Oecologia (1993) 93:165–170

Oecologia

Photosynthetic induction times in shade-tolerant species with long and short-lived leaves

Thomas A. Kursar, Phyllis D. Coley

Department of Biology, University of Utah, Salt Lake City, UT 84112, USA

Received: 3 September 1991 / Accepted: 15 September 1992

Abstract. In the understory of a tropical rainforest, light flecks can contribute 10–80% of the total light flux. We investigated the capacity of eight shade-tolerant species to use light flecks by examining the time required for full induction of photosynthesis during an artificial light fleck. CO_2 fixation rates were measured with a portable LiCor gas-exchange system for plants growing in the field on Barro Colorado Island, Panama. In all species induction to 50% of maximum CO_2 fixation occurred quickly, from 1 to 3 min. In species with short leaf lifetimes (1 year), induction to 90% of maximum also occurred quickly, in 3–6 min. In contrast, the species with longer lived leaves (> 4 years) required 11–36 min for induction to 90% of maximum. Induction times for leaves from gap and understory plants of the same species were indistinguishable. Elevated CO_2 did not eliminate the slow induction phase of long-lived leaves. This suggests that slow induction did not result from stomatal limitation. O_2 evolution, measured on excised leaf disks, induced in 3–4 min in species with short-lived leaves, and 4–8 min in species with long-lived leaves. The rapid induction of O_2 evolution indicates that the slower induction of CO_2 fixation in long-lived leaves was not caused by a delay in the induction of electron transport. Activation of rubisco may be the major factor limiting response times in species with long-lived leaves. Species from Panama with short-lived leaves had remarkably rapid induction times that are comparable to those of algae or higher plant chloroplasts. We also found that understory forest plants induced two to seven times more quickly than did potted plants.

Key words: Photosynthesis – Induction – Light flecks – Leaf lifespan – Rainforest

Plants in the understory of a tropical rainforest receive very low levels of diffuse light along with occasional periods of direct sunlight or light flecks. Diffuse light levels in the understory are often less than 20 μmol $m^{-2}s^{-1}$, whereas light flecks can reach 200 μmol $m^{-2}s^{-1}$ or more (Chazdon 1986; Pearcy 1988; Sasaki and Mori 1981). Although each light fleck may last only seconds, they contribute 10–80% of the total light flux (Chazdon 1988). Hence light flecks represent an important resource for understory plants, possibly accounting for up to 60% of the total carbon gain (Chazdon 1988). In order to take full advantage of a light fleck, a leaf must shift quickly from a low photosynthetic rate to a high photosynthetic rate. However, few studies report rates of photosynthetic induction in response to natural or simulated light flecks (Chazdon and Pearcy 1986). Even though species differ in their rate of photosynthetic induction, there are few examples where inter-specific differences in induction times have been correlated with plant life history or environmental parameters.

To investigate inter-specific differences in the capacity of plants to use light flecks, we measured the induction of photosynthesis in eight shade-tolerant species in a rainforest in Panama. We created artificial light flecks in the field and monitored how fast leaves reached maximum photosynthesis. The study species included shrubs, small trees, and canopy trees and species with short and long-lived leaves (Table 1). Here we report that in some species photosynthesis induces very rapidly and that species differ in their ability to respond photosynthetically to light flecks. These differences appear to be related to leaf lifetime.

Materials and methods

Study site and study species

The study was carried out on Barro Colorado Island, Panama during the rainy season of 1990. The semi-evergreen moist forest supports a highly diverse community of shade-tolerant woody species (Croat 1978; Leigh et al. 1982). Average annual rainfall is 260 cm (Windsor 1990) and most falls during the rainy season, May through December. The understory and light gap environments on

