

# Effects of elevated CO<sub>2</sub> and light availability on the photosynthetic light response of trees of contrasting shade tolerance

MARK E. KUBISKE and KURT S. PREGITZER

School of Forestry and Lake Superior Ecosystems Research Center, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931, USA

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**Summary** Photosynthetic light response curves ( $A/PPFD$ ), leaf N concentration and content, and relative leaf absorbance ( $\alpha_r$ ) were measured in 1-year-old seedlings of shade-intolerant *Betula papyrifera* Marsh., moderately shade-tolerant *Quercus rubra* L. and shade-tolerant *Acer rubrum* L. Seedlings were grown in full sun or 26% of full sun (shade) and in ambient (350 ppm) or elevated (714 ppm) CO<sub>2</sub> for 80 days. In the shade treatments, 80% of the daily PPFD on cloud-free days was provided by two 30-min sun patches at midday. In *Q. rubra* and *A. rubrum*, leaf N concentration and  $\alpha_r$  were significantly higher in seedlings in the shade treatments than in the sun treatments, and leaf N concentration was lower in seedlings in the ambient CO<sub>2</sub> treatments than in the elevated CO<sub>2</sub> treatments. Changes in  $\alpha_r$  and leaf N content suggest that reappportionment of leaf N into light harvesting machinery in response to shade and elevated CO<sub>2</sub> tended to increase with increasing shade tolerance of the plant. Shifts induced by elevated CO<sub>2</sub> in the  $A/PPFD$  relationship in sun plants were largest in *B. papyrifera* and least in *A. rubrum*: the reverse was true for shade plants. Elevated CO<sub>2</sub> resulted in increased light-saturated  $A$  in every species  $\times$  light treatment combination, except in shaded *B. papyrifera*. The light compensation point ( $\Gamma$ ) decreased in response to shade in all species, and in response to elevated CO<sub>2</sub> in *A. rubrum* and *Q. rubra*. *Acer rubrum* had the greatest increases in apparent quantum yield ( $\phi$ ) in response to shade and elevated CO<sub>2</sub>. To illustrate the effects of shifts in  $A$ ,  $\Gamma$  and  $\phi$  on daily C gain, daily integrated C balance was calculated for individual sun and shade leaves. Ignoring possible stomatal effects, estimated daily (24 h) leaf C balance was 218 to 442% higher in the elevated CO<sub>2</sub> treatments than in the ambient CO<sub>2</sub> treatments in both sun and shade seedlings of *Q. rubra* and *A. rubrum*. These results suggest that the ability of species to acclimate photosynthetically to elevated CO<sub>2</sub> may, in part, be related to their ability to adapt to low irradiance. Such a relationship has implications for altered C balance and nitrogen use efficiency of understory seedlings.

**Keywords:** *Acer rubrum*, *Betula papyrifera*, leaf nitrogen, photosynthesis, *Quercus rubra*.

## Introduction

It is predicted that increased atmospheric CO<sub>2</sub> concentration will have pronounced effects on species composition of future landscapes, as a result of selection for C<sub>3</sub> over C<sub>4</sub> species (Zangerl and Bazzaz 1984, Johnson et al. 1993) and altered drought tolerance and plant water relations (Tolley and Strain 1984, Miao et al. 1992). Elevated CO<sub>2</sub> may also influence the competitive ability of seral species by differentially altering their C balance depending on light conditions (Bazzaz and McConnaughay 1992). For example, Reekie and Bazzaz (1989) suggested that the competitive ability of some tropical species is enhanced as a result of improved photosynthetic rates at low irradiances. Other studies have demonstrated differences in the growth response of successional tree species to elevated CO<sub>2</sub> (Bazzaz et al. 1990, Bazzaz and Miao 1993). Such differential responses to elevated CO<sub>2</sub> have the potential to alter the species composition and successional dynamics of temperate communities in the future, but a pattern on which predictions may be based has not been elucidated. A mechanistic approach to comparing responses to elevated CO<sub>2</sub> among seral tree species may provide insight about these differential responses.

Direct effects of elevated CO<sub>2</sub> on C<sub>3</sub> plants include reduced photosynthetic capacity (i.e., photosynthesis in saturating CO<sub>2</sub> and light) but enhanced net photosynthetic rates ( $A$ ) at the growth CO<sub>2</sub> concentration, increased apparent quantum yield ( $\phi$ ), decreased leaf N concentration, and decreased dark respiration rates ( $R_d$ ) (Ehleringer and Björkman 1977, Tolbert and Zelitch 1983, Teskey and Shrestha 1985, Bunce 1992a). Because these responses are not consistent among all species, it has been suggested that they are transitory responses to down-regulation of the photosynthetic apparatus (Arp 1991, Socias et al. 1993). However, recent reports indicate that CO<sub>2</sub> enhancement of  $A$  and growth may be sustained in field plants in which unrestricted rooting volume provides an adequate sink for increased photosynthate production (Idso and Kimball 1991, Long and Drake 1991, Thomas and Strain 1991, Bunce 1992b, Gunderson et al. 1993, Tissue et al. 1993).

