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Photosynthetic sunfleck utilization potential of understory saplings growing under elevated CO₂ in FACE

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Abstract Few studies have evaluated elevated CO₂ responses of trees in variable light despite its prevalence in forest understories and its potential importance for sapling survival. We studied two shade-tolerant species (*Acer rubrum*, *Cornus florida*) and two shade-intolerant species (*Liquidambar styraciflua*, *Liriodendron tulipifera*) growing in the understory of a *Pinus taeda* plantation under ambient and ambient+200 ppm CO₂ in a free air carbon enrichment (FACE) experiment. Photosynthetic and stomatal responses to artificial changes in light intensity were measured on saplings to determine rates of induction gain under saturating light and induction loss under shade. We expected that growth in elevated CO₂ would alter photosynthetic responses to variable light in these understory saplings. The results showed that elevated CO₂ caused the expected enhancement in steady-state photosynthesis in both high and low light, but did not affect overall stomatal conductance or rates of induction gain in the four species. Induction loss after relatively short shade periods (<6 min) was slower in trees grown in elevated CO₂ than in trees grown in ambient CO₂ despite similar decreases in stomatal conductance. As a result leaves grown in elevated CO₂ that maintained induction well in shade had higher carbon gain during subsequent light flecks than was expected from steady-state light response measurements. Thus, when frequent sunflecks maintain stomatal conductance and photosynthetic induction during the day, enhancements of long-term carbon gain by elevated CO₂ could be underestimated by steady-state photosynthetic measures. With respect to species differences, both a toler-

ant, *A. rubrum*, and an intolerant species, *L. tulipifera*, showed rapid induction gain, but *A. rubrum* also lost induction rapidly (*c.* 12 min) in shade. These results, as well as those from independent studies in the literature, show that induction dynamics are not closely related to species shade tolerance. Therefore, it cannot be concluded that shade-tolerant species necessarily induce faster in the variable light conditions common in understories. Although our study is the first to examine dynamic photosynthetic responses to variable light in contrasting species in elevated CO₂, studies on ecologically diverse species will be required to establish whether shade-tolerant and -intolerant species show different photosynthetic responses in elevated CO₂ during sunflecks. We conclude that elevated CO₂ affects dynamic gas exchange most strongly via photosynthetic enhancement during induction as well as in the steady state.

Key words Elevated CO₂ · Shade tolerance · Photosynthetic induction · Stomatal conductance · Understory trees

Introduction

Rising atmospheric CO₂ is likely to have large impacts on both overstory and understory components of forest ecosystems (Körner 1996; Saxe et al. 1998). Tree seedling growth responses to elevated CO₂ differ greatly among species and are often affected by the availability of other resources such as light (Williams et al. 1986; Bazzaz and Miao 1993). Research on comparing tree species of different “functional” groups such as shade tolerance is rare (Eamus 1996), although some studies indicate that shade-intolerant species may benefit more from elevated CO₂ than tolerant species (Bolker et al. 1995; Rochefort and Bazzaz 1992). In contrast to that prediction, a recent analysis of studies of shade tolerance and CO₂ responses showed that tolerant species generally have greater CO₂ enhancements of photosynthesis and biomass than less tolerant species (Kerstiens 1998).

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Even for shade-tolerant species characteristic of forest understories, most elevated CO₂ studies have been conducted with plants growing under high-light conditions or artificial, homogeneous shade (Bazzaz et al. 1990; Saxe et al. 1998). Light conditions in forests are much more complex, with periods of low diffuse light alternating with sunflecks, defined as short periods of high light intensities (Chazdon 1988). Sunflecks have the potential to greatly contribute to the daily carbon gain in understory species since they represent around half of the daily photosynthetically active radiation under the canopies of temperate forests (Chazdon 1988). The efficient utilization of sunflecks may thus be crucial to carbon gain in understory plants. Elevated CO₂ should enhance carbon gain in forest environments with variable light levels, since photosynthesis is generally enhanced under elevated CO₂ at both low and saturating light (Osborne et al. 1997). Yet virtually no studies have examined elevated CO₂ effects on plant performance in variable light that occurs in forest understories.

For leaves maintained in shade, photosynthetic responses to sudden increases in light via sunflecks are not instantaneous because photosynthetic enzymes are deactivated and stomata are partially closed (Percy et al. 1994). Thus, to rapidly reach light saturated photosynthesis (A_{sat}) after a shade period, leaves must be capable of (1) rapid light activation of photosynthetic enzymes, chiefly Rubisco, (2) rapid stomatal opening, and (3) the maintenance of high enzyme activation and high stomatal conductance (g) during low-light periods (Chazdon 1988; Percy et al. 1994). Elevated CO₂ may potentially influence the ability to rapidly reach light saturation, since elevated CO₂ can decrease the amount of the primary carboxylating enzyme Rubisco or its activity (Sage et al. 1989; Sage 1994; Drake et al. 1997). Further, elevated CO₂ plants often have decreased g (Drake et al. 1997; Saxe et al. 1998). Thus, even if actual induction rates are not altered by elevated CO₂, the reduced maximum activity of Rubisco and rate of g should be reached faster in elevated CO₂ plants than ambient ones. So far only one study has examined the effects of elevated CO₂ on gas exchange rates under variable light. Stomata of a C₄ grass responded to elevated CO₂ with overall reduced g , leading to faster stomatal opening during sunflecks (Knapp et al. 1994).

Plant species can differ in their capacity to utilize sunflecks (e.g., Chazdon and Percy 1986a, 1986b; Tinoco-Ojanguren and Percy 1993a; Küppers et al. 1996) and elevated CO₂ may potentially affect species utilization of sunflecks through its effects on photosynthesis and stomatal conductance. Since sunfleck responses have important implications for photosynthesis in understories that can translate into growth differences (Percy 1983; Oberbauer et al. 1988; Watling et al. 1997), the possibility exists that relative species importance will shift in an elevated-CO₂ atmosphere as a result of interactions with shade tolerance.

We studied the effect that growth [CO₂] has on both steady-state and dynamic gas exchange rates in four tree

species with different ecological traits. Using field-grown understory saplings that were exposed to ambient and ambient+200 ppm CO₂ for 2 years, we addressed the following questions regarding their gas exchange responses to light intensity changes:

1. Does elevated CO₂ affect induction dynamics in temperate hardwood species?
2. Do species of contrasting ecology differ in their response to elevated CO₂ and in their induction dynamics?

We investigated these questions using *Acer rubrum* L. and *Cornus florida* L., two species that tolerate shading well, and *Liquidambar styraciflua* L. and *Liriodendron tulipifera* L., which are considered shade intolerant (Baker 1949; Peet and Christensen 1980; Burns and Honkala 1990).

Methods

Study site

The study was conducted at the FACTS-1 site in Duke Forest, North Carolina (USA) which is equipped with six free-air CO₂ enrichment rings (described in Hendrey et al. 1999). The site is located in a *Pinus taeda* plantation established in 1983. No understory species control measures were taken after planting. Consequently, regeneration of hardwood species is widespread in the subcanopy and understory. Three rings are operating at ambient atmospheric [CO₂] and three controlled to maintain ambient+200 ppm CO₂ in the *P. taeda* canopy. Ambient- and elevated-CO₂ rings are paired based on overstory pine and soil nutritional properties. At the height of the study saplings in the center of the ring, mean daytime [CO₂] was 569±24 ppm (mean±1 SD) for $n=3$ elevated CO₂ rings and ~365 ppm in the ambient rings (G.R. Hendrey, K.F. Lewin, J. Nagy, unpublished work; see also Hendrey et al. 1999). A more detailed description of the site can be found in Ellsworth et al. (1995) and Hendrey et al. (1999).