Correspondence to: T.A. Kursar

Table 1. Study species

	Family	ID	Growth Form	Lifetime
Hybanthus prunifolius (Schult.)Schultze	Violaceae	HYBP	shrub	1
Alseis blackiana Hemsl.	Rubiaceae	ALSB	canopy tree	1
Psychotria horizontalis Sw.	Rubiaceae	PSYH	shrub	1
Swartzia simplex Benth. in Mart.	Caesalpinioideae	SWAS	treelet	4
Ouratea lucens (H.B.K.)Engler in Mart.	Ochnaceae	OURL	treelet	5
Aspidosperma cruenta Woods.	Apocynaceae	ASPC	canopy tree	5
Calophyllum longifolium Willd.	Clusiaceae	CALL	canopy tree	5
Rheedia edulis (Seem.)Planch. & Tr.	Clusiaceae	RHEE	treelet	5

ID is the species code used in the figures. Lifetime is in years

Barro Colorado Island resemble those of other rainforest sites. Understory light conditions are as described above. Light gaps receive 100–2000 μmol $m^{-2}s^{-1}$ during a 6–8 h period of high light.

We studied three species with short leaf lifetimes, about 1 year, and five species with longer leaf lifetimes, 4–5 years (Table 1). Two species are shrubs, three are small trees (treelets), and two were saplings of canopy tree species. All of the study species are shade-tolerant and able to survive in the understory. All five species of shrubs and small trees can produce flowers and fruit in the shaded understory, another indication of shade tolerance.

Nearly all of the study plants were growing naturally in the forest. Induction was also measured in potted plants of *Hybanthus* and *Ouratea*. *Hybanthus* plants were rooted from cuttings. *Ouratea* was collected from a site near Barro Colorado Island. Plants were rooted in 2 liter pots in a greenhouse for 1 year and then transplanted into 15 liter pots. The pots were then placed in the forest understory and buried up to the top of the pot. After two years, the plants were removed from the forest, placed in the shade and induction was measured within 10 days of moving the plants.

Leaf lifetimes

Lifetimes of *Ouratea* were determined by marking a cohort of leaves and determining the time to 50% mortality. Other lifetime data were obtained from Coley (1983) and Aide (1989).

CO_2 fixation

Respiration and net photosynthesis were measured for mature leaves in the field. In the afternoon of the day before a measurement, plants were shaded with black plastic and the light level at the leaf prior to measuring induction did not exceed 10 μmol $m^{-2}s^{-1}$. In some species, touching the leaf appeared to have a strong inhibitory effect on induction. For this reason, a leaf was placed in the cuvette without a top late in the afternoon of the day prior to measurement and leaves were primarily handled by the petiole. On most days, only two leaves were measured. The second leaf was allowed to recover from being placed in the cuvette before measurements were started. For all species but *Psychotria*, the entire leaf was placed in the cuvette and sealed at the petiole. For *Psychotria*, a pair of leaves was placed in the cuvette and sealed at the stem.

The protocol for measuring induction times was to determine dark respiration (lasting about 15 min), illuminate the leaf at 5 μmol $m^{-2}s^{-1}$ for 15 min, and then rapidly increase PPFD to a level that saturated photosynthesis (250–600 μmol $m^{-2}s^{-1}$ depending on the species). This was done at either ambient CO_2 or 800 ppm CO_2. Nearly all measurements were made between 9:00 A.M. and 1:00 P.M. On the morning after CO_2 induction was measured, a leaf disk was collected for the analysis of O_2 induction.

CO_2 fixation was measured using a LI-6200 field photosynthesis system (LiCor, Lincoln, NB, USA). The cuvettes were lined with teflon film (Saunders, Los Angeles, CA, USA) and the system volume was adjusted using different cuvettes to accommodate leaves of different sizes and photosynthetic rates. The minimum and maximum system volumes were 498 ml and 1944 ml. Air was well-mixed using Micronel fans (Vista, CA, USA). Leaf temperature was maintained at 29–30° C using Peltier units (Melcor, Trenton, NJ, USA) mounted on the leaf cuvette. Long exposure of the Vaisala humidity sensor to high vapor pressure made the calibration unreliable. Therefore conductance was not determined. Vapor pressure was monitored using a dewpoint hygrometer (General Eastern, Hygro E1) and maintained at 20–30 mb. Light from 12V, 75W narrow spot lamps (Sylvania, Hillsboro, NH, USA) was passed through infra-red filters (Stock Hot Mirrors, OCLI, Santa Rosa, CA, USA).

