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# The photosynthetic response of eight species of *Acer* to simulated light regimes from the centre and edges of gaps

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## Summary

1. Seedlings of eight *Acer* species grown under two light treatments simulating forest gap edge (photosynthetic photon flux density, PPFD =  $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; R:FR = 0.6) and gap centre (PPFD =  $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; R:FR = 1.1) were studied to explore the effect of growth irradiance on transient- and steady-state photosynthesis.
2. The increase in maximum photosynthetic rate ( $A_{\text{max}}$ ) from gap edge- to gap centre-grown seedlings ranged between 20% in *Acer saccharum* and 138% in *Acer ginnala*.  $A_{\text{max}}$  differed significantly among species (2.3 to  $12.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) but assimilation rates under dim light ( $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) were more similar (0.6 to  $1.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).
3. Significant differences among species in stomatal conductance indicate that species of high photosynthetic performance maintain higher dim light conductance and show a much greater excursion in stomatal opening under saturating light.
4. Lightfleck response based on actual photosynthetic rates was more rapid in gap centre- vs gap edge-grown plants but the latter demonstrated more rapid rates of photosynthetic induction (PI).
5. We suggest that the estimation of photosynthetic induction state is prone to an inverse relationship with maximum photosynthetic rate ( $A_{\text{max}}$ ) and so may not be directly related to efficiency in sunfleck response. Conversely, higher  $A_{\text{max}}$  can result in low PI but is also associated with higher transient rates of assimilation during a lightfleck and, therefore, be equally relevant as induction properties.
6. It appears that leaves with characters such as greater specific leaf mass and area-based leaf N, even within the same irradiance treatment, may confer a carboxylation advantage to sunfleck utilization not reflected in PI. However, whether the total carbon return on such a leaf is better assessed by PI or transient photosynthetic rate remains to be determined.

*Key-words:* Aceraceae, growth irradiance, Maple, photosynthetic induction, stomatal conductance

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## Introduction

Light plays a dominant role in the growth and survival of understorey plants. Their light environment consists of a complex sequence of sunflecks and low-intensity diffused light that varies greatly with weather, season, site characteristics and geographical location (Endler 1993; Lei *et al.* in press). Understorey plants may experience less than 60 min of sunflecks on a clear day but these could contribute as much as 80% of the total light energy received (Chazdon 1988). Because whole-plant performance of forest understorey plants is associated with the available sunflecks (Pearcy 1983), understorey species are

expected to show adaptive properties that maximize the utilization of the fluctuating light source. Physiologically, shade plants can improve light capture by reaching higher levels of  $\text{CO}_2$  uptake through a quick photosynthetic response to sunflecks (i.e. becoming photosynthetically induced) and by maintaining a minimum loss of induction between sunflecks (Chazdon & Pearcy 1986a,b; Chazdon 1988; Pearcy 1990). At present, a large part of our understanding of induction is based on tropical and herbaceous species (e.g. Gross & Chabot 1979; Gross 1982; Chazdon & Pearcy 1986a,b; Kirschbaum & Pearcy 1988a,b; Kirschbaum, Gross & Pearcy 1988; Pearcy 1990; Tinoco-Ojanguren & Pearcy 1992, 1993). A lack of comparable data on temperate woody plants (Küppers & Schneider 1993; Tang *et al.* 1994),

particularly among forest species, is clearly evident. In this study we compare lightfleck responses among eight congeners grown in two contrasting light environments and reconsider the relationship and ecological significance of photosynthetic induction and transient rates of CO<sub>2</sub> uptake. In the temperate forest, many Maple (*Acer* L.) species must complete their juvenile stage growing in the forest understorey. Some, like *Acer saccharum*, require periodic gaps to reach maturity in the forest crown (Canham 1985) while others (e.g. *Acer pensylvanicum*) remain in the subcanopy through life. While Maple seedlings show significant growth response to forest gaps (Wilson & Fischer 1977; Canham 1988), their persistence from germination to the occurrence of a forest gap, which may last more than a decade, must depend on an effective balance of carbon to production and structure. Previous studies have shown that Maple seedlings vary in a large suite of traits among species and among light treatments (Lei & Lechowicz 1990; Lei 1992; Sipe & Bazzaz 1994, 1995). Here we focus on the variation in transient and steady-state photosynthesis in eight *Acer* species grown under low and moderate light levels. We estimate various photosynthetic induction properties in four census periods during the growing season and examine their consistency with expected shade-adaptation under the dynamic light environment of the forest gap.

### Materials and methods

Eight species of *Acer* were used in this study, each represented by two populations (seed sources given in Lei 1992). The species are: *A. macrophyllum* Pursh., *A. platanoides* L., *A. rubrum* L., *A. saccharum* Marsh., *A. ginnala* Maxim., *A. palmatum* Thunb., *A. pensylvanicum* L. and *A. spicatum* Lam. The first four species mature at heights > 15 m while the last four species reach heights < 15 m. Seedlings were 3–4 years old and raised from seed under a common greenhouse environment in the McGill Phytotron. They were planted in cylindrical Plexiglas tubes (7.7-cm diameter and 61 cm in height) filled with commercial top soil. In April 1990, the seedlings were placed under two experimental light treatments just as bud-break began. The construction of the simulated gap edge (PPFD = 30 μmol m<sup>-2</sup> s<sup>-1</sup>; R:FR = 0.55) and simulated gap centre (400 μmol m<sup>-2</sup> s<sup>-1</sup>; R:FR = 1.1) environments is described in detail elsewhere (Lei 1992). During the experiment, seedlings were fertilized with Hoagland's solution (Dunn & Arditti 1968, Version 2) once a week and watered regularly. The total number of seedlings used in this study was 160.