Two separate data sets were collected at the site. The first set was collected during July and August 1997 when precipitation was 70% of normal in nearby Chapel Hill. Only one shade-tolerant species, *A. rubrum* and one shade-intolerant species, *L. styraciflua*, were measured in 1997. The second data set was collected in June 1998 after an unusually wet spring with close to normal June precipitation. In addition to *A. rubrum* and *L. styraciflua*, *C. florida* and *L. tulipifera* were measured in 1998 to give two replicate species for both shade-tolerant and intolerant classes.

For the gas exchange measurements, saplings approximately 2.0–4.5 m in height and between 1.0 and 2.5 cm diameter at 1.4 m were selected in each ring. For one branch on each sapling, the light environment was evaluated as percent diffuse light transmission using two LI-190 PAR sensors (LI-COR, Lincoln, Neb., USA) on a cloudy day (Messier and Puttonen 1995; Gendron et al. 1998). In addition, photodiodes (GaAsP G1118, Hamamatsu, Bridgewater, N.J., USA) were used to determine light regimes for 24 saplings during the summer of 1997. The photodiodes were calibrated against a LI-190 photosynthetically active radiation (PAR) sensor and connected to a Campbell 21X data logger and storage module (Campbell Scientific, Lodgen, Utah, USA). The logger was recording instantaneous readings at 5-s intervals for 8 h approximately centered around solar noon (830–1630 hours Eastern Standard Time, EST). From the photodiode data, frequency histograms for sunfleck duration and intensity as well as shade duration were generated. Light intensities above 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$

(photosynthetic photon flux density, PFD) were considered to be sunflecks.

Gas exchange measurements

Combined CO₂ and H₂O exchange was measured for two saplings per day on leaves that had been enclosed in shade cloth since the previous afternoon and were therefore uninduced. The measurement of the first sapling began at 0700 hours local time and of the second sapling approximately 3 h later. A single leaf per sapling was enclosed in a miniature controlled-environment chamber of the CIRAS-1 open photosynthesis system (PP-Systems, Hitchin, UK). The flow rate of the system was set to 200 ml min⁻¹ for all measurements. The detection lag times for changes in CO₂ in the air-stream for the gas exchange system were determined by injecting a steady stream of CO₂ with a fine tube into the chamber. At the measurement flow rate, a change in the chamber [CO₂] was detected within 15 s and the measurements reached 90% of the actual value within 35 s.

Chamber conditions were controlled by the system to supply CO₂ equivalent to the growth [CO₂] and constant water vapor. Leaf temperature was set to a constant 28°C resulting in about 1.6 kPa leaf-to-air vapor pressure deficit or 60% relative humidity during measurements. Light values in the chamber were controlled with a halogen slide projector bulb (Sylvania EXT 50 W 12 V) and neutral density window film (3M Corporation, Minneapolis, Minn., USA).

For each of the measurement sets, a leaf was exposed to an arbitrary light regime under otherwise constant environmental conditions to determine both induction gain under high light and induction loss during shade. The light regime used was a sequence of ≥15 min at low light followed by a period of high light until the leaf reached constant gas exchange rates for 5 min, followed by shade periods of 6, 2, and 12 min length. These shade periods were each separated by high-light periods long enough to attain the maximum steady rates prior to shading. This sequence of alternating saturating and shade light was chosen to allow determination of rates of both induction gain and loss, which are important for the efficiency of photosynthesis during sunflecks (e.g., Chazdon and Pearcy 1986b; Valladares et al. 1997). The recording interval during the measurement runs was 10 s. Light intensities for low and high light were ~50 and ~1000 μmol m⁻² s⁻¹, respectively. Both high and low light levels represent intensities that the saplings would experience during overstory *P. taeda* shade and sunflecks. Based on the system lag response results, the gas exchange data were offset with the light change by 10 s, e.g., the first measurement under high light was assigned to the shade period while the second measurement represents the first high-light data point. Since light intensity was changed immediately after a CIRAS recording, the second measurement after a light change was >15 s after that change.

After the completion of the light measurement sets, photosynthetic responses to [CO₂] (called *A/c_i* curves) were determined to evaluate biochemical induction states (Küppers and Schneider 1993) and determine carboxylation efficiency using the model of Farquhar and von Cammerer (1982).

In 1997, the experimental light regime for the measurements was similar to that used in 1998. However, the leaves were only exposed to the initial low-light level for 3 min, which was insufficient to reach full equilibrium gas exchange rates at low light. The 1997 measurements were conducted with an earlier model of the temperature-controlled chamber used in the 1998 measurements. Since flow was separated between the upper and lower leaf surfaces in this earlier chamber configuration, measurements with this chamber resulted in erroneously low values of stomatal conductance in hypostomatous leaves while *A* was not affected (Keith Parkinson, PP-Systems, personal communication). Thus only the *A* responses to light changes are reported for the 1997 data.

Data analyses

Gas exchange values during the initial low-light period were used as shade equilibrium values, while the maximum values reached

during the subsequent high-light period were considered light saturated. Light saturation in the saplings was measured via light response curves and was reached around 600 μmol m⁻² s⁻¹. Photosynthetic induction (IS) was evaluated by the method described in Chazdon and Pearcy (1986a):

$$IS = (A_{60s} - A_{shade}) / (A_{high} - A_{shade}) \times 100,$$

where *A*_{60s} represents the photosynthetic rate at 60 s into the high-light period, *A*_{shade} the rate during the initial low-light period and *A*_{high} the rate just prior to the shade period in question, or, for the determination of the initial low light, the maximal rate during the subsequent high-light period. Since the 1997 data set did not provide steady-state low-light *A* because of the short initial equilibration time, low-light *A* at the end of the 6 min shade period was used for the calculation. We compared in the 1998 data set *A*_{shade} with *A* at the end of the 6-min shade period and found no significant difference in the values. Due to the short low-light equilibration in 1997, initial low-light IS is not reported.

To determine actual carbon gain after the shade periods, photosynthetic rates were multiplied by the measurement time interval of 10 s and summed up for 2 min after the light increase. The resulting integrated rates of photosynthesis (*A*_{int}) are comparable to rates that would be achieved during a 2-min lightfleck, except that our analysis does not include post-illumination carbon fixation. Post-illumination fixation generally lasts for around 10 s and decreases in importance for lightfleck photosynthesis with increasing lightfleck duration (Chazdon and Pearcy 1986b). Further, species do not differ in post-illumination fixation, which is a function of maximal photosynthetic rates (Pearcy et al. 1996). Thus, while our analysis does underestimate expected lightfleck photosynthesis, it should not affect any observed differences among species or CO₂ treatments.