Photosynthesis was measured by depletion and the system remained closed throughout the measurement of induction. The LI-6200 was set to calculate photosynthetic rates every 20 or 30 s period for up to 50 min. A small amount of high CO_2 air was injected into the system every 1–1.5 min in order to replenish the CO_2 consumed in photosynthesis. Data points obtained during the 30–40 s required for the injected CO_2 to become fully mixed were discarded. In general one photosynthetic measurement was made every 1–1.5 min. During a photosynthetic measurement, the mean CO_2 concentration was 350 ppm and CO_2 dropped 15–35 ppm. System response time was approximately 25 s, but all results are reported as the original times uncorrected for the system response time. Since a data point was collected every 1.5 min, the induction times are reported only to the nearest minute. Data were collected until photosynthesis reached a maximum. This was 15 min for species with rapid induction and up to one hour for the species with the slowest induction. The induction curves were fitted by eye and the times to 50% and 90% of maximum were determined.

Induction of oxygen evolution

O_2 evolution from 10 cm^2 leaf disks was determined with a Clark electrode (Model LD1, Hansatech, Norfolk, England). Light was supplied with the 12V lamps described above. The closed chamber

contained air with 8–20% CO_2, and was maintained at 30° C, a temperature typically experienced by illuminated leaves in the field. Leaves were placed in 20% CO_2 and the chamber sealed. Dark respiration was determined and the leaf was placed at 5 μmol $m^{-2}s^{-1}$ for 15 min and the light increased to saturation. When the CO_2 dropped below 8%, the chamber was flushed by gas containing 15%–20% CO_2. In the range of 8–20% CO_2, no effect of CO_2 on leaf response was noted. The system response time was 1.5 min. Induction times are reported without correcting for system response.

The Hansatech LD1 does not permit control of the atmosphere in the cuvette so a plexiglass insert with valves was added to the LD1. We also have noted artifactual induction-like signals from the LD1 oxygen electrode following a step change in PPFD with a paper disk in the chamber. This may result from the temperature sensitivity of the Clark electrode and the fact that the electrode is in the path of the light beam. To reduce the system volume and eliminate the light artifact a plexiglass cylinder about 3 cm in diameter was inserted between the leaf and the electrode. System volume was 3.4–5 ml. The modified system did not respond to a step change in PPFD.

When leaves are maintained at 10 μmol $m^{-2}s^{-1}$ and the PPFD increased to saturating levels, a burst of O_2 evolution is observed (Kirschbaum and Pearcy 1988). We observed the same effect in leaf disks. While this effect interfered with the determination of the time to 50% of maximum O_2 evolution, it remained possible to calculate the time to 90% of maximum.

Sample sizes and statistical analyses

Data were collected from three to six leaves per species. Each leaf was from a different plant. Differences among species were tested using ANOVA and the Waller-Duncan K-ratio *t*-test (SAS 1987). Differences between the two classes of leaf lifetimes, short and long, and the three classes of growth form, shrub, treelet and tree, were also tested by ANOVA (SAS 1987).

Results

The initial stage of induction of CO_2 assimilation was rapid for all species

The induction of CO_2 assimilation to 50% of maximum occurred very quickly for all eight study species, ranging from 1 to 3 min (Figs. 1, 2A). Species with short-lived leaves required 1 min to induce to 50% of the maximum rate of CO_2 fixation and induced significantly faster than the 2 min required by long-lived leaves (Fig. 2A, ANOVA, $P=0.02$, averaged by species).