In low-irradiance phenotypes growing under limiting light conditions, leaf carbon balance is improved by increased  $\phi$  and decreased  $R_d$  (Ehleringer and Björkman 1977, Teskey and

Shrestha 1985). This plasticity in photosynthetic light response is particularly well developed in shade-tolerant species (Teskey and Shrestha 1985). Similarly, the responses of  $\phi$ ,  $R_d$  and  $A$  to elevated  $\text{CO}_2$  have the potential to induce a shift in the photosynthetic light response at low irradiances. We postulated that, at low irradiances, this type of acclimation to elevated  $\text{CO}_2$  leads to increased carbon balance that varies directly with the intrinsic plasticity of the photosynthetic apparatus and hence, shade tolerance of the species.

We tested the hypothesis that elevated  $\text{CO}_2$  shifts the photosynthetic light response of shade-tolerant species growing in low irradiance in a manner that results in increased daily carbon balance. Because shade-intolerant species photosynthesize most efficiently in full sun, we also tested the hypothesis that shade-intolerant species exhibit the greatest  $\text{CO}_2$ -induced increase in daily carbon gain at high irradiances. These hypotheses were tested by growing species representing stages of a typical Lake States forest sere under a simulated forest canopy in open-top, elevated  $\text{CO}_2$  exposure chambers.

## Methods

### Experimental design

One-year-old seedlings of *Betula papyrifera* Marsh., *Quercus rubra* L. and *Acer rubrum* L. were obtained from a commercial nursery in Michigan. These species have been ranked as shade intolerant, moderately shade tolerant and shade tolerant, and as early, mid and late successional, respectively (Burns and Honkala 1990). In May 1993, two seedlings of each species in leafless condition were planted in each of 12 open-bottom wooden boxes ( $0.7 \times 0.7 \times 0.7$  m) that were lined with plastic and buried in Rubicon sand (frigid Entic Haplorthod) at the University of Michigan Biological Station in northern Lower Michigan ( $45^\circ 33' 30''$  N,  $84^\circ 4' 28''$  W). The boxes were filled with C horizon material of the Rubicon sand (bottom 0.4 m of each box) overtopped by a 1/2 (v/v) mixture of A horizon (Kalkaska sand) and C horizon material.

An open-top chamber approximately  $1 \text{ m}^3$  (cf. Curtis and Teeri 1992, Zak et al. 1993) was placed over each soil box. In six of the chambers, atmospheric  $\text{CO}_2$  was elevated to approximately twice ambient by injecting  $\text{CO}_2$  into a blower system. Half of the chambers in each  $\text{CO}_2$  treatment ( $r = 3$ ) were covered with neutral density shade cloth. Two parallel slots, 10 cm wide and 30 cm apart, were cut in the shade cloth extending up the south face and across the top of each shaded chamber to allow two sun patches of about 30-min duration to pass across the seedlings about 1.5 h apart.

### Data collection

Air temperature and incident photosynthetic photon flux density (PPFD) were recorded every 15 min within a sunlit and shaded chamber with a shaded thermocouple and an LI-190SA quantum sensor connected to an LI-1000 data logger (Li-Cor Inc., Lincoln, NE). Chamber relative humidities were monitored with hygrometers calibrated every 4–5 days.

In late August 1993, photosynthetic light response ( $A$ /PPFD curve) was determined on a fully developed, midcrown leaf

excised from one seedling of each species per chamber ( $n = 3$  for each species  $\times$   $\text{CO}_2$   $\times$  light combination) at the growth  $\text{CO}_2$  concentration. The excised leaves were hydrated for 30 min in the dark before measurement, and the petioles remained submerged in distilled water during generation of the  $A$ /PPFD curves (cf. Ellsworth and Reich 1992). Two LCA-2 photosynthesis systems (ADC Ltd., Hoddesdon, U.K.) were used concurrently, one for each of the  $\text{CO}_2$  treatments. One cuvette was supplied with ambient air, the other with 700 ppm  $\text{CO}_2$  by supplementing ambient air with bottled  $\text{CO}_2$  by means of a Wösthoff Model G18/3A gas mixing pump. Saturating light was supplied by a 50-W halogen projector bulb for 10 min, and incrementally reduced in 9–11 steps over a 20-min period by means of multiple layers of neutral density filters. Use of decreasing rather than increasing PPFD reduced the equilibration time required for stomatal opening and photosynthetic induction following each incremental change in PPFD. Preliminary trials indicated that  $A$  reached steady state within 2 min following each incremental decrease in PPFD. Measurements were performed on one block per day in random order so that temperature differences among the 3 days were included as a block effect in the analysis of variance. Cuvette temperature fluctuated by no more than  $0.7^\circ\text{C}$  during each leaf measurement and by no more than  $2.5^\circ\text{C}$  on any one measurement day.

To test the validity of the photosynthetic light response measurements on excised leaves, light-saturated  $A$  was measured on a fully expanded leaf of each study seedling *in situ* at midday on relatively cloud-free days in mid-August 1993. The shaded seedlings were equilibrated for 20 min in full sun before measurement. The values of directly measured light-saturated  $A$  were then compared to  $A_{\text{sat}}$  values obtained from the  $A$ /PPFD curves. *In situ* measurements of light-saturated  $A$  were not significantly different from values of  $A_{\text{sat}}$  determined from photosynthetic light response curves ( $t$ -test,  $P = 0.57$ ). The two values were highly correlated across all species and treatments ( $r = 0.74$ ,  $P < 0.05$ ; data not shown).