The biochemical induction state (BIS) was determined by expressing *A* as a function of the leaf-intercellular [CO₂] (*c_i*). The slope that a point of the *A/c_i* relationship during induction gain creates with the light-independent CO₂ compensation point (Γ*) and *A* at Γ* is divided by the slope of *A/c_i* curve to calculate BIS (Küppers and Schneider 1993). Γ* was calculated using the formula of Brooks and Farquhar (1985). BIS is expressed as a percentage. For about 2 min into a light increase, BIS reflects the combined effect of Rubisco and RuBP-regeneration enzymes. Since the latter enzymes activate rapidly, subsequent increases in BIS reflect Rubisco activity (Woodrow and Mott 1989; Ernsten et al. 1997).

A crucial assumption in this analysis is that stomata are not patchy during induction, so that the calculation of *c_i* is accurate. If stomata become patchy in response to a light change, then *c_i* could be overestimated. However, a recent modeling study showed that stomatal apertures must have very specific distributions of apertures (that are rarely observed) to yield large *c_i* errors, thus greatly reducing the number of situations where stomatal patchiness affects *c_i* calculations (Mott and Buckley 1998). Also, patchiness requires several minutes after a light change to develop and in some species requires some water stress (Eckstein et al. 1996). Thus it is unlikely that the calculation of BIS directly after a shade period would have been affected especially for the 1998 data when sufficient precipitation precluded water stress.

Rates of increases in photosynthesis, stomatal conductance, and BIS in response to high light were evaluated by exponential curves fit to the data, e.g.:

$$A(\text{time}) = A_{low} + (A_{high} - A_{low}) \times (1 - \exp^{-\text{time}/\tau}),$$

where *A*(time) is the photosynthetic rate as a function of minutes since the light increase, *A*_{low} the rate of *A* prior to the light increase, *A*_{high} the maximal rate achieved during the high-light period, and 1/τ the time constant when 63% of the change has occurred.

In cases where photosynthetic or stomatal responses exhibited a lag greater than about 1 min, a logistic curve was used instead (Fig. 1a), e.g.:

$$g(\text{time}) = g_{low} + \frac{g_{high} - g_{low}}{1 + (\text{time}/a)^b},$$

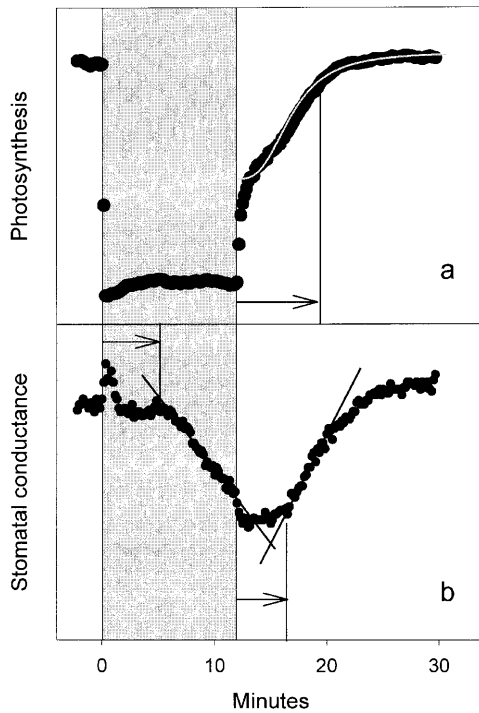


Fig. 1a,b Description of analyses conducted on the light regime data with the example of a 12-min shade period (darker column). **a** The photosynthetic response to a light increase was fit by a logistic curve to determine the time to 90% change (arrow). **b** Stomatal response to shade showing linear regression fits to determine rates of stomatal opening/closing and lag times (arrows)

where $g(\text{time})$ is the stomatal conductance as a function of minutes since the light increase, g_{high} the maximal rate of g achieved after the light increase, g_{low} the minimum rate of g in response to the shade period, a the inflection point, and b the slope parameter of the curve. The curves were fit in SigmaPlot 4.0 (SPSS Inc., Evanston, Ill., USA) using least-squares non-linear regression. From these curves the time required to achieve 90% of maximal photosynthesis ($t_{90\%A}$) (Fig. 1a), stomatal conductance ($t_{90\%g}$), and BIS ($t_{90\%B}$) were estimated during the initial induction phase and after the 12-min shade period.

Stomatal closure in response to the shade periods was evaluated by visually determining the minimum g reached in response to the shade period. Due to stomatal response lags, this minimum often occurred during the subsequent high-light period (e.g., Fig. 1). To evaluate stomatal opening and closing rates, linear regression lines were fit to the linear portion of the closing response during the 12 min shade period and to the opening response after the 12 min shade as well as the initial induction phase (Tinoco-Ojanguren and Pearcy 1993a; Fig. 1b). The other shade periods were excluded because they were too short to allow this analysis. The lag time of stomatal response to the light intensity change was calculated by taking the intersection of the regression line with the previous maximum or minimum conductance (Fig. 1b).

Variables that were measured after each of the shade periods, i.e. IS, A integrated for 2 min, g_{min} , and BIS were analyzed with repeated measures ANOVA. Main factors were species, growth $[\text{CO}_2]$, block, and shade length as the repeated factor. For the blocking factor, each pair of ambient and elevated CO_2 rings were considered a different block. Since these variables all showed a significant species \times shade length interaction, responses after each shade period were then analyzed in separate ANOVAs. The remaining variables were analyzed by a fixed-model ANOVA with species, growth $[\text{CO}_2]$, and block as the main factors and species \times CO_2 interaction. For all analyses, the average of the saplings per species and CO_2 treatment ring were used, resulting in a sam-

ple size of 3. Data sets that did not meet assumptions of homogeneity of variance or normality were log-transformed and then analyzed. For the percentage data sets an arcsin transformation was used. All analyses were carried out in SAS version 6.12 for Windows (SAS Institute, Cary, N.C., USA).

Results

Understory light environment

The pine forest understory was characterized by frequent sunflecks. If sunflecks are defined as $\text{PFD} > 100 \mu\text{mol m}^{-2} \text{s}^{-1}$, then nearly 50% of sunflecks lasted less than 30 s and were of low PFD ($100\text{--}200 \mu\text{mol m}^{-2} \text{s}^{-1}$). The highest intensity sunflecks ($\text{PFD} > 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) generally lasted between 5 and 20 min. Shade periods following sunflecks were mostly of short duration (< 2 min), with 86% of all shade periods falling into this class. Shade periods greater than 20 min occur on average two to three times a day. The proportion of diffuse light above the measurement branches, an index of overall light availability to understory plants (Messier and Puttonen 1995) was approximately 8% in early September 1998 (range 3–15%) and was not significantly different among species or between growth CO_2 regimes.