Experimental plants were blocked within each light treatment. Analysis of variance showed no significant block effect in measured traits, therefore only pooled results are presented. Gas-exchange measurements were taken indoors (by random treatment and block) under standard lighting conditions. Photosynthesis,

leaf internal CO<sub>2</sub> and stomatal conductance were determined with a Li-6200 Portable Photosynthetic System (Li-Cor, Inc., Lincoln, NE, USA). Plants were acclimated under dim light for at least 1 h. Lighting was supplied by a mixed array of fluorescent tubes and incandescent bulbs; mean PPFD was 29 μmol m<sup>-2</sup> s<sup>-1</sup> at 124 cm from the source. Photosynthesis was measured under dim light on one randomly selected leaf per plant after the acclimation period. Seedlings were then moved under a GE Cool Beam Flood Lamp (300 W PAR 56/2MFL) suspended over a 5-cm thick thermal barrier. Mean PPFD was 1260 μmol m<sup>-2</sup> s<sup>-1</sup>. Estimates of photosynthesis after 30 s, 270 s and 1470 s of exposure to this saturating light were taken on the same leaf measured under dim light. This procedure simulates the photosynthetic induction response of a dim light-acclimated leaf to a saturating sunfleck of the three durations. Photosynthesis at 1470 s is referred to as  $A_{\max}$  based on preliminary determinations that the seedling response curves began to plateau at approximately 10 min in all the *Acer* species. Repeated measurements of the same leaf at these time intervals had no effect on the photosynthetic activities. During the growing season of 1990, four complete sets of lightfleck response measurements were taken: 15–25 June, 16–20 July, 6–16 August and 5–13 September.

Photosynthetic induction was calculated, following Chazdon & Pearcy (1986a), as:

$$\text{Induction state (\%)} = \frac{A_t - A_{\text{dim}}}{A_{\max} - A_{\text{dim}}} \times 100 \quad \text{eqn 1}$$

where  $A_t$  is the transient photosynthesis 30 s and 270 s after the onset of saturating light, and  $A_{\text{dim}}$  and  $A_{\max}$  are the steady-state photosynthesis under dim light (29 μmol m<sup>-2</sup> s<sup>-1</sup>) and saturating light (1260 μmol m<sup>-2</sup> s<sup>-1</sup>) after 1470 s. The three photosynthetic measurements after exposure to saturating light correspond approximately to the three phases of photosynthetic induction (Pearcy 1990): (1) at 30 s, the rate during RuBP regeneration, (2) at 270 s, the Rubisco activation phase and (3) at 1470 s, the stomatal conductance limitation phase. We focused on the comparative progression of photosynthetic induction among species and between treatments to stable state at these discrete time intervals instead of the rapid photosynthetic response to dynamic light fluctuations. Variation in photosynthetic rate during the induction process affected by light treatment and species was analysed using analysis of variance (SAS 1988) for repeated measures at the four census periods (Potvin, Lechowicz & Tardif 1990).

### Results

#### PHOTOSYNTHETIC INDUCTION PROPERTIES

Overall, Maple seedlings grown in simulated gap centre achieved higher  $A_{\max}$  (steady state  $A$  at 1470 s,

Fig. 1, Appendix 1) than gap edge-grown plants. Among species, *A. macrophyllum* and *A. ginnala* consistently maintained higher  $A_{\max}$  in both centre and edge treatments over the summer while the lowest  $A_{\max}$  was observed in *A. saccharum* in both light treatments (Fig. 1). Photosynthesis in dim light ( $A$  at 0 s) is significantly correlated with  $A_{\max}$  for the gap centre ( $r=0.77$ ,  $P<0.001$ ,  $n=32$ ) and gap edge ( $r=0.38$ ,  $P=0.03$ ,  $n=32$ ) treatments, using pooled data of species means in the four censuses. This indicates that species that attained higher  $A_{\max}$  also maintained higher dim light photosynthesis. During the photosynthetic induction process, transient photosynthesis (at 30 s and 270 s) was generally higher in plants grown under the higher irradiance treatment (Fig. 1). Within treatment, species reaching higher  $A_{\max}$  (e.g. *A. macrophyllum*) also showed a more rapid rise in transient rates than those with low  $A_{\max}$  (e.g. *A. saccharum*). However, calculated photosynthetic induction state showed a reversed pattern where *A. saccharum* was quicker in becoming fully induced than *A. macrophyllum*, reaching 80% full induction (vs 60% for *A. macrophyllum*) at 270 s (Fig. 1).

Photosynthetic rate ( $A$ ) at the four exposure times to saturating light differed significantly over the season but showed a tendency to increase later in the growing season (Fig. 2; Table 1, census effect within subject). Because the same leaf on each plant was measured at every census, this is apparently an effect of leaf age. The correspondence in between transient and steady-state photosynthesis under dim and saturating light is

large, and conserved over the season (Table 1, census by species) and among species (Fig. 2). Changes in  $A$  at different leaf ages are not only species specific and dependent of the growth light regime (Table 1, significant interaction between light regime and species) but also vary with the time of exposure to saturating light during lightfleck measurements. In general, a higher  $A$  in gap centre vs gap-edge seedlings (Table 1, census by light) was expressed with longer exposure time (at 270 s and 1470 s, Fig. 2). Conversely, at 0 s and 30 s, species such as *A. macrophyllum* grown in gap centre showed distinctly lower  $A$ , indicating that higher growth irradiance reduced photosynthesis under dim light and the initial response of the leaf to saturating light.