Relative light absorbance ( $\alpha_r$ ) of photosynthetically active radiation was nondestructively determined on a sample of three leaves from each of the six study seedlings in each chamber with a chlorophyll meter (Model SPAD-502, Minolta) before the initiation of  $A$ /PPFD measurements. The Minolta meter uses a scale of  $-9.9$  to  $99.9$  from least to greatest absorbance and has been found to estimate relative differences in leaf chlorophyll content reliably (Yadava 1986, Marquard and Tipton 1987). Leaf N concentration (%) was determined on one leaf from each of the six study seedlings per chamber with a Carlo Erba CHN analyzer (Model NA 1500). Leaf mass per area was determined on the leaves sampled for photosynthetic light response measurements and was used to calculate leaf N per unit area.

### Data analysis

Photosynthetic light response functions were formulated based on a rectangular hyperbolic model (Givnish 1988, Long and Hällgren 1993) and calculations were made with PROC NLIN (SAS Institute Inc., Cary, NC):

$$A = \frac{A_{\text{sat}} \text{PPFD}}{(K + \text{PPFD})} - R_d, \quad (1)$$

where  $A_{\text{sat}}$  is the light-saturated photosynthetic rate,  $K$  is the light saturation constant (defined as one half of the saturating PPFD), and  $R_d$  is the dark respiration rate. The model was fit to pooled data ( $n = 3$ ) for each of the 12 species  $\times$  treatment combinations to evaluate differences in overall  $A/\text{PPFD}$  curves. Contrasts were formed by all pair-wise comparisons among treatments within a species and among species within a CO<sub>2</sub>  $\times$  light treatment (Potvin et al. 1990).

Differences in light response curves were examined by fitting Equation 1 to data from each leaf for statistical comparison of  $A_{\text{sat}}$ ,  $K$ ,  $R_d$  and the light compensation point ( $\Gamma$ ). The apparent photosynthetic quantum yield ( $\phi$ ) was determined as the initial slope above  $\Gamma$ .

To place the treatment responses of  $A/\text{PPFD}$  parameters in the context of diurnal carbon gain, a leaf-level simulation was constructed. Diurnal PPFD recorded on a cloud-free day was used to interpolate diurnal  $A$  ( $A'$ ) from the  $A/\text{PPFD}$  function for each seedling. Estimated daily (24 h) integrated leaf C balance was calculated from diurnal  $A'$  and  $R_d$  from the fitted  $A/\text{PPFD}$  model. These calculations were based solely on the response of  $A$  to PPFD and ignored possible changes in stomatal conductance to CO<sub>2</sub> and light and nocturnal decreases in  $R_d$ .

All parameters were analyzed by a split-plot analysis of variance with chambers as the whole units and species as the subunits in three replicate blocks (SAS Institute Inc.). Means were compared by Fisher's least significant difference procedure at the 0.05 level of significance.

## Results

### Microenvironment

Throughout the experiment, atmospheric CO<sub>2</sub> concentrations averaged  $374.8 \pm 2.9$  and  $714 \pm 2.4$  ppm in the ambient and elevated CO<sub>2</sub> chambers, respectively. On cloud-free days, daily (0500 to 2000 h solar time) integrated PPFD in the shaded chambers was approximately 26% of that of the unshaded chambers, and the two sun patches accounted for 80% of the daily PPFD in the shaded chambers (Figure 1). These values are within the range reported for natural, temperate deciduous forest understories (Chazdon 1988). Low points in midday PPFD of the sunlit chambers were caused by shadows cast over the sensor by the chamber rim. Daily relative humidity was higher and temperature was lower in the shaded than in the sunlit chambers ( $t$ -test,  $P < 0.05$ ).

### Leaf nitrogen

For all species and light treatments, percent leaf N (% N) was significantly lower in seedlings grown in elevated CO<sub>2</sub> than in seedlings grown in ambient CO<sub>2</sub>, except for *B. papyrifera* sun leaves (Figure 2a). Shade leaves of *Q. rubra* and *A. rubrum* had significantly higher % N than sun leaves, whereas sun and shade leaves of *B. papyrifera* had similar % N. Among species in all treatments, *B. papyrifera* leaves had the highest % N and