The final phase of induction of CO_2 assimilation was more rapid in short-lived than long-lived leaves

The time to 90% of the maximum CO_2 fixation rate varied considerably among species, from 3 to 36 min. The species with short-lived leaves, *Hybanthus, Alseis,* and *Psychotria,* induced to 90% of the maximum photosynthetic rate in 3–5 min (Figs. 1, 2B). Four of the species with long-lived leaves, *Swartzia, Ouratea, Aspidosperma,* and *Calophyllum,* induced to 90% of the maximum in 10–13 min and *Rheedia,* the fifth long-lived species, in 36 min. Even when *Rheedia* was excluded, induction to 90% of maximum was significantly slower in long-lived leaves (ANOVA, $P=0.0007$).

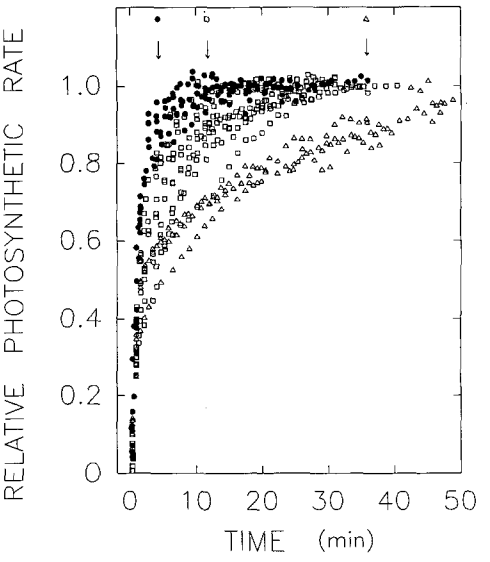

Fig. 1. Induction of CO_2 fixation in understory plants of the eight study species. The photosynthetic rate was normalized to 1.0 for the average maximum rate. After induction, the measured photosynthetic rate varied by 2–5% about the mean. For this reason, some of the normalized values exceed 1.0. The closed circles are the species with short-lived leaves, the open squares are four of the species with long-lived leaves (*Rheedia* is excluded), and the open triangles are for *Rheedia*. Only understory plants are included. The arrow indicates the times to 90% of maximum CO_2 fixation for each group. The times, averaged by species, were 4, 12, and 36 min for short-lived, long-lived excluding *Rheedia,* and *Rheedia,* respectively

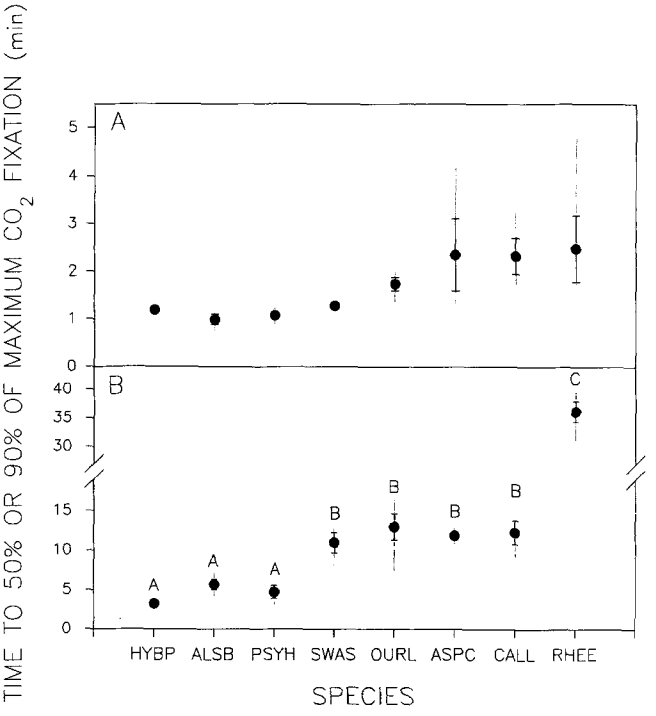

Fig. 2A, B. Means, one standard error, and ranges of induction times for understory plants. The vertical lines indicate the range for each species. The key to the species codes is given in Table 1. **A.** The time to 50% of maximum CO_2 fixation. Differences among species means were not significant ($P=0.26$, ANOVA), but differences among short- and long-lived leaves were significant ($P=0.02$). **B.** The time to 90% of maximum CO_2 fixation. Note the range break on the y-axis. The letters indicate which species had significantly different induction times ($P<0.05$, Waller-Duncan K-ratio *t*-test, ANOVA, SAS, 1987)