The contrasting patterns of seedling response to saturating light represented by photosynthetic rates vs photosynthetic induction state (PI) seen in Fig. 1 prevailed among species and census periods. There was a clear relationship between  $A$  and PI where higher transient  $A$  is found in gap centre plants but gap edge plants attained higher PI (Fig. 3). Because the initial rise in  $A$  is similar (cf. Fig. 2 from 0 s to 30 s) even between species that are greatly different in  $A_{\max}$ , the calculation of PI will yield high values when  $A_{\max}$  is low. As Fig. 3 shows, mean species values support the general conclusion that among *Acer* seedlings, those grown in the higher irradiance level were slower in photosynthetic induction than those in the lower irradiance treatment but attained higher carbon fixation in the initial minutes of exposure to saturating light.

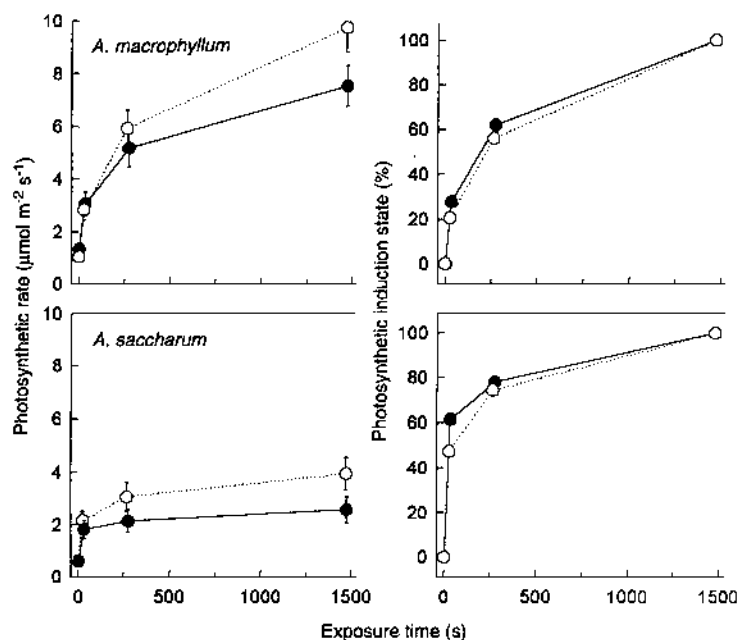


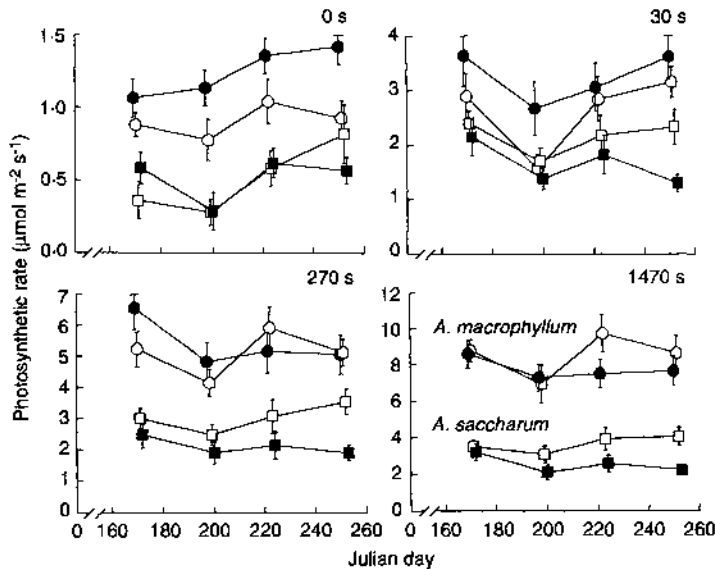
Fig. 1. Response patterns of photosynthesis and photosynthetic induction in two representative *Acer* species grown under gap-centre (open symbols; PPF $D=300\ \mu\text{mol m}^{-2}\text{s}^{-1}$ ) and gap-edge (closed symbols; PPF $D=30\ \mu\text{mol m}^{-2}\text{s}^{-1}$ ) treatments. Photosynthesis of the same leaf was first measured after acclimation to dim light ( $30\ \mu\text{mol m}^{-2}\text{s}^{-1}$ ; at time = 0 s), then under bright light ( $1260\ \mu\text{mol m}^{-2}\text{s}^{-1}$ ) after 30 s, 270 s and 1470 s of exposure. The photosynthetic rate at 1470 s is taken as  $A_{\max}$ . Graph shows the August 1990 measurements. Each data point represents the mean value ( $\pm 1\text{SE}$ ) of 10 plants.