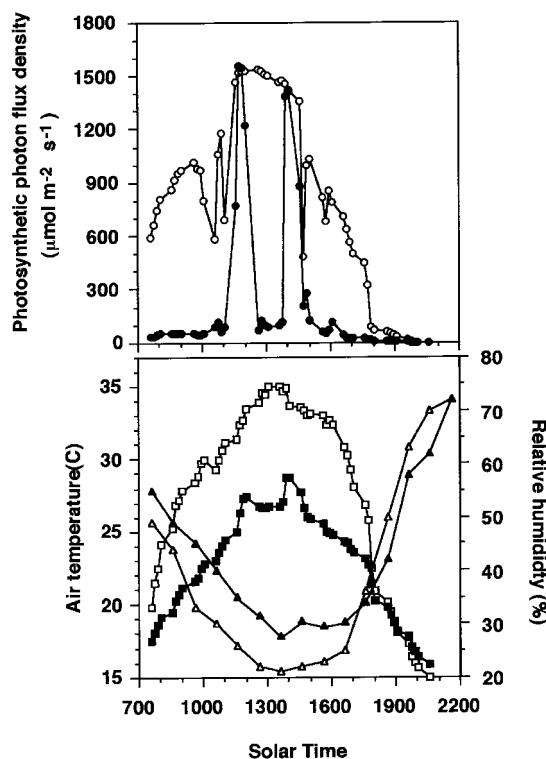


Figure 1. Representative microenvironment on cloudless days in shaded (closed symbols) and unshaded (open symbols) open-top CO<sub>2</sub> chambers. In the lower panel, squares represent air temperature and triangles represent relative humidity.

*A. rubrum* leaves had the lowest. Leaf N content (expressed on a leaf area basis) of *A. rubrum* was not significantly affected by any of the treatments (Figure 2b). In *B. papyrifera* and *Q. rubra*, elevated CO<sub>2</sub> only decreased leaf N content of sun leaves, whereas the shade treatment decreased leaf N content of seedlings in both CO<sub>2</sub> treatments. In all treatments, leaf N content was significantly lower in *A. rubrum* than in the other two species.

The effect of irradiance on  $\alpha_r$  was similar to that on % leaf N, i.e.,  $\alpha_r$  was significantly higher in shade plants than in sun plants of *Q. rubra* and *A. rubrum* (Figure 2c). Shade-treated plants of these two species had lower  $\alpha_r$  in the elevated CO<sub>2</sub> treatments than in the ambient CO<sub>2</sub> treatments.

### Photosynthetic light response

All pair-wise comparisons of  $A/\text{PPFD}$  curves within or among species were significant ( $P < 0.05$ ) except for elevated versus ambient CO<sub>2</sub> for shade plants of *B. papyrifera* (Figure 3). Consequently, the large difference in  $A/\text{PPFD}$  curves between sun and shade leaves of *B. papyrifera* was enhanced by the elevated CO<sub>2</sub> treatment. Both sun and shade leaves of *Q. rubra* and *A. rubrum* exhibited CO<sub>2</sub>-induced shifts in  $A/\text{PPFD}$ . Sun leaves of *Q. rubra* exhibited a greater CO<sub>2</sub>-induced shift in  $A/\text{PPFD}$  than shade leaves, whereas the magnitudes of the CO<sub>2</sub>-induced shifts in  $A/\text{PPFD}$  were similar for sun and shade leaves of *A. rubrum*. In general, the  $A/\text{PPFD}$  curves tended to saturate more abruptly for shade leaves than for sun leaves and

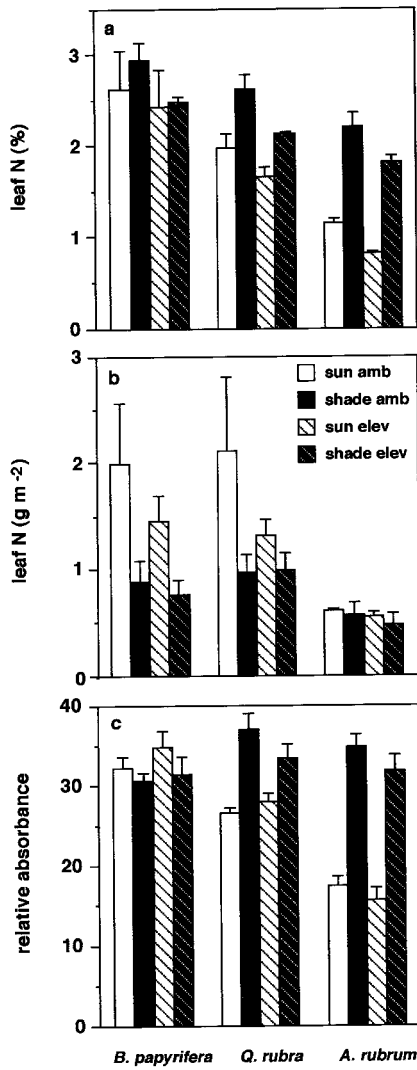


Figure 2. (a) Total leaf N concentration (per unit dry mass), (b) leaf N content per unit area, and (c) relative leaf absorbance (scale = 9.9 to 99.9) of seedlings grown in four treatment combinations of sun, shade, ambient CO<sub>2</sub> (amb) and elevated CO<sub>2</sub> (elev). Vertical lines represent SE.

for leaves in the elevated CO<sub>2</sub> treatment than for leaves in the ambient CO<sub>2</sub> treatment.

