sun and shade leaves of canopy sweetgum trees during the first full year of the Duke Forest FACE experiment. Elevated CO\(_2\) enhanced \(A_{\text{sat}}\) and daytime carbon gain more in sun leaves than in shade leaves. Quantum yield was stimulated by CO\(_2\) enrichment, but did not show a CO\(_2\) \times\) leaf position interaction. Sun leaves had greater leaf mass per unit area, leaf N per unit leaf area, chlorophyll per unit leaf area and light-saturated photosynthetic rates than shade leaves. The greater CO\(_2\) enhancement of light-saturated photosynthesis in sun leaves than in shade leaves was probably associated with a greater amount of leaf N per unit leaf area in sun leaves compared with shade leaves. Despite showing a smaller stimulation by elevated CO\(_2\), shade leaves make up a large component of the sweetgum canopy and, as a result, are important to whole-canopy photosynthesis. If atmospheric CO\(_2\) enrichment stimulates quantum yield, trees may be able to maintain greater leaf area in the shade, thus increasing LAI of the forest canopy to a new equilibrium. In order to understand the effects of increasing atmospheric CO\(_2\) concentrations on forest ecosystems, one must consider the complex nature of the light environment.

Acknowledgments

The authors thank Drs. David Myers and Evan DeLucia for guidance on the field and technical aspects of this project. Dr. James McGraw for statistical consultation and Jeff Pippen and Chris Nacci for assistance in data collection. We thank Christine Muth and Dr. David Myers for helpful comments on this manuscript. We thank Dr. Jerry Leverenz for assistance with curve fitting of the photosynthetic data. We acknowledge the Brookhaven/Duke Forest FACE site supported by the U.S. Department of Energy and the Duke University Phytotron staff. This research was supported through the NSF/DOE/NASA/USDA/EP/A/NOAA Interagency Program on Terrestrial Ecology and Global Change (TECO) and by the U.S. Department of Energy Program for Ecosystem Studies Grant DE-FG02-95ER62124.

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