#### PHOTOSYNTHETIC INDUCTION, STOMATAL CONDUCTANCE AND INTERNAL $\text{CO}_2$ PARTIAL PRESSURE

Among *Acer* species, those with lower  $A_{\max}$  (e.g. *A. saccharum* and *A. pensylvanicum*) showed only a marginal increase in  $g_s$  from dim light to steady state under saturating light. But in species with high  $A_{\max}$ ,  $g_s$  increased by twofold during the same period (e.g. *A. macrophyllum* and *A. ginnala*, Figs 1 and 4). Seedlings also varied in dim light  $g_s$  with *A. ginnala* maintaining a substantially higher level than the others. In some species (e.g. *A. macrophyllum*), the greatest increase in  $g_s$  occurred after 270 s under saturating light when photosynthesis has reached 60% of maximum  $A$  (Figs 1 and 4) while others, such as *A. saccharum*, showed only marginal or no increases in the same time period. Mean  $g_s$  for all eight species was  $0.06$  ( $0.04\text{--}0.10$ )  $\text{mol m}^{-2}\text{s}^{-1}$  under dim light and  $0.10$  ( $0.04\text{--}0.24$ )  $\text{mmol m}^{-2}\text{s}^{-1}$  at  $A_{\max}$ . The correlation between  $A$  and  $g_s$  using population means was weak in the dim light (Pearson  $r=0.21$ ,  $P=0.24$ ,  $n=32$ ) but increased with the length of exposure to saturating light (30 s:  $r=0.75$ ; 270 s:  $r=0.90$ ; 1470 s:  $r=0.96$ ;  $P>0.001$  for all three,  $n=32$ ).

Leaf internal  $\text{CO}_2$  partial pressure ( $c_i$ ) of all species in dim light was similar at  $33.6 \pm 2$  Pa at a mean photo-

synthetic rate of  $0.89 \pm 0.04 \mu\text{mol m}^{-2} \text{s}^{-1}$  (August measurements). With the onset of saturating light, there was a rapid decrease in  $c_i$  from the dim light level to  $28.6 \pm 4 \text{ Pa}$  as  $A$  rose to  $1.97 \pm 0.11 \mu\text{mol m}^{-2} \text{s}^{-1}$  after 30 s. Internal  $\text{CO}_2$  stabilized at 25.5 and 25.1 Pa after 270 s and 1470 s while  $A$  continued to increase reaching  $3.01 \pm 0.20$  and  $4.84 \pm 0.33 \mu\text{mol m}^{-2} \text{s}^{-1}$  respectively. The time course of  $c_i$  in individual species (Fig. 4) showed a large decrease from the onset of saturating light to 270 s. As leaves approach steady state (270 s),  $c_i$  stabilized along with rapid stomatal opening (Fig. 4) but only in *A. ginnala* and *A. macrophyllum*.



**Fig. 2.** Variations in the seasonal pattern of steady-state and transient photosynthetic rate (mean  $\pm$  1 SE,  $n=10$ ) in two representative *Acer* species. Open symbols, plants grown in the brighter gap-centre light regime; solid symbols, plants grown in the shadier gap-edge light regime. Steady-state photosynthetic rate under dim light ( $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and under saturating light ( $1260 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) are shown as at time = 0 s and 1470 s respectively. Transient photosynthetic rates are given at 30 s and 270 s of exposure to saturating light. Budbreak in the Maple seedlings occurred at Julian day 125–130.

## Discussion

### INDUCTION STATE AND TRANSIENT PHOTOSYNTHETIC RATE

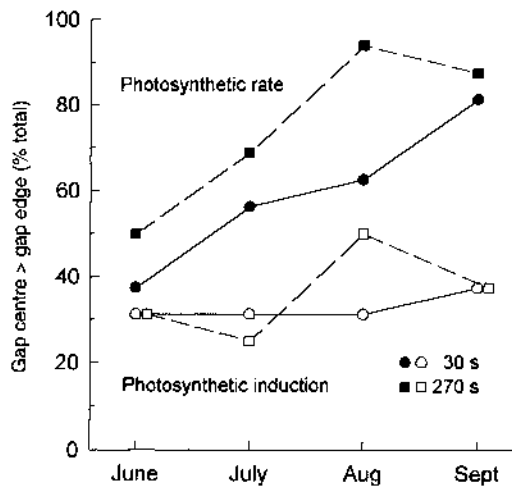
Overall, Maple seedlings responded to the sudden onset of bright light in an adaptive fashion in terms of photosynthetic induction, similar to the European Beech (Küppers & Schneider 1993) and tropical species (Chazdon & Pearcy 1986a,b). This first report on lightfleck response among congeners revealed considerable species-specific treatment response in transient and steady-state photosynthesis, and in photosynthetic induction properties. Among species, differences in response appear to be associated with their ecological light requirement as juveniles (e.g. higher in *A. macrophyllum* than in *A. saccharum*, Fried, Tappeiner & Hibbs 1988), a pattern similar to those observed among divergent taxa (e.g. Chazdon & Pearcy 1986a).

Among Maples, photosynthetic induction state was lower for gap centre- vs gap edge-grown seedlings at early onset of saturating light, a consistent pattern over the season (Fig. 3). These results indicate that Maple seedlings grown in lower irradiance showed physiological adjustment consistent with that expected in shade adaptation (e.g. Pearcy 1990). However, the higher absolute rates of photosynthesis in gap-centre plants during the same exposure period suggest that a leaf capable of high  $A_{\text{max}}$  also carries an advantage over gap-edge plants in carbon fixation during lightflecks. This advantage is facilitated by comparable dim light photosynthetic rates (Figs 2 and 4, Appendix 1) and dark respiration (Lei 1992) between plants grown in the two irradiance levels. The apparent contrast between transient photosynthetic rate and photosynthetic induction in this study was not only observed among treatment but also within treatment (e.g. between *A. macrophyllum* and *A. saccharum*, Fig. 1).