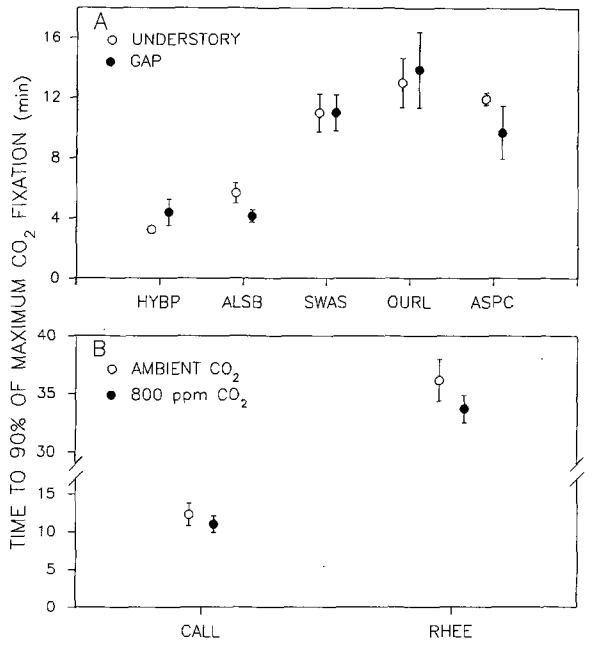

Fig. 3A, B. The effects of light environment and CO_2 concentration on the time to 90% of maximum CO_2 fixation. Means plus or minus one SE are indicated. The key to the species codes is given in Table 1. **A.** The effect of light environment on the time to 90% of maximum CO_2 fixation. Each species was tested for the effect of light environment on induction time using Student's *t*-test. *P* values range from a low of 0.19 for *Alseis* to 0.99 for *Swartzia*. **B.** The effect of CO_2 concentration on the time to 90% of maximum CO_2 fixation. Note the range break on the y-axis. Each species was tested for the effect of CO_2 concentration on induction time using Student's *t*-test. *P* values were 0.58 for *Calophyllum* and 0.41 for *Rheedia*

Growth form had no significant effect on induction times to 90% of maximum CO_2 fixation when both leaf lifetime and growth form were entered as main effects (ANOVA, $P=0.20$).

Leaves that developed in the understory or light gaps did not differ in induction times

The leaves of two short-lived species, *Hybanthus* and *Alseis*, induced to 90% of maximum assimilation in 3–6 min regardless of whether they developed in the understory or light gaps (Fig. 3A) (Student's *t*-test by species, $P=0.36$ for *Hybanthus* and $P=0.19$ for *Alseis*). Leaves of the long-lived species, *Swartzia, Ouratea,* and *Aspidosperma,* induced to 90% of maximum assimilation in 10–14 min, again with no effect of habitat ($P>0.40$ for all species). Furthermore, there were no significant differences between shade and sun leaves for either induction of CO_2 fixation to 50% of maximum (ANOVA, $P=0.20$) or induction of O_2 evolution to 90% of maximum (ANOVA, $P=0.12$). Gap plants had respiratory and photosynthetic rates that were twofold or more greater than understory plants (Table 2). Among gap plants, we found a weak negative relationship between the light-saturated photosynthetic rate and the time to 90% of maximum induction ($P=0.07$).

Induction of CO_2 fixation in ambient CO_2 and 800 ppm of CO_2 did not differ

To determine whether stomatal aperture might limit the rate of induction of photosynthesis, we measured induction times under 800 ppm CO_2 for *Calophyllum* and *Rheedia,* two species with long-lived leaves. The CO_2 concentration did not affect the time until leaves induced either to 50% or 90% of maximum CO_2 assimilation (Fig. 3B) (Student's *t*-test, for time to 90% of maximum $P=0.60$ for *Calophyllum* and $P=0.90$ for *Rheedia*).