Elevated CO<sub>2</sub> resulted in significantly higher  $A_{\text{sat}}$  in sun plants of all three species, and in shade plants of *Q. rubra* and *A. rubrum* (Table 1). There was no significant CO<sub>2</sub>-induced increase in  $A_{\text{sat}}$  of shaded *B. papyrifera*. For *B. papyrifera* and *Q. rubra*, sun leaves had higher  $A_{\text{sat}}$  than shade leaves, but this pattern was reversed in shade-tolerant *A. rubrum*. Thus, the highest  $A_{\text{sat}}$  occurred in elevated CO<sub>2</sub> in sun plants of *B. papyrifera* and *Q. rubra* and in shade plants of *A. rubrum*. Among sun plants of all three species, *B. papyrifera* had the highest  $A_{\text{sat}}$  ( $P < 0.05$ ) in both CO<sub>2</sub> treatments. However, species ranking of  $A_{\text{sat}}$  in shade plants was altered by elevated CO<sub>2</sub> and was highest in *Q. rubra* ( $P < 0.05$ ). The CO<sub>2</sub>- and light-induced increases in  $A_{\text{sat}}$  were generally accompanied by significant

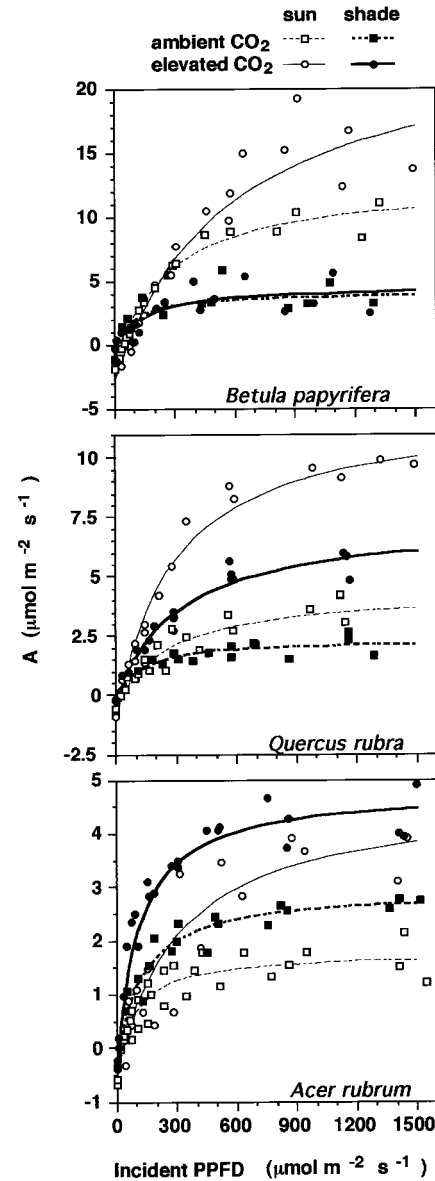


Figure 3. Net photosynthetic rate ( $A$ ) versus incident photosynthetic photon flux density (PPFD) of seedlings grown in four combinations of sun (thin lines), shade (heavy lines), ambient CO<sub>2</sub> (broken lines) and elevated CO<sub>2</sub> (solid lines). Corresponding light response parameters are given in Table 1.

increases in the light saturation constant ( $K$ ), and species ranking of  $K$  was generally consistent with that of  $A_{\text{sat}}$ . In *A. rubrum*, however, the shade-induced increase in  $A_{\text{sat}}$  was accompanied by a decrease in  $K$  in the elevated CO<sub>2</sub> treatments.

Respiration rate ( $R_d$ ), as determined from  $A/\text{PPFD}$  relationships, was significantly lower in shade plants than in sun plants for all species  $\times$  CO<sub>2</sub> combinations, except *A. rubrum* in elevated CO<sub>2</sub> (Table 1). Elevated CO<sub>2</sub> only induced a significant decrease in  $R_d$  in *Q. rubra* shade plants and *A. rubrum* sun plants. Among species in all treatments, the highest ( $P < 0.05$ )  $R_d$  occurred in *B. papyrifera*.

Table 1. Photosynthetic light response parameters of leaves of shade-intolerant *Betula papyrifera*, moderately shade-tolerant *Quercus rubra*, and shade-tolerant *Acer rubrum* seedlings grown in sun or shade and 350 (ambient) or 714 (elevated)  $\mu\text{mol mol}^{-1}\text{CO}_2$ . Means ( $\pm$  SE) of a parameter within a row or column with the same letter are not significantly different ( $P > 0.05$ ). Corresponding functions are shown in Figure 3.