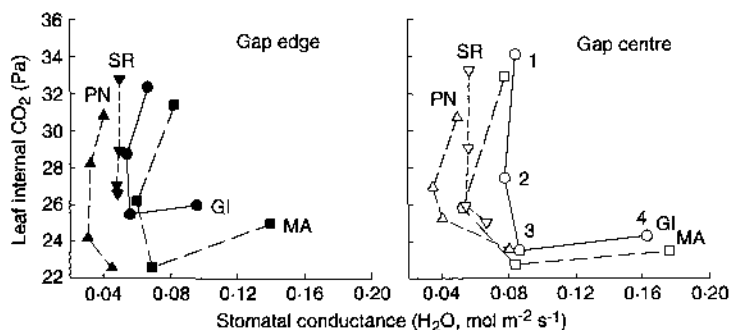
**Table 1.** Analysis of variance of photosynthetic rate at four different exposure times to saturating light measured repeatedly at four census periods (15–25 June, 16–20 July, 6–16 August and 5–13 September) during the summer of 1990. The analysis assumes a fixed model with two light regimes and eight *Acer* species. The Huyn-Feldt  $\epsilon$  values are close to 1 indicating that the corrected Huyn-Feldt significance level (asterisks) can be applied to the  $F$  values given in the table

Source of variation	df	Exposure time(s)			
		0 ( $A_{\text{dim}}$ )	30	270	1470 ( $A_{\text{max}}$ )
<b>Within subject</b>					
Huyn-Feldt $\epsilon$		0.97	0.95	1.03	1.06
Census	3	8.9***	25.3***	11.4***	15.6***
Census $\times$ light	3	6.0***	7.5***	9.9***	10.9*
Census $\times$ species	21	0.8 <sup>NS</sup>	1.8*	1.5 <sup>NS</sup>	0.8 <sup>NS</sup>
Census $\times$ light $\times$ species	21	0.8 <sup>NS</sup>	0.8 <sup>NS</sup>	0.7 <sup>NS</sup>	0.9 <sup>NS</sup>
<b>Between subjects</b>					
Light	1	4.5*	6.5*	24.4***	78.9***
Species	7	10.9***	13.4***	26.4***	30.3***
Light $\times$ species	7	1.3 <sup>NS</sup>	4.0***	4.3***	2.5*

\*\*\* $P \leq 0.001$ ; \*\* $P \leq 0.01$ ; \* $P \leq 0.05$ ; NS is  $P > 0.05$ .



**Fig. 3.** Proportion of *Acer* species with higher values of transient photosynthetic rates (after 30 s and 270 s exposure to saturating light) and photosynthetic induction state in gap-centre vs gap-edge treatments. Across the four census periods, the gap-centre seedlings of most species were higher in photosynthetic rates (>50%) but lower in induction states (<50%) than gap-edge plants. Data points represent the ratio of the number of gap-centre:gap edge species populations (four species  $\times$  two populations = eight) in the measured traits over the total of 16 species populations. There were five seedlings in each species population of each treatment.



**Fig. 4.** Time course of stomatal conductance and leaf internal  $\text{CO}_2$  as dim light-acclimated leaves (1) were exposed to saturating light after 30 s (2), 270 s (3) and 1470 s (4). Measurements taken in August 1990. Species codes are GI, *A. ginnata*; MA, *A. macrophyllum*; PN, *A. pensylvanicum*; SR, *A. saccharum*. Each data point is the mean of five measurement (one per replicate plant).

The contrasting patterns of lightfleck response of transient photosynthesis vs induction state is also evident in several other studies. Chazdon & Pearcy (1986a,b) reported higher photosynthetic induction response in *Alocasia macrorrhiza*, an Australian rain forest understory herb, than *Toona australis* seedlings, a canopy tree less tolerant of shade. While the high light-grown *T. australis* showed a slower induction rate, its transient photosynthetic rates were consistently higher than *A. macrorrhiza* during the induction process. Even with its greater stomatal and biochemical limitations in sunfleck response, *T. australis* is capable of higher  $\text{CO}_2$  assimilation. Similarly, in a simulated model of sunfleck response in *Fragaria virginiana*, Gross (1982) found high light-grown plants performed consistently better than those grown

in low light. Specifically, the proportion of carbon uptake during a single sunfleck of 0.5, 1 and 2 min in duration to the total in an hour was 30–40% higher for high light-grown plants despite their slower response time in induction (Gross & Chabot 1979). Typical lightfleck response patterns of *Piper auritum* clearly showed a twofold advantage in *A* for sun- over shade-grown plants spanning the entire course of induction (Tinoco-Ojanguren & Pearcy 1993). In *Quercus serata*, seedlings grown in high light attained higher *A* within 5 s of exposure to saturating light compared with those grown in low light, yet induction rates showed the reverse pattern in agreement with the shade-adaptation argument (Tang *et al.* 1994). Evidently, in every case, because the dim light photosynthetic rates were similar between treatments, any demonstrable advantage in induction state for a shade-grown plant is achieved by virtue of its lower steady-state photosynthetic rate.