For species with long-lived leaves, O_2 evolution induced more rapidly than CO_2 fixation

In the three study species with short-lived leaves, O_2 evolution and CO_2 fixation induced to 90% of maximum at similar rates (Fig. 4). In the species with long-lived leaves, induction of O_2 evolution to 90% of the maximum was significantly shorter than CO_2 induction times (Fig. 4). For *Rheedia,* induction of O_2 evolution required 8 min as compared to 36 min for CO_2 fixation. For the other four species with long-lived leaves, induction of O_2 evolution required 4–5 min as compared to 11–13 min for CO_2 fixation. In addition, leaf lifetime had a marginal effect on the induction of O_2 evolution (ANOVA, $P=0.06$) that was much weaker when *Rheedia* was excluded from the data set ($P=0.09$).

Table 2. Dark respiration and light-saturated CO_2 fixation rates

	Dark respiration		Light-saturated CO_2 fixation	
	Understory	Gap	Understory	Gap
Hybanthus prunifolius	0.083	0.47	3.4	8.2
Alseis blackiana	0.087	0.36	2.8	8.1
Psychotria horizontalis	0.099	ND	2.2	ND
Swartzia simplex	0.103	0.27	5.3	7.2
Ouratea lucens	0.091	0.26	2.9	5.3
Aspidosperma cruenta	0.095	0.34	3.1	5.7
Calophyllum longifolium	0.120	ND	4.7	ND
Rheedia edulis	0.076	ND	2.5	ND

The dark respiration rate is for CO_2 release. ND indicates that no data were taken. Each datum represents 3–6 plants and one leaf per plant

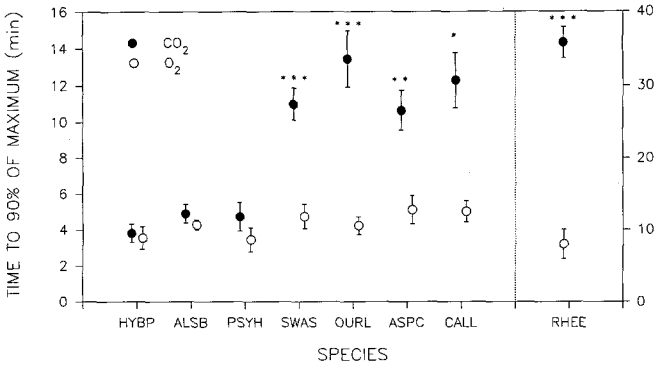

Fig. 4. The induction of CO_2 fixation and O_2 evolution to 90% of maximum. Means plus or minus one SE are indicated. The key to the species codes is given in Table 1. Understory and gap samples were combined. Differences between the rate of CO_2 fixation and O_2 evolution were tested using Student's *t*-test. One, two, and three stars indicate significance at the $P<0.05$, 0.005, and 0.001 levels, respectively

Potted plants induced more slowly than forest plants

Plants of *Hybanthus* and *Ouratea* were placed in pots in the forest for one to two years and then moved to a shaded site on the edge of a large clearing where induction of CO_2 fixation was determined. Induction in the plotted plants was slower than for plants growing naturally in the forest despite similar light conditions. For potted *Hybanthus,* the time to 50% of maximum was 2 min (SE = 0.49, $n=6$) as compared to 1 min for naturally growing plants. The times to 90% of maximum were 16 min (SE = 3.9) for potted *Hybanthus* and 3 for forest plants. For potted and forest *Ouratea,* the times to 50% of maximum were 13 min (SE = 1.8, $n=5$) and 2 min, respectively and the times to 90% of maximum were 24 min (SE = 2.8, $n=5$) and 13 min, respectively. Vapor pressure effects cannot explain the slower induction of the potted plants since the vapor pressure deficit during the induction measurements was less for the potted plants than for the forest plants.