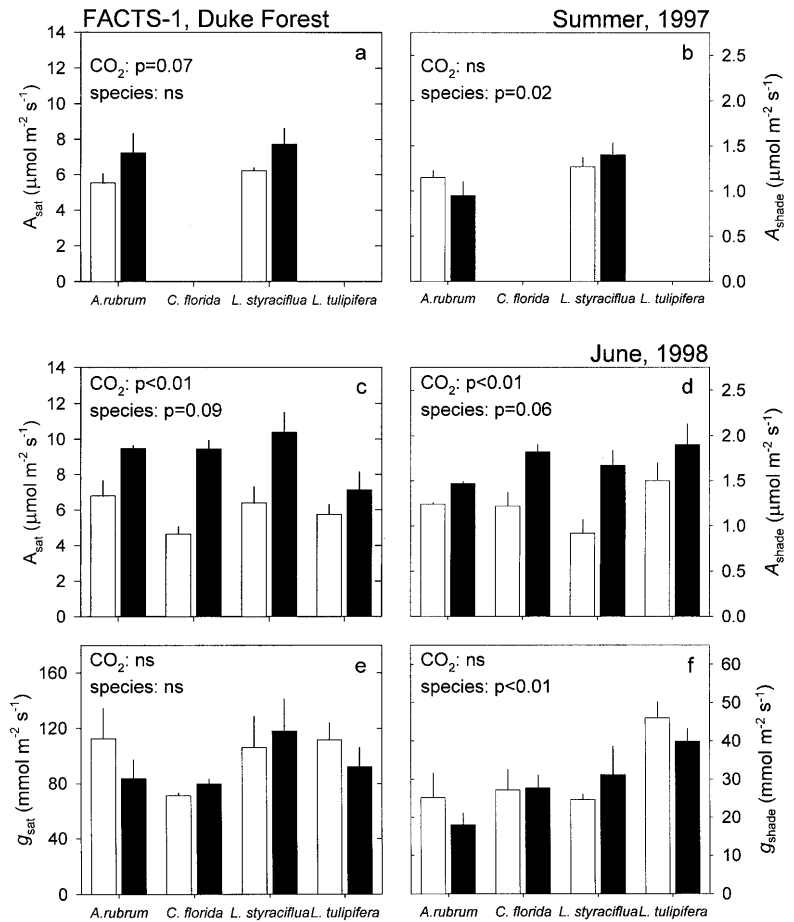
Steady state gas exchange rates

In 1997, light-saturated photosynthetic rates (A_{sat}) were similar for both species, but during the initial low-light period *Liquidambar styraciflua* had significantly higher A_{shade} than *A. rubrum* ($P=0.02$). Elevated CO_2 had a not quite significant effect on A_{sat} ($P=0.07$) with an average enhancement of 1.3 for both species (Fig. 2a). At low light, elevated CO_2 did not enhance photosynthesis relative to the ambient plants (Fig. 2b).

In 1998, A_{sat} values were not quite significantly different among species ($P=0.09$) with *Liriodendron tulipifera* having the lowest and *Liquidambar styraciflua* the overall highest rate of the species (Fig. 2c) while no significant species differences in g_{sat} existed (Fig. 2e). Species differed marginally significantly in A_{shade} ($P=0.06$) and significantly in g_{shade} ($P<0.01$) with *Liriodendron tulipifera* having significantly higher rates (Fig. 2d,f). Thus overall species differences in steady state gas exchange are largely due to high g_{shade} in *L. tulipifera* which also had the highest specific leaf area of the species (data not shown). Elevated CO_2 increased A_{sat} and A_{shade} significantly for all species by an average factor of 1.6 and 1.4, respectively. Species differences in A_{sat} enhancement ratios (Fig. 2c) were not significant. Neither g_{sat} nor g_{shade} were significantly affected by growth $[\text{CO}_2]$ (Fig. 2e,f) which was unexpected given that stomatal responses to elevated CO_2 are commonly assumed to occur.

Carboxylation efficiency of fully induced leaves differed significantly among species ($P=0.04$) but was not significantly affected by growth $[\text{CO}_2]$ ($P=0.14$, Fig. 3a). The species \times CO_2 interaction was also not significant

Fig. 2. a–d Steady state photosynthesis and e,f stomatal conductance of the four study species at light saturation (~1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$; a,c,e) and low light (~50 $\mu\text{mol m}^{-2} \text{s}^{-1}$; b,d,f) in two years. In 1997, only *Acer rubrum* and *Liquidambar styraciflua* were measured; in 1998, *Cornus florida* and *Liriodendron tulipifera* were also measured. Open bars represent saplings growing at ambient $[\text{CO}_2]$ and filled bars saplings growing at ambient+200 ppm $[\text{CO}_2]$. Bars represent means of 3 treatment rings with ± 1 SEM



($P=0.18$). Overall, the two shade-intolerant species *L. tulipifera* and *Liquidambar styraciflua* had the highest and lowest carboxylation efficiency respectively (Fig. 3a). When *C. florida* was analyzed separately, plants grown in elevated CO_2 had significantly higher carboxylation efficiency than plants grown in ambient despite growing in a similar light environment of 5.3% and 5.9% diffuse light transmission for saplings in ambient and elevated CO_2 , respectively. Therefore, the species as a group showed no overall photosynthetic adjustments to elevated CO_2 with respect to either biochemistry or stomatal conductance.

Dynamic gas exchange rates

Both biochemical induction state (BIS) and photosynthetic induction (IS) determined 60 s into the first high-light period were significantly different among species in 1998 ($P<0.01$). *Liriodendron tulipifera* had the highest and *A. rubrum* the lowest BIS and IS (Fig. 4 at continuous low light). Growth $[\text{CO}_2]$ had no significant effect on BIS or IS after low light.

Photosynthetic induction loss during shade assessed via IS differed significantly among species both in 1997 and in 1998 ($P<0.01$, Table 1, Fig. 4a) and was closely related to the effect of shade on minimum stomatal con-

ductance and BIS (Fig. 4b,c). In both years *A. rubrum* had significantly lower IS than the other species after the 6- and 12-min shade periods due to significantly larger decreases in g and BIS. The greater stomatal closure in *A. rubrum* was related to both lower lag times and higher closing rates than in the other species (Fig. 5). After 12 min shade IS, BIS, and g of *A. rubrum* leaves were similar to those prior to high-light induction (Fig. 4). In 1997, IS after 2 and 6 min shade (Table 1) and in 1998 after 6 min was not quite significantly higher for elevated

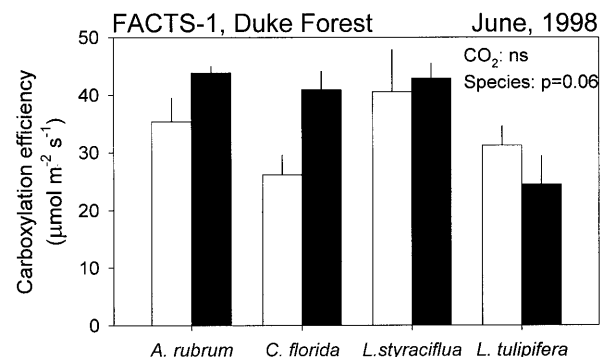


Fig. 3 Carboxylation efficiency of saplings grown in ambient (open bars) and elevated CO_2 (black bars). Bars represent means of 3 treatment rings with ± 1 SEM

Table 1 ANOVA results for dynamic gas exchange data ($t_{90\%A}$ photosynthetic induction gain, IS induction state after various shade periods) collected on *Acer rubrum* and *Liquidambar styraciflua* in summer 1997. A blocking factor was included in the analysis but is not presented. Shown are *F*-statistics, *P*-values, and means for significant species or CO₂ effects (*Ar* *A. rubrum*, *Ls* *L. styraciflua*)