These findings raise the question of the relative ecological significance of photosynthetic induction vs the actual transient assimilation rate. What are the relevant parameters for evaluating sunfleck response and inferring shade adaptation? Higher transient *A* in plants with 'sun' type leaf construction appears to be the result of proportionally large pool size of RuBP and Rubisco even under conditions of partial activation, relative to the 'shade' leaf. Furthermore, the second phase of induction involving Rubisco activation has been found not to vary among species and light treatments, and thus plays only a minor role in improved lightfleck-use efficiency relative to the maintenance of high  $c_i$  and  $g_s$  (Seemann *et al.* 1988; Woodrow & Mott 1989; Tinoco-Ojanguren & Pearcy 1992, 1993). Therefore, empirically, the 'sun' leaf could achieve higher carbon fixation quicker than a 'shade' leaf when artificially exposed to a sunfleck. By calculating photosynthetic induction using  $A_{\text{max}}$  as a denominator (see Materials and methods), an inverse relationship  $A_{\text{max}}$  and PI will likely be expressed. Can we infer from the low PI in a sun leaf the lack of adaptation to sunflecks simply because it has a high  $A_{\text{max}}$ ?

Although plants grown in high light also show a more rapid loss of induction that appears to be closely associated with the regeneration of RuBP (Tinoco-Ojanguren & Pearcy 1993), by virtue of their high *A*, the 'advantage' in carbon gain will likely be preserved. For a shade plant, even by maintaining high  $g_s$  and high induction states during darkflecks (interval between sunflecks), it may be constrained by its low carboxylation potential that places an upper limit on assimilation rate. Even in post-illuminative  $\text{CO}_2$  fixation after short sunflecks that carry significant ecological importance to understory plants (Pearcy 1990), light-grown Beech seedlings consistently out-performed shade-grown ones at all induction states (Küppers & Schneider 1993). Is sunfleck adaptation of a leaf better evaluated from induction properties

that are highly dependent of  $A_{\max}$ , or on transient rates of carbon fixation? Ultimately, it may be necessary to evaluate the benefit as the life-time return in carbon of a leaf exposed to sunflecks and determine whether  $A$  or  $PI$  is the better correlate with total carbon gain.

#### STOMATAL CONDUCTANCE AND LEAF INTERNAL $CO_2$

Stomatal response in Maple seedlings was slow during the initial stages of exposure to bright light before showing large increases in some species (Fig. 4). For *A. macrophyllum* and *A. ginnala*, the pattern is consistent with other reports that 10–40 min is required to reach maximum conductance (Pfirsch & Pearcy 1989a; Tinoco-Ojanguren & Pearcy 1992). Reaching and maintaining high  $g_s$  under fluctuating light is now recognized as a key factor in increasing the utilization efficiency of sunflecks (Pearcy 1990; Tinoco-Ojanguren & Pearcy 1992). Higher initial  $g_s$ , as is the case for *A. macrophyllum* and *A. ginnala*, leads to a faster induction by improving the relative concentrations of  $CO_2$  vs  $O_2$  for Rubisco (Ehleringer & Björkman 1987). If a plant can maintain a modest level of  $g_s$  (i.e. high  $c_i$ ) in dim light, then the carbon gain during a subsequent sunfleck will be largely limited (>85%) by carboxylation factors alone (Pearcy, Osteryoung & Calkin 1985; Chazdon & Pearcy 1986a; Pfirsch & Pearcy 1989b; Pearcy 1990). Interestingly, those species with low photosynthetic performance (e.g. *A. pensylvanicum* and *A. saccharum*) (Table 1, Fig. 2) were also low in steady-state  $g_s$  under dim and high light. The conservative nature of photosynthesis in these two species is also observed by Sipe & Bazzaz (1994). While the modest gas-exchange capacity appears correlated with poor growth and survival in *A. saccharum*, *A. pensylvanicum* can show significant height growth despite being limited in instantaneous carbon gain (Sipe & Bazzaz 1995; T. Lei, unpublished data). This points to the importance of the long-term consequences of carbon allocation among Maple species (Lei & Lechowicz 1990).

Virtually all plants show morphological and physiological acclimation to changes in growth light environments (e.g. Boardman 1977; Björkman 1981; Evans, von Caemmerer & Adams 1988; Newell *et al.* 1993). An important question is whether all the characters are functionally adaptive in the existing light conditions, and whether an adaptive advantage is demonstrable? The Maple seedlings in this study were found to show allocation patterns in chlorophyll and nitrogen consistent with the expected shade acclimation (T. Lei, unpublished data). Such changes were only substantiated by transient photosynthetic response to lightflecks based on induction and not absolute rates. In a lucerne canopy, Evans (1993) found similar shade-

adaptive acclimation in total leaf N, proportional N to chlorophyll and electron-transport capacity but it is not clear how these adjustments contribute to sunfleck responses. In a revealing study using *Alocasia*, Sims & Pearcy (1993) demonstrated that the initial physiological adjustment at the leaf level is determined by the mean PPFD in the growth environment and independent of the frequency pattern of light (i.e. sunflecks). However, the subsequent whole-plant growth is affected by the pattern of simulated sunflecks, not mean PPFD. Clearly, shade acclimation syndromes, such as the co-ordinated regulation of N allocation to light and dark reaction components, do not respond directly or adaptively to sunflecks *per se*. Rather, adaptive response to sunflecks appears to be a secondary effect of the overall leaf adjustment to the average light level in the environment.