Discussion

The rapidity of photosynthetic induction of rainforest plants

Forest plants from Panama induced rapidly. They required 1–3 min to attain 50% of the maximum rate of CO_2 assimilation. Seven out of eight of the Panama species induced to 90% of maximum in 3–13 min. The shortest induction times of the Panama species are nearly as fast as for isolated chloroplasts, 1–2 min to maximum photosynthesis (Edwards and Walker 1983). We found that CO_2 fixation in potted plants induced two to seven times more slowly than for forest plants.

Other field studies suggest rapid photosynthetic induction. Stomatal conductance reached a maximum in 2 min for beech, 10–11 min for maple and oak, and 20 min for yellow poplar (Woods and Turner 1971). In *Euphorbia forbesii* and *Claoxylon sandwichense* from a mesic Hawaiian forest, induction of CO_2 fixation may occur in less than 4 min (Pearcy and Calkin 1983). *Argyrodendron perulatum,* an Australian rainforest tree, induced to 50% of maximum in about 3 min and 90% of maximum in about 9 min (Pearcy 1988). *Adenocaulon bicolor,* an herb that occurs in redwood forest, induced to 50% of the maximum in about 1.5 min and 90% of maximum in about 6 min (Pfitsch and Pearcy 1989).

Our data and the field studies cited above differ from the results of Chazdon and Pearcy (1986); they found that the induction of assimilation to 90% of maximum in two rainforest species required about 20 min. As was noted above, we found that field plants induced more quickly than potted plants of the same species. Some of the discrepancy among data sets may arise from differences between potted and forest plants. In our study, the forest plants required 1–3 min to attain 50% of their maximum rate. This was substantially faster than the 9–12 min for potted plants of *Alocasia macrorrhiza* and *Toona australis,* two understory species of Australian tropical rainforest (Chazdon and Pearcy 1986). Seven of the eight Panamanian species induced to 90% of maximum in 3–13 min. This was faster than the 22–27 min found for *Alocasia* and *Toona* (Chazdon and Pearcy 1986). The wide differences among species in the speed of induction and the discrepancy between forest and potted plants deserve further investigation.

Patterns of photosynthetic induction in relation in leaf lifetime and environment

Our study species differed substantially in the time to 90% of the maximum rate of CO_2 fixation. In species with short-lived leaves, CO_2 fixation reached 90% of maximal rates in about 3 to 6 min (Fig. 2B). In contrast, four of the species with long-lived leaves, *Aspidosperma, Ouratea, Calophyllum,* and *Swartzia,* had induction times to 90% of maximum of 11–13 min. *Rheedia,* the fifth species with long-lived leaves, had the longest time to 90% of maximum that has been reported, 36 min. Our results suggest that there is a tradeoff between leaf lifetime and the rapidity of photosynthetic induction. It is unclear what physiological factors might lead to such a tradeoff.

In order to investigate environmental plasticity, induction times of leaves that developed in the understory and light gaps were compared. Understory and gap leaves had induction times that were indistinguishable (Fig. 3A), indicating that induction time was not affected by the light environment in which leaves develop. For *Alocasia,* the growth PPFD had little effect on the rate of photosynthetic induction (Chazdon and Pearcy 1986).

We also compared shrubs, treelets and saplings of trees and found no relationship between growth form and the time to 90% of maximum CO_2 fixation (ANOVA, $P=0.12$). With only eight study species, it is difficult to draw any conclusions about phylogenetic patterns. We found that both species of Rubiaceae, *Alseis* and *Psychotria,* had rapid induction and both species of Clusiaceae, *Calophyllum* and *Rheedia,* had slow induction.