		Factors			Effects	
		Species	CO ₂	Species×CO ₂	Species	CO ₂
$t_{90\%A}$ Initial	<i>F</i>	12.7	0.2	2.3	Ls>Ar	
	<i>P</i>	0.02	ns	ns	(34.4, 16.8)	
$t_{90\%A}$ 12 min shade	<i>F</i>	24.1	1.3	0.2	Ar>Ls	
	<i>P</i>	<0.01	ns	ns	(11.0, 2.5)	
IS-12 min shade	<i>F</i>	98.3	2.1	1.1	Ls>Ar	
	<i>P</i>	<0.01	ns	ns	(67.7, 26.4)	
IS-6 min shade	<i>F</i>	111.9	4.4	0.3	Ls>Ar	Elev.>amb.
	<i>P</i>	<0.01	0.08	ns	(86.7, 68.1)	(82.0, 77.4)
IS-2 min shade	<i>F</i>	0.1	16.2	2.7		Elev.>amb.
	<i>P</i>	ns	0.01	ns		(98.9, 94.0)

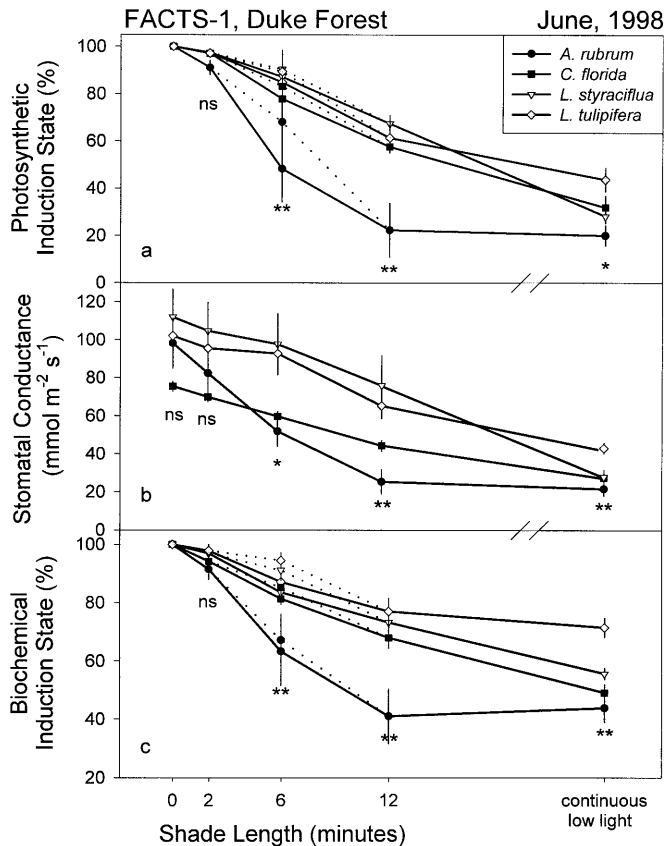


Fig. 4a-c Species responses to shade periods of varying lengths. Values at zero shade length represent maximal steady state rates under saturating light. Values at continuous low light are steady-state values reached during the initial low-light period. Values are averaged over both CO₂ treatments with ± 1 SEM except after 6 min shade where photosynthetic induction (IS) and biochemical induction state (BIS) show separate species means for leaves grown in ambient and elevated CO₂. Growth [CO₂] did not affect any of the variables except IS and BIS after 6 min shade ($P=0.07$) where the lines split to show the higher IS and BIS of plants grown in elevated CO₂ (dashed lines). Species difference significant at * $P<0.05$ and ** $P<0.01$

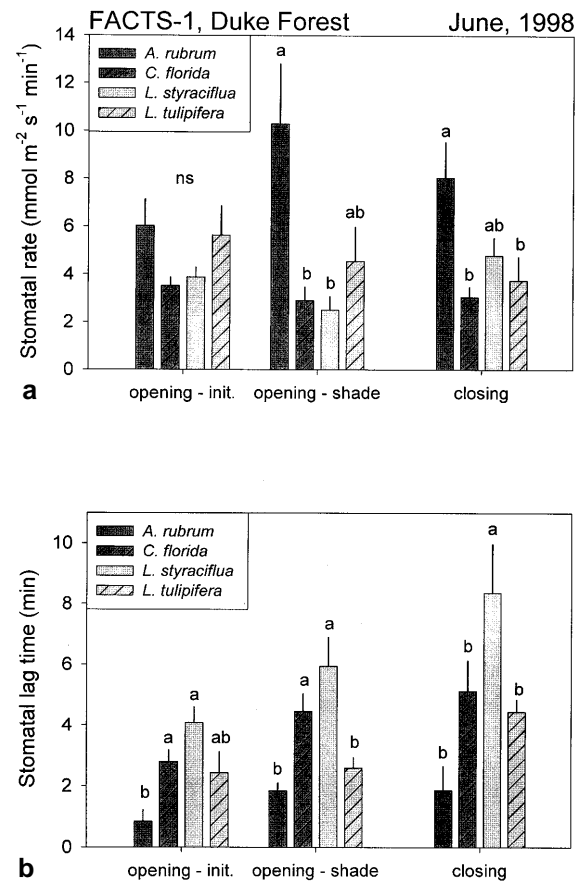


Fig. 5 a Rates of stomatal opening and closing and **b** lag times in stomatal responses during the initial induction gain and in response to the 12-min shade period. Darker bars represent the two shade-tolerant species. Values are means of plants grown in both ambient and elevated CO₂ with 1 SEM. Growth [CO₂] had no effect on either variable. Bars with different letters indicate significant species differences for each variable

ed CO₂ plants ($P=0.08$, data not shown), indicating slower induction loss during shade. In 1998 higher IS after 6 min shade was linked to not quite significantly higher BIS ($P=0.07$, data not shown).

As for induction gain of low-light acclimated leaves, the time to reach 90% of maximum photosynthetic rate

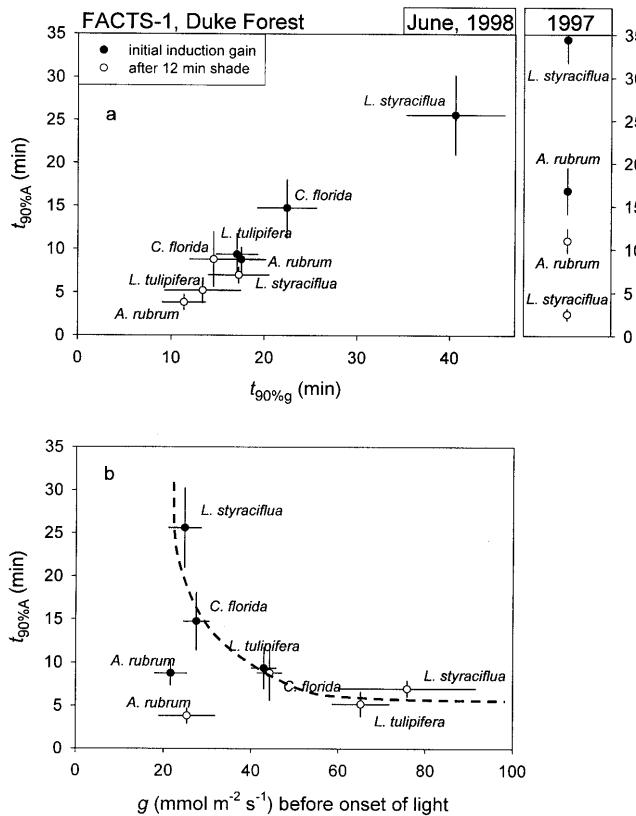


Fig. 6 Time required until 90% of maximal photosynthesis was reached as a function of **a** the time until 90% of maximal conductance and **b** the minimum conductance due to shade. Both **a** and **b** include data collected after the initial shade period (●) and after 12 min shade (○). For 1997, no stomatal conductance data was available. Dashed line in **b** shows the relationship between stomatal conductance prior to high light and the time required to reach 90% of A_{sat} . Note that *A. rubrum* does not fit this relationship

($t_{90\%A}$) differed significantly among species in 1997 and 1998 ($P < 0.01$, Fig. 6 closed symbols, Table 1) but was unaffected by growth [CO_2]. In both years *Liquidambar styraciflua* was the slowest of the species with respect to $t_{90\%A}$ and $t_{90\%g}$ (Fig. 6). No significant species differences existed in the time until 90% of BIS ($t_{90\%B}$, data not shown). Differences in the rates of stomatal opening were reflected in significant differences in stomatal lag times ($P < 0.01$, Fig. 5). While species differences were apparent in the rate of stomatal opening during the linear portion response, these were not significant (Fig. 5).