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**Appendix 1.** Photosynthetic rate (mean  $\pm$  1 SE,  $n = 10$ ) at four exposure times to saturating light for the eight Maple species grown under the two simulated (gap centre and gap edge) light regimes. Measurements were repeated four times during the growing season indicated by census 1 (15–25 June), 2 (16–20 July), 3 (6–16 August) and 4 (5–13 September). At measurement time = 0 s, the photosynthetic rate represents steady-state level under dim light ( $29 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) and steady-state maximum photosynthetic rate is indicated by values at 1470 s. Species abbreviations are: GI, *A. ginnala*; MA, *A. macrophyllum*; PA, *A. palmatum*; PL, *A. platanoides*; PN, *A. pensylvanicum*; RU, *A. rubrum*; SP, *A. spicatum*; SR, *A. saccharum*

Species	census	0 s		30 s		270 s		1470 s	
		Centre	Edge	Centre	Edge	Centre	Edge	Centre	Edge
GI	1	0.52 $\pm$ 0.24	1.01 $\pm$ 0.09	3.26 $\pm$ 0.33	2.37 $\pm$ 0.30	5.38 $\pm$ 0.56	3.39 $\pm$ 0.63	7.90 $\pm$ 0.72	5.99 $\pm$ 0.36
	2	0.56 $\pm$ 0.10	0.62 $\pm$ 0.09	2.57 $\pm$ 0.46	1.66 $\pm$ 0.19	5.02 $\pm$ 0.74	2.92 $\pm$ 0.17	7.79 $\pm$ 0.64	4.36 $\pm$ 0.53
	3	0.76 $\pm$ 0.10	0.83 $\pm$ 0.08	2.93 $\pm$ 0.47	2.08 $\pm$ 0.17	5.31 $\pm$ 0.86	2.75 $\pm$ 0.22	8.35 $\pm$ 0.83	4.64 $\pm$ 0.41
	4	1.02 $\pm$ 0.10	1.00 $\pm$ 0.22	3.45 $\pm$ 0.37	1.94 $\pm$ 0.21	6.00 $\pm$ 0.69	3.08 $\pm$ 0.30	9.15 $\pm$ 0.61	4.41 $\pm$ 0.39
MA	1	0.88 $\pm$ 0.08	1.07 $\pm$ 0.13	2.90 $\pm$ 0.42	3.64 $\pm$ 0.56	5.23 $\pm$ 0.57	6.57 $\pm$ 0.70	8.78 $\pm$ 1.03	8.59 $\pm$ 0.77
	2	0.78 $\pm$ 0.14	1.14 $\pm$ 0.12	1.57 $\pm$ 0.26	2.68 $\pm$ 0.49	4.15 $\pm$ 0.43	4.83 $\pm$ 0.61	6.94 $\pm$ 1.04	7.30 $\pm$ 0.74
	3	1.04 $\pm$ 0.15	1.36 $\pm$ 0.12	2.84 $\pm$ 0.41	3.06 $\pm$ 0.44	5.92 $\pm$ 0.68	5.16 $\pm$ 0.70	9.74 $\pm$ 0.95	7.50 $\pm$ 0.78
	4	0.93 $\pm$ 0.12	1.42 $\pm$ 0.12	3.15 $\pm$ 0.28	3.61 $\pm$ 0.42	5.12 $\pm$ 0.42	5.05 $\pm$ 0.62	8.65 $\pm$ 0.92	7.65 $\pm$ 0.80
PA	1	0.55 $\pm$ 0.22	0.67 $\pm$ 0.18	2.15 $\pm$ 0.33	2.07 $\pm$ 0.33	2.80 $\pm$ 0.36	2.30 $\pm$ 0.23	5.78 $\pm$ 0.61	3.60 $\pm$ 0.34
	2	0.37 $\pm$ 0.07	0.48 $\pm$ 0.11	1.72 $\pm$ 0.25	1.62 $\pm$ 0.19	2.43 $\pm$ 0.35	2.24 $\pm$ 0.26	4.87 $\pm$ 0.63	3.50 $\pm$ 0.33
	3	0.65 $\pm$ 0.08	0.75 $\pm$ 0.08	2.66 $\pm$ 0.29	1.83 $\pm$ 0.25	3.85 $\pm$ 0.30	2.34 $\pm$ 0.35	6.24 $\pm$ 0.25	3.27 $\pm$ 0.44
	4	1.00 $\pm$ 0.24	0.65 $\pm$ 0.09	2.29 $\pm$ 0.15	1.80 $\pm$ 0.26	3.88 $\pm$ 0.43	2.31 $\pm$ 0.36	6.17 $\pm$ 0.60	2.97 $\pm$ 0.39