	Ambient CO <sub>2</sub>		Elevated CO <sub>2</sub>	
	Sun	Shade	Sun	Shade
<i>Light-saturated photosynthetic rate (<math>A_{\text{sat}}</math>, <math>\mu\text{mol m}^{-2}\text{s}^{-1}</math>)</i>				
<i>B. papyrifera</i>	10.53 $\pm$ 2.55 b	4.08 $\pm$ 0.85 c	17.86 $\pm$ 4.82 a	4.43 $\pm$ 0.86 c
<i>Q. rubra</i>	3.88 $\pm$ 0.41 c	2.38 $\pm$ 0.23 d	9.96 $\pm$ 1.26 b	6.27 $\pm$ 0.60 a
<i>A. rubrum</i>	1.78 $\pm$ 0.20 a	2.72 $\pm$ 0.38 d	3.15 $\pm$ 0.64 d	4.42 $\pm$ 0.25 c
<i>Saturation constant (<math>K</math>, <math>\mu\text{mol m}^{-2}\text{s}^{-1}</math>)</i>				
<i>B. papyrifera</i>	246 $\pm$ 5 b	85 $\pm$ 15 c	626 $\pm$ 96 a	135 $\pm$ 56 c
<i>Q. rubra</i>	252 $\pm$ 17 b	121 $\pm$ 15 c	330 $\pm$ 55 d	324 $\pm$ 48 bd
<i>A. rubrum</i>	146 $\pm$ 86 c	117 $\pm$ 24 c	253 $\pm$ 84 d	107 $\pm$ 38 c
<i>Dark respiration rate (<math>R_d</math>, <math>\mu\text{mol m}^{-2}\text{s}^{-1}</math>)</i>				
<i>B. papyrifera</i>	1.27 $\pm$ 0.34 a	0.69 $\pm$ 0.19 b	1.40 $\pm$ 0.40 a	0.75 $\pm$ 0.27 b
<i>Q. rubra</i>	0.62 $\pm$ 0.06 b	0.36 $\pm$ 0.09 c	0.86 $\pm$ 0.20 b	0.20 $\pm$ 0.02 a
<i>A. rubrum</i>	0.62 $\pm$ 0.04 b	0.39 $\pm$ 0.05 c	0.43 $\pm$ 0.12 c	0.38 $\pm$ 0.09 c
<i>Light compensation point (<math>\Gamma</math>, <math>\mu\text{mol m}^{-2}\text{s}^{-1}</math>)</i>				
<i>B. papyrifera</i>	54.9 $\pm$ 14.0 a	16.4 $\pm$ 2.1 b	55.9 $\pm$ 11.2 a	30.5 $\pm$ 18.0 b
<i>Q. rubra</i>	48.9 $\pm$ 6.1 a	23.7 $\pm$ 7.0 b	26.1 $\pm$ 1.7 b	10.7 $\pm$ 1.5 c
<i>A. rubrum</i>	35.8 $\pm$ 6.4 a	20.2 $\pm$ 6.2 b	22.2 $\pm$ 4.3 b	9.8 $\pm$ 3.4 c
<i>Apparent quantum yield (<math>\Phi</math>, <math>\text{mol C mol}^{-1}</math>)</i>				
<i>B. papyrifera</i>	0.022 $\pm$ 0.007 a	0.021 $\pm$ 0.001 a	0.024 $\pm$ 0.006 a	0.024 $\pm$ 0.005 a
<i>Q. rubra</i>	0.011 $\pm$ 0.002 b	0.013 $\pm$ 0.001 bc	0.023 $\pm$ 0.005 a	0.018 $\pm$ 0.001 ac
<i>A. rubrum</i>	0.007 $\pm$ 0.002 d	0.017 $\pm$ 0.003 ab	0.010 $\pm$ 0.003 d	0.035 $\pm$ 0.007 e

The elevated CO<sub>2</sub> treatment resulted in lower ( $P < 0.05$ ) light compensation points ( $\Gamma$ ) in both sun and shade plants of *Q. rubra* and *A. rubrum*, but not in *B. papyrifera* (Table 1). There were no significant species differences with respect to the effects of light or CO<sub>2</sub> treatments on  $\Gamma$ . In all species, shade plants had significantly lower  $\Gamma$  than sun plants.

Apparent photosynthetic quantum yield ( $\Phi$ ) tended to increase with elevated CO<sub>2</sub> but the increase was only statistically significant ( $P < 0.05$ ) in sun plants of *Q. rubra* and shade plants of *A. rubrum* (Table 1). Among species, light had the greatest effect on  $\Phi$  in *A. rubrum*, particularly in the elevated CO<sub>2</sub> treatments; therefore, shade plants of *A. rubrum* in elevated CO<sub>2</sub> had the highest  $\Phi$  of all study species and treatments.

#### Daily C balance

Estimated diurnal  $A$  ( $A'$ ) gave a theoretical indication of the effect of elevated CO<sub>2</sub> on the daily carbon balance of sun and shade leaves based on the light environments shown in Figure 1. Shade leaves of *B. papyrifera* had similar diurnal  $A'$  in both CO<sub>2</sub> treatments and sun leaves had similar  $A'$  at low PPFD (Figure 4). At high PPFD (i.e., between 0800 and 1700 h), *B. papyrifera* sun leaves had higher  $A'$  in elevated CO<sub>2</sub> than in ambient CO<sub>2</sub>. Shade leaves of *Q. rubra* had higher  $A'$  in elevated CO<sub>2</sub> than in ambient CO<sub>2</sub> primarily during light patches, whereas sun leaves tended to have higher  $A'$  at all PPFDs greater than  $\Gamma$ . The data obtained for *A. rubrum* were similar to those for *Q. rubra* except for higher  $A'$  in shade leaves than in sun leaves during light patches.

In response to elevated CO<sub>2</sub>, daily (24 h) integrated leaf C

balance, based on diurnal  $A'$  and  $R_d$ , significantly increased in sun and shade leaves of *Q. rubra* and *A. rubrum*, but not in *B. papyrifera* (Figure 5a). Daily C balance was lower in shade leaves than in sun leaves of *B. papyrifera* and *Q. rubra*, but was similar among sun and shade leaves of *A. rubrum* in a given CO<sub>2</sub> treatment. In the elevated CO<sub>2</sub> treatment, daily C balance of shade leaves tended to increase with the shade tolerance of the species, whereas daily C balance was similar among species in the ambient CO<sub>2</sub> treatment.