Induction gain after the 12-min shade period in all species proceeded faster than during the initial induction gain both in 1997 and 1998 (Fig. 6a). Despite the large induction loss in *A. rubrum* in 1998 (Fig. 4), no significant species differences ($P > 0.1$) were found in $t_{90\%A}$ or $t_{90\%g}$ among species in 1998 (Fig. 6a, open symbols). Rates of stomatal opening and lag times after the 12-min shade period differed significantly among species ($P = 0.04$ and $P < 0.01$, respectively, Fig. 5). *A. rubrum* showed the most rapid rates of stomatal opening in combination with low lag times. *A. rubrum* rates of stomatal opening were actually faster than during the initial in-

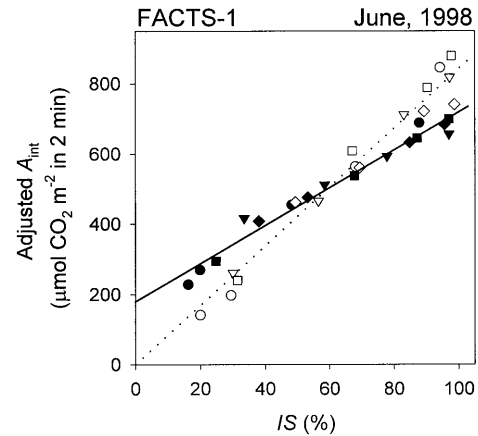


Fig. 7 Adjusted 2-min integrated rates of photosynthesis (A_{int}) of individual saplings in relation to induction state (IS). Adjusted A_{int} was obtained by subtracting the significant effect of A_{sat} and the elevated CO_2 model intercept from the measured A_{int} . Models for plants grown in ambient and elevated CO_2 differed significantly ($P < 0.01$) in intercept and slope. Shown are the regression lines obtained using individual saplings measured in 1998 (solid line ambient, dashed line elevated). For clarity, data points show means of species by CO_2 treatments after the shade periods shown in Fig. 4 (● ○ *A. rubrum*, ▼ ▽ *C. florida*, ■ □ *Liquidambar styraciflua*, ◆ ◇ *Liriodendron tulipifera*, with closed and open symbols representing ambient and elevated treatments, respectively)

duction gain (Fig. 5), thus explaining its more rapid recovery after shade. For $t_{90\%B}$, species differed significantly ($P = 0.01$) with *L. styraciflua* and *Liriodendron tulipifera* requiring less time to recover high BIS than *A. rubrum* (data not shown).

Overall species differences in $t_{90\%A}$ both during initial induction and after 12 min shade were related to stomatal behavior: $t_{90\%A}$ increased with increasing $t_{90\%g}$ (Fig. 6a). Further, $t_{90\%A}$ showed a decreasing exponential relationship with g_{min} for three species (Fig. 6b) as previously suggested by Valladares et al. (1997). This suggests that rates of stomatal conductance before a lightfleck will control how quickly induction gain will proceed. However, *A. rubrum* deviated from this relationship due to responsive stomata that opened quickly after short lag times (Fig. 5).

Photosynthesis integrated for 2 min after a shade period (A_{int}) decreased significantly with increasing shade duration. In addition, elevated CO_2 significantly increased A_{int} . Species also differed in their integrated A in that *Liquidambar styraciflua* had the overall highest rates, while *A. rubrum* showed the greatest decrease with increasing shade length (data not shown). The latter is related to the more rapid decay of IS in *A. rubrum* in comparison with the other study species (Fig. 4b). To explore the relationship between IS and integrated A further, we regressed A_{int} against IS and A_{sat} in a multiple regression. Two models, one for plants grown in ambient and one for plants grown in elevated CO_2 , were parameterized and tested for differences in both slope and intercept. Both models were highly significant and had significant differences in the slope parameter for IS and in-

tercept. The models were: for saplings grown in ambient CO_2 , $A_{\text{int}}=75.0 \times A_{\text{sat}}+5.4 \times \text{IS}-316.1$; and for saplings grown in elevated CO_2 , $A_{\text{int}}=75.0 \times A_{\text{sat}}+8.4 \times \text{IS}-495.6$. Based on these models, saplings grown in elevated CO_2 that had similar A_{sat} values to saplings grown in ambient CO_2 had higher 2-min lightfleck photosynthesis than plants grown in ambient CO_2 if they had an induction state greater than $\sim 60\%$ (Fig. 7). Below 60%, ambient plants of similar A_{sat} would gain more carbon. In the data set, A_{sat} values ranged between 3.0 and 8.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and between 5.5 and 12.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for plants grown in ambient and elevated CO_2 , respectively. Thus, some saplings measured in this study do meet the criterion of similar A_{sat} .

Discussion

Based on our results, the largest effect that elevated CO_2 will have on photosynthesis in understory vegetation is likely a function of the photosynthetic enhancement ratio under steady-state conditions, since photosynthetic enhancement was the strongest effect we observed both for steady-state photosynthesis and 2-min integrated photosynthesis in lightflecks after shade. However, while elevated CO_2 overall showed limited effects on photosynthetic dynamics in response to light, some significant trends were apparent. First, after shorter shade periods, which predominate at the study location, elevated CO_2 plants had higher induction states (Table 1, Fig. 4). Second, plants grown in elevated CO_2 with similar A_{sat} values to plants grown in ambient CO_2 differed in integrated lightfleck photosynthesis from plants grown in ambient CO_2 depending on their induction state (Fig. 7). Combined, these effects could lead to greater photosynthetic enhancement than expected based on the steady-state enhancement in elevated CO_2 plants in a light environment with short shade periods that allows plants to maintain high induction states throughout the day.

Strong photosynthetic enhancements in 1998, especially for *C. florida*, were related to the lack of photosynthetic downregulation in all species (Fig. 3) and the lack of significant decreases in stomatal conductance (Fig. 2). Both results are unexpected given that numerous studies have demonstrated these effects of elevated CO_2 on plants grown in chamber or greenhouse studies (see Drake et al. 1997; Wolfe et al. 1998). For example, herbaceous species often show large stomatal responses to CO_2 (Field et al. 1995), while long-term effects of elevated CO_2 on stomata of tree species are much less consistent (Saxe et al. 1998). In woody species, the decrease in g under elevated CO_2 is small but most pronounced in long-term experiments of unstressed plants (Curtis 1996). Similar to our results, Ellsworth (1999) found no effects of CO_2 on g in the overstory *P. taeda* at this site, and studies on several hardwood tree species also did not find reductions in g (Bunce 1992; Gunderson et al. 1993; Hogan et al. 1996; Heath and Kerstiens 1997). Thus, it appears that, at least early in the growing season, under-

story trees growing in forest conditions may not show significant photosynthetic down-regulation or adjustments in steady state g to elevated CO_2 .