PL	1	0.57 $\pm$ 0.08	1.01 $\pm$ 0.15	2.96 $\pm$ 0.28	2.86 $\pm$ 0.37	4.34 $\pm$ 0.50	3.66 $\pm$ 0.42	6.62 $\pm$ 0.58	4.39 $\pm$ 0.56
	2	0.67 $\pm$ 0.09	0.72 $\pm$ 0.09	1.78 $\pm$ 0.27	1.67 $\pm$ 0.25	2.92 $\pm$ 0.50	2.69 $\pm$ 0.22	5.13 $\pm$ 0.71	3.37 $\pm$ 0.28
	3	0.86 $\pm$ 0.08	1.01 $\pm$ 0.12	2.70 $\pm$ 0.45	1.74 $\pm$ 0.22	4.48 $\pm$ 0.70	2.49 $\pm$ 0.31	7.02 $\pm$ 0.70	3.41 $\pm$ 0.46
	4	1.05 $\pm$ 0.11	0.73 $\pm$ 0.06	2.37 $\pm$ 0.21	1.60 $\pm$ 0.27	3.37 $\pm$ 0.37	2.38 $\pm$ 0.40	5.95 $\pm$ 0.58	2.95 $\pm$ 0.33
PN	1	0.45 $\pm$ 0.20	1.01 $\pm$ 0.15	1.03 $\pm$ 0.29	1.99 $\pm$ 0.30	1.58 $\pm$ 0.41	2.20 $\pm$ 0.42	3.71 $\pm$ 0.56	4.21 $\pm$ 0.38
	2	0.79 $\pm$ 0.10	0.50 $\pm$ 0.11	1.02 $\pm$ 0.23	0.97 $\pm$ 0.18	1.46 $\pm$ 0.33	1.17 $\pm$ 0.23	4.12 $\pm$ 0.55	2.52 $\pm$ 0.42
	3	1.06 $\pm$ 0.14	0.77 $\pm$ 0.12	1.90 $\pm$ 0.30	1.09 $\pm$ 0.26	2.50 $\pm$ 0.44	1.46 $\pm$ 0.27	5.64 $\pm$ 0.55	3.17 $\pm$ 0.35
	4	0.91 $\pm$ 0.53	0.78 $\pm$ 0.11	2.26 $\pm$ 0.26	1.47 $\pm$ 0.27	3.16 $\pm$ 0.43	1.82 $\pm$ 0.32	5.01 $\pm$ 0.54	3.11 $\pm$ 0.30
RU	1	0.97 $\pm$ 0.10	1.33 $\pm$ 0.15	2.25 $\pm$ 0.44	3.26 $\pm$ 0.54	2.89 $\pm$ 0.44	4.65 $\pm$ 0.53	5.87 $\pm$ 0.67	6.05 $\pm$ 0.52
	2	0.98 $\pm$ 0.10	0.82 $\pm$ 0.15	1.05 $\pm$ 0.22	1.29 $\pm$ 0.23	2.70 $\pm$ 0.52	2.91 $\pm$ 0.43	4.98 $\pm$ 0.75	3.71 $\pm$ 0.45
	3	0.86 $\pm$ 0.13	0.96 $\pm$ 0.20	1.09 $\pm$ 0.28	1.49 $\pm$ 0.31	3.27 $\pm$ 0.69	2.54 $\pm$ 0.46	6.07 $\pm$ 0.86	3.59 $\pm$ 0.60
	4	1.01 $\pm$ 0.28	0.69 $\pm$ 0.10	1.59 $\pm$ 0.30	1.21 $\pm$ 0.30	2.96 $\pm$ 0.65	2.69 $\pm$ 0.49	5.38 $\pm$ 0.61	3.66 $\pm$ 0.67
SP	1	0.82 $\pm$ 0.13	1.09 $\pm$ 0.16	2.10 $\pm$ 0.29	2.74 $\pm$ 0.29	3.33 $\pm$ 0.49	4.09 $\pm$ 0.33	5.46 $\pm$ 0.56	5.08 $\pm$ 0.33
	2	0.80 $\pm$ 0.18	0.87 $\pm$ 0.09	1.89 $\pm$ 0.23	1.11 $\pm$ 0.20	2.78 $\pm$ 0.27	1.61 $\pm$ 0.30	4.84 $\pm$ 0.47	2.54 $\pm$ 0.39
	3	0.97 $\pm$ 0.16	1.15 $\pm$ 0.13	1.87 $\pm$ 0.32	1.96 $\pm$ 0.20	2.97 $\pm$ 0.35	2.59 $\pm$ 0.26	5.49 $\pm$ 0.66	4.14 $\pm$ 0.26
	4	1.00 $\pm$ 0.19	1.06 $\pm$ 0.13	2.49 $\pm$ 0.35	1.50 $\pm$ 0.25	3.01 $\pm$ 0.53	1.71 $\pm$ 0.38	5.02 $\pm$ 0.64	3.38 $\pm$ 0.32
SR	1	0.36 $\pm$ 0.13	0.58 $\pm$ 0.11	2.39 $\pm$ 0.24	2.10 $\pm$ 0.33	2.99 $\pm$ 0.32	2.47 $\pm$ 0.42	3.48 $\pm$ 0.39	3.19 $\pm$ 0.44
	2	0.28 $\pm$ 0.09	0.29 $\pm$ 0.13	1.70 $\pm$ 0.25	1.39 $\pm$ 0.21	2.47 $\pm$ 0.33	1.90 $\pm$ 0.35	3.07 $\pm$ 0.46	2.08 $\pm$ 0.40
	3	0.58 $\pm$ 0.12	0.62 $\pm$ 0.10	2.17 $\pm$ 0.36	1.82 $\pm$ 0.35	3.07 $\pm$ 0.54	2.14 $\pm$ 0.43	3.93 $\pm$ 0.61	2.57 $\pm$ 0.49
	4	0.82 $\pm$ 0.20	0.57 $\pm$ 0.09	2.33 $\pm$ 0.32	1.30 $\pm$ 0.16	3.53 $\pm$ 0.41	1.90 $\pm$ 0.24	4.05 $\pm$ 0.51	2.24 $\pm$ 0.28