#### Discussion

The study species exhibited widely contrasting responses to light and elevated CO<sub>2</sub>. The two most shade-tolerant species, *Q. rubra* and *A. rubrum*, had increased % leaf N and  $\alpha_r$  when grown in shade (cf. Björkman and Holmgren 1963, Loach 1967, Wallace and Dunn 1980, St-Jacques et al. 1991). The greater effect of shade on  $\alpha_r$  than on leaf N content suggests that a greater proportion of leaf N was partitioned to chlorophyll in shade leaves than in sun leaves of *Q. rubra* and *A. rubrum*. Plasticity in partitioning of leaf N between light harvesting and carbon reduction pools is particularly well developed in shade-tolerant species (Givnish 1988, Evans 1989). In shade, N reapportionment in favor of light harvesting machinery ensures that RuBP regeneration, which depends in part on ATP production in photosynthetic light reactions, remains in balance with Rubisco activity (cf. von Caemmerer and Farquhar 1981). This shade-induced N reapportionment response has implications for photosynthetic acclimation to

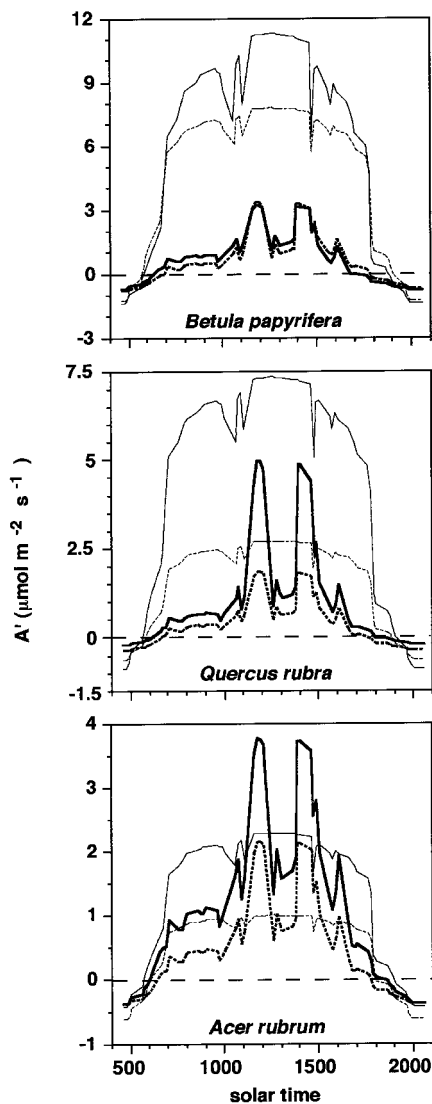


Figure 4. Diurnal leaf photosynthetic rates ( $A'$ ) interpolated from photosynthetic light response curves and the diurnal light environment of seedlings grown in four combinations of sun (thin lines), shade (heavy lines), ambient  $\text{CO}_2$  (broken lines) and elevated  $\text{CO}_2$  (solid lines).

elevated  $\text{CO}_2$ , because high  $\text{CO}_2$  availability tends to increase Rubisco activity but not RuBP regeneration capacity (cf. Bowes 1991). For example, we found that the elevated  $\text{CO}_2$  treatment caused a reduction in the leaf N content of sun leaves (cf. Coleman et al. 1991, Owensby et al. 1993, Tissue et al. 1993); however, there was no  $\text{CO}_2$ -induced decrease in  $\alpha_r$ , suggesting that sun leaves had a greater proportion of leaf N in light harvesting machinery in elevated  $\text{CO}_2$  than in ambient  $\text{CO}_2$ . In other species, elevated  $\text{CO}_2$  caused greater decreases in Rubisco activity than in chlorophyll content, resulting in lower total leaf N (cf. von Caemmerer and Farquhar 1984, Tissue et al. 1993). In the present study, this phenomenon increased with shade tolerance rank, reflecting the plasticity for N partitioning of shade-tolerant species (cf. Evans 1989).

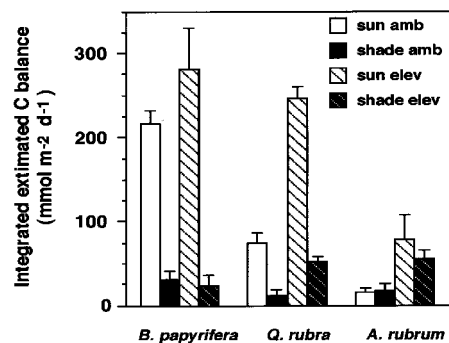


Figure 5. Daily (24 h) integrated leaf carbon balance, based on interpolated diurnal photosynthetic rates shown in Figure 4. Seedlings were grown in four combinations of sun, shade, ambient  $\text{CO}_2$  and elevated  $\text{CO}_2$ . Vertical lines represent SE.