Giving the lack of significant photosynthetic down-regulation or stomatal response observed in the species studied, it is not surprising that elevated CO_2 had a small impact on the dynamic gas exchange responses to light. In contrast to our study, stomatal dynamics of a C_4 grass were affected by decreased g_{sat} under elevated CO_2 , which allowed faster induction gain in comparison to ambient plants (Knapp et al. 1994). Still, in our study loss of photosynthetic induction after the shorter shade periods as well as the loss of biochemical induction after 6 min shade were lower in elevated CO_2 (Table 1, Fig. 4). The longer maintenance of high induction states in shade, despite similar g responses under elevated CO_2 , would suggest that elevated CO_2 decreased photosynthetic enzyme deactivation rates in shade. It is unclear which photosynthetic enzymes were affected, since biochemical induction states at 60 s into the high-light period are at the transition from limitations due to enzymes in the ribulose-1,5-bisphosphate (RuBP) regeneration cycle to those due to Rubisco (Seeman et al. 1988; Sassenrath-Cole and Pearcy 1992; Ernstsens et al. 1997).

High induction states are crucial to achieving high rates of photosynthesis during sunflecks as has been shown in previous studies (e.g., Chazdon and Pearcy 1986b; Valladares et al. 1997) and our study (Fig. 7). As a consequence of the observed enhanced induction states, elevated CO_2 saplings could achieve higher daily photosynthetic enhancement ratios than expected based on enhancement ratios observed during steady state conditions. The vast majority (93%) of shade periods at the study site were shorter than 6 min, so the study species, with the exception of *A. rubrum*, are likely to maintain relatively high induction states during the day (Fig. 4). This is especially true for *Liriodendron tulipifera*, which has shade light-induction states close to 50%. With these higher induction states, elevated CO_2 plants showed higher rates of lightfleck carbon gain than ambient ones even when the effect of higher A_{sat} was accounted for (Fig. 7). Therefore, the photosynthetic enhancement during a 2-min lightfleck after short shade periods exceeds that expected from the enhancement of A_{sat} . A possible exception to this greater than expected enhancement is for *A. rubrum* saplings which, due to rapid induction loss during shade, would benefit less from elevated CO_2 than the other species. If the study species, however, were growing under a light regime with short, infrequent sunflecks, then plants grown in elevated CO_2 would have smaller than expected daily photosynthetic enhancements since induction states after long shade periods appear not to be enhanced by elevated CO_2 , and sunfleck carbon gain corrected for the A_{sat} effect is actually lower in elevated than in plants grown in ambient CO_2 . This demonstrates that general predictions on the effects of elevated CO_2 on understory daily carbon gain are difficult to make in the absence of actual field measurements, since elevated CO_2 carbon gain depends not only on

Table 2 Summary of rates of light-saturated photosynthesis (A_{sat}), induction gain ($t_{90\%A}$ for photosynthesis and $t_{90\%g}$ for stomatal conductance) and photosynthetic induction state after shade (IS) in woody species. Shade-tolerance ratings were based on authors' descriptions or were taken from Baker (1949) and Burns and Honkala (1990). Data are split into angiosperms and

gymnosperms due to the apparent slower induction gain in the latter. Species within each group are sorted according to time constants for induction gain. Data published by Küppers et al. (1996) and Schneider et al. (1993) were excluded from the table since the authors only reported biochemical induction dynamics, e.g., BIS in the current study

Species	Growth environment ^a	Shade tolerance	A_{sat} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	$t_{90\%A}$ (min)	$t_{90\%g}$ (min)	IS after 10 min shade	Reference
Angiosperms							
<i>Hybanthus prunifolius</i> ^b	US	Tolerant	3.4	3			Kursar and Coley 1993
<i>Psychotria horizontalis</i> ^b	US	Tolerant	2.2	5			Kursar and Coley 1993
<i>Quercus serrata</i>	GC-50 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Intolerant		5.5			Yanhong et al. 1994
<i>Alseis blackiana</i> ^b	US	Tolerant	2.8	6			Kursar and Coley 1993
<i>Salix spp.</i>	GC-250 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Intolerant		7.1		76 ^d	Ögren and Sundin 1996
<i>Cornus amomum</i>	GH-100%	Tolerant			7.6 ^c		Pereira and Kozlowski 1977
<i>Physocarpus opulifolius</i>	GH-100%	Tolerant			7.6 ^c		Pereira and Kozlowski 1977
<i>Acer saccharinum</i>	GH-100%	Tolerant			8.3 ^c		Pereira and Kozlowski 1977
<i>Juglans nigra</i>	GH-100%	Intolerant			8.9 ^c		Pereira and Kozlowski 1977
<i>Ulmus americana</i>	GH-100%	Intermediate			12.2 ^c		Pereira and Kozlowski 1977
<i>Acer rubrum</i>	?	Tolerant			15 ^c		Davies and Kozlowski 1975
<i>Acer rubrum</i>	US	Tolerant	6.8	8.8	17.5	22 ^e	Current study
<i>Betula pubescens</i>	GC-250 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Intolerant		9.2			Ögren and Sundin 1996
<i>Liriodendron tulipifera</i>	US	Intolerant	5.7	9.4	17.1	61 ^e	Current study
<i>Populus fremontii</i>	Open	Intolerant		9.9			Roden and Pearcy 1993
<i>Cecropia obtusifolia</i> ^b	US-Gap	Intolerant	7.5 ^f	9.9		43	Poorter and Oberbauer 1993
<i>Populus tremuloides</i>	Open	Intolerant		10			Roden and Pearcy 1993
<i>Aspidosperma cruenta</i> ^b	US	Tolerant	3.1	12			Kursar and Coley 1993
<i>Calophyllum longifolium</i> ^b	US	Tolerant	4.7	12			Kursar and Coley 1993
<i>Swartzia simplex</i> ^b	US	Tolerant	5.3	12			Kursar and Coley 1993
<i>Ouratea lucens</i> ^b	US	Tolerant	2.9	13			Kursar and Coley 1993
<i>Acer saccharum</i>	?	Tolerant			18 ^c		Davies and Kozlowski 1975
<i>Cornus amomum</i>	?	Tolerant			18 ^c		Davies and Kozlowski 1975
<i>Cornus florida</i>	US	Tolerant	4.6	14.8	22.4	57 ^e	Current study
<i>Shorea leprosula</i> ^b	US	Tolerant	3.5	16.0	17.8	64	Zipperlen and Press 1997
<i>Dipteryx panamensis</i> ^b	US	Tolerant	4.5 ^f	16.3		60	Poorter and Oberbauer 1993
<i>Ulmus americana</i>	?	Intermediate			22 ^c		Davies and Kozlowski 1975
<i>Dryobalanops lanceolata</i> ^b	US	Intermediate	3.0	21.2	24.7	65	Zipperlen and Press 1997
<i>Toona australis</i> ^b	GH-100%	Intolerant	12.3	21.8			Chazdon and Pearcy 1986a
<i>Fraxinus americana</i>	?	Intermediate			27 ^c		Davies and Kozlowski 1975
<i>Liquidambar styraciflua</i>	US	Intolerant	6.4	25.6	40.6	67 ^e	Current study
<i>Rheedia edulis</i> ^b	US	Tolerant	2.5	37			Kursar and Coley 1993
<i>Isertia henkeana</i> ^b	Open	Intolerant	19.5			33 ^d	Valladares et al. 1997
<i>Palicourea guianensis</i> ^b	Gap	Intermediate	9.5			49 ^d	Valladares et al. 1997
<i>Psychotria limonensis</i> ^b	US	Tolerant	4.9			63 ^d	Valladares et al. 1997
<i>Psychotria acuminata</i> ^b	US	Tolerant	3.9			68 ^d	Valladares et al. 1997
<i>Psychotria marginata</i> ^b	US	Tolerant	4.8			68 ^d	Valladares et al. 1997
<i>Piper auritum</i> ^b	GH-1%	Intolerant	4.5			75 ^e	Tinoco-Ojanguren and Pearcy 1993a,1993b
<i>Piper aequale</i> ^b	GH-1%	Tolerant	3.0			81 ^e	Tinoco-Ojanguren and Pearcy 1993a,1993b
<i>Psychotria micrantha</i> ^b	Gap	Intermediate	10.8			85 ^d	Valladares et al. 1997
Gymnosperms							
<i>Picea sitchensis</i>	GC-250 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Tolerant		21.5			Ögren and Sundin 1996
<i>Tsuga heterophylla</i>	GC-250 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Tolerant		27.7			Ögren and Sundin 1996
<i>Pseudotsuga menziesii</i>	Open	Intermediate		30 ^g			Pepin and Livingston 1997
<i>Pseudotsuga menziesii</i>	open US	Intermediate				33	Chen and Klinka 1997
<i>Pinus sylvestris</i>	GC-250 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Intolerant		30.7		76 ^d	Ögren and Sundin 1996
<i>Thuja plicata</i>	Open	Tolerant		32 ^g			Pepin and Livingston 1997
<i>Tsuga heterophylla</i>	Open	Tolerant		39 ^g			Pepin and Livingston 1997
<i>Pinus taeda</i>	Open	Intolerant		115			Whitehead and Teskey 1995