Because partitioning of leaf N in shade-tolerant species occurs in response to either shade or elevated  $\text{CO}_2$ , these species may be able to acclimate to elevated  $\text{CO}_2$  by leaf N partitioning more readily than shade-intolerant species. We emphasize that acclimation to elevated  $\text{CO}_2$  by means of leaf N partitioning differs from photosynthetic down-regulation due to sink strength limitations observed in potted plants exposed to elevated  $\text{CO}_2$ .

The photosynthetic light response curves were representative of shade-intolerant, moderately shade-tolerant and shade-tolerant species. For example, leaves that developed in sun in the presence of an elevated  $\text{CO}_2$  concentration tended to exhibit delayed saturation of photosynthesis, evidenced by higher  $K$ , as a result of light attenuation through the thickness of the leaf (Ramos and Grace 1990, Riddoch et al. 1991). In addition, at high irradiances, shade leaves of *A. rubrum* had  $A'/\text{PPFD}$  curves positioned above those of sun leaves, a phenomenon that has been reported previously for some (Björkman and Holmgren 1963, Bazzaz and Carlson 1982), but not all shade-tolerant species (Loach 1967, Wallace and Dunn 1980). Typical of shade-intolerant species, *B. papyrifera* exhibited much larger light-induced shifts in  $A_{\text{sat}}$  than did the shade-tolerant species *Q. rubra* and *A. rubrum* (Loach 1967, Wallace and Dunn 1980, Bazzaz and Carlson 1982, Teskey and Shrestha 1985, Ramos and Grace 1990). Bazzaz and Carlson (1982) suggested that the large variability in  $A'/\text{PPFD}$  relationships of shade-intolerant species is associated with a high adaptive ability to variation in light environment. Teskey and Shrestha (1985) argued that because shade-tolerant species tend to exhibit a smaller shade-induced change in their  $A'/\text{PPFD}$  relationship than shade-intolerant species, they experience less shade-induced stress and therefore exhibit greater plasticity to changes in irradiance. Our findings of larger light-induced shifts in % leaf N,  $\alpha_r$ ,  $\phi$  and  $\Gamma$  in *Q. rubra* and *A. rubrum* than in *B. papyrifera* support the latter interpretation.

*Quercus rubra* and *A. rubrum* exhibited  $\text{CO}_2$ -induced decreases in  $\Gamma$  and increases in  $\phi$ . Under current ambient  $\text{CO}_2$  conditions, the affinity of Rubisco for  $\text{O}_2$  may result in a

photorespiratory loss of up to 50% of carbon fixed (Tolbert and Zelitch 1983). Increasing the atmospheric CO<sub>2</sub>/O<sub>2</sub> ratio allows a greater proportion of absorbed light energy to be utilized for net carbon fixation, thus altering the A/PPFD relationship (Ehleringer and Björkman 1977, Tolbert and Zelitch 1983, Long and Drake 1991). Consequently, increases in  $\phi$  in response to elevated atmospheric CO<sub>2</sub> have been related primarily to increased carboxylase compared to oxygenase activity of Rubisco in C<sub>3</sub> plants (Ehleringer and Björkman 1977, Pearcy and Björkman 1983, Long and Drake 1991). Because plants grown in low irradiance are essentially carbon limited (Bazzaz and McConnaughay 1992), an increase in  $\phi$  should translate to an increase in the ability of understory plants to compete for light, irrespective of whether the  $\phi$  shift is induced by low light or by elevated CO<sub>2</sub>.

We found that the various CO<sub>2</sub>-induced shifts in light response parameters interacted to produce different predictions for leaf-level C balance under different light conditions, with the effects of shade being most pronounced in the most shade-tolerant species. Although the lower diurnal temperatures in the shaded chambers than in the sunlit chambers may have served to depress  $R_d$  and further enhance daily C balance, the observed shifts in estimated daily leaf C balance are consistent with other studies. For example, shade-tolerant species exhibited greater relative increases in biomass than less shade-tolerant species in elevated CO<sub>2</sub>, and late-successional species exhibited greater CO<sub>2</sub>-induced increases in growth in shade than in sun (Bazzaz et al. 1990, Bazzaz and Miao 1993).

If the variation among the study species in photosynthetic response to elevated CO<sub>2</sub> at low irradiance is directly related to the intrinsic shade tolerance of the species, then acclimation to elevated CO<sub>2</sub>, which results in increased N use efficiency, may operate by one of the mechanisms underlying photosynthetic acclimation to shade. Furthermore, elevated CO<sub>2</sub> may facilitate the ability of shade-tolerant plants to compete for light and improve their carbon balance (cf. Pearcy and Björkman 1983). However, elevated CO<sub>2</sub> may affect the competitive ability of understory plants for resources other than light, such as water and nutrients. In addition, increased leaf-level photosynthetic rate may not necessarily translate to increased whole-plant carbon balance (Givnish 1988, Bazzaz and McConnaughay 1992). Notwithstanding these complications and our limited sample size, our conclusions are consistent with the results obtained from studies of whole-plant growth (Teskey and Shrestha 1985, Reekie and Bazzaz 1989, Bazzaz et al. 1990, Bazzaz and Miao 1993). We conclude that if responses to elevated atmospheric CO<sub>2</sub> parallel the successional status of tree species, the composition and dynamics of successional forest communities will be greatly affected by the predicted increase in atmospheric CO<sub>2</sub>.

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