^a GC growth chamber with light intensity, GH greenhouse with % of full sun, US forest understory, Gap forest gap

^b Tropical/subtropical species

^c Time until maximal conductance instead of 90% of maximum

^d Ratio of A at 60 s to A_{sat} : $\text{IS}^{\text{d}} = 100 \times A_{60} / A_{\text{sat}}$

^e After 12 min shade

^f Estimated average from Fig. 6

^g At 20°C; from Fig. 2a

photosynthetic enhancements measured under steady state conditions but also on characteristics of the light environment and species-specific differences in induction dynamics.

Species differences in induction dynamics were related to stomatal dynamics, as evidenced by the similarity in species differences in time constants for A and g ($t_{90\%A}$ and $t_{90\%g}$; Fig. 6a) and the lack of significant species differences in biochemical induction gain. *A. rubrum*, which both gains and loses induction rapidly, had the most responsive stomata which showed both low lag times and the most rapid rates of opening and closing (Fig. 5). *L. tulipifera*, the other species with rapid induction gain, was intermediate in its stomatal responsiveness (Fig. 5), but had the highest g_{shade} of the species thus allowing rapid induction gain. In contrast to *A. rubrum*, *L. tulipifera* however maintained induction during shade as well as the other two species that were slow in induction gain. Induction loss in the species paralleled both decreases in g and BIS, the two components of IS. It thus appears that the components of IS vary in a coordinated fashion, even though during induction different components may be limiting at different times after the light change (Percy et al. 1996).

Previous studies have suggested that shade-tolerant species have induction characteristics allowing a more efficient utilization of sunflecks than intolerant species (e.g., Schneider et al. 1993; Küppers et al. 1996). For example, shade-tolerant or late successional species can gain induction faster than less tolerant species (Lei and Lechowicz 1997; Ögren and Sundin 1996; Schneider et al. 1993; Chazdon and Percy 1986a) and maintain it longer under low light (Poorter and Oberbauer 1993; Tinoco-Ojanguren and Percy 1993b; Chazdon and Percy 1986a). In this study we had both a shade-tolerant (*A. rubrum*) and a shade-intolerant species (*L. tulipifera*) that gained induction rapidly, and a shade-tolerant species (*A. rubrum*) that lost induction rapidly. Further, a comparison across all published studies of which we are aware does not support a shade-tolerance trend with respect to induction gain/loss rates for woody species in general (Table 2). In fact, both shade-tolerant and intolerant species have a wide range of induction time constants. The only apparent trend for induction dynamics in woody plants is that gymnosperms tend to take longer to induce photosynthesis than angiosperms (13 vs. 42 min, respectively). As for the maintenance of induction, four out of seven shade intolerant and three out of eight shade-tolerant species maintained induction states of 66% or greater after shade (Table 2). Therefore, species differences in induction dynamics should relate not to shade tolerance per se but some other characteristic.

As an alternative, the responsiveness to changes in light intensity could be driven by the relative tradeoffs between water use and carbon gain. Knapp and Smith (1989) suggested that species with higher intrinsic gas exchange rates would achieve greater increases in water use efficiency by closing stomata during low light than

species with inherently lower rates. Consequently, species with high rates should have stomata that are responsive to light changes. The gas exchange rates in this study are low in comparison to those of the more responsive species previously investigated (Knapp 1992; Knapp and Smith 1989), and three of the species showed slow stomatal responses to shade (Fig. 4b). The species in Table 2 show a general trend towards decreasing induction states after shade with increasing light-saturated rates of photosynthesis when two species (*A. rubrum* and *Psychotria micrantha*) are removed from the analysis ($IS = -2.4A_{\text{sat}} + 75.6$, $n=14$, $P < 0.01$, $r^2 = 0.67$). Including these species, the trend is still negative but no longer significant ($P = 0.07$, $r^2 = 0.21$).

In summary, in the absence of photosynthetic down-regulation and decreases in stomatal conductance, the largest effect elevated CO_2 has on dynamic gas exchange is enhanced photosynthesis. A lesser effect was a reduction in induction loss during short shade periods, but this effect increased lightfleck carbon gain more than expected based solely on the enhancement of light-saturated photosynthesis. The impact of the CO_2 effect of induction loss on daily photosynthesis will depend on the frequency and distribution of sunflecks as well as the photosynthetic capacity of the species, since A_{sat} can be a good indicator of induction loss rates (Table 2; see also Knapp and Smith 1989). Our literature review also indicated a few species that do not follow this overall pattern, suggesting the need for additional experiments evaluating the ecological determinants of species variation in induction loss. Since no significant $\text{CO}_2 \times \text{species}$ interactions were observed for any parameter, our data do not support the contention that shade-tolerant species will experience short-term or daily photosynthetic enhancements that are greater than for intolerant species. While our study of four species has provided an initial direct test of hypotheses concerning shade tolerance $\times \text{CO}_2$ interactions in an actual forest understory, a more complete test for such interactions will require large and diverse understory CO_2 enrichment experiments. At present, no other forest elevated- CO_2 experiment includes understory trees despite their importance for understanding the successional trajectory of forest development with changing atmospheric CO_2 .

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