Mechanisms restricting photosynthetic induction times

In the absence of conductance measurements, we cannot assess stomatal limitations to photosynthesis directly. For two species with long-lived leaves, *Rheedia* and *Calophyllum*, we found that the slow phase of induction did not differ at ambient CO_2 concentrations of 350 and 800 ppm (Fig. 3B). In *Alocasia*, the time to 90% of maximum was 22 min in 350 ppm of CO_2 and 13 min in 844 ppm of CO_2 (Chazdon and Pearcy 1986). Even with such a substantial reduction in induction time at high CO_2, they concluded that, at most, only 30% of the limitation to photosynthesis was stomatal. The large effect of high CO_2 on induction for *Alocasia* and the absence of such of an effect in *Rheedia* and *Calophyllum* suggests that slow induction in *Rheedia* and *Calophyllum* and the three other species with long-lived leaves did not result from stomatal limitation. Reduction of stomatal aperture by high CO_2 would confound this interpretation.

Our results suggest that the slow induction of long-lived leaves was not due to slow induction of O_2 evolution and electron transport. In long-lived leaves, we found that O_2 evolution induced more quickly than did CO_2 fixation (Fig. 4). This indicates that, as expected, electron transport induced quickly and did not delay induction of CO_2 fixation. Concurrent measurements of O_2 evolution and CO_2 fixation in *Alocasia* support this interpretation (Kirschbaum and Pearcy 1988).

Rubisco activation appears to be the primary factor limiting the rate of assimilation during the first 5–15 min of induction in *Alocasia* (Seemann et al. 1988) and spinach (Woodrow and Mott 1989). In the final phase of photosynthetic induction, increases in photosynthesis may also be due to an increase in the stomatal aperture (Chazdon 1988; Pearcy 1988). Slow induction of photosynthesis in the Panama species with long-lived leaves may be due to a slow activation of rubisco, although this remains to be determined.

Acknowledgments. We thank Li Chen, Patricia Escobar-Paramo and Denise Thorin for running the O_2 electrode and Weishan Jin and Julie Glick for technical assistance. We are grateful to the Smithsonian Tropical Research Institute for providing research facilities. The research was supported by NSF grants BSR–8407712 (to PDC) and BSR–8806080 (to TAK & PDC).

References

Aide TM (1989) The relationship between leaf phenology and herbivory in a tropical understory community. PhD Dissertation, University of Utah

Chazdon RL (1986) Light variation and carbon gain in rainforest understorey palms. J Ecol 74:995–1012

Chazdon RL (1988) Sunflecks and their importance to forest understorey plants. Adv Ecol Res 18:1–63

Chazdon RL, Pearcy RW (1986) Photosynthetic responses to light variation in rainforest species I. Induction under constant and fluctuating light conditions. Oecologia 69:517–523

Coley PD (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecol Monogr 53:209–233

Croat TB (1978) Flora of Barro Colorado Island, Stanford Univ Press, Stanford Calif

Edwards G, Walker D (1983) C3, C4: Mechanisms, and Cellular and Environmental Regulation, of Photosynthesis. Univ of California Press, Berkeley, Calif

Kirschbaum MUF, Pearcy RW (1988) Concurrent measurements of oxygen- and carbon-dioxide exchange during lightflecks in *Alocasia macrorrhiza* (L.) G. Don. Planta 74:527–533

Leigh EG, Rand AS, Windsor DM (eds) (1982) The Ecology of a Tropical Forest: Seasonal Rhythms and Long Term Changes. Smithsonian Institution Press, Washington, D.C.

Pearcy RW (1988) Photosynthetic utilisation of lightflecks by understory plants. Aust J Plant Physiol 15:223–238

Pearcy RW, Calkin HW (1983) Carbon dioxide exchange of C_3 and C_4 tree species in the understory of a Hawaiian forest. Oecologia 58:26–32

Pfitsch WA, Pearcy RW (1989) Steady-state and dynamic photosynthetic response of *Adenocaulon bicolor* (Asteraceae) in its redwood forest habitat. Oecologia 80:471–476

Sasaki S, Mori T (1981) Growth responses of dipterocarp seedlings to light. Malaysian Forester 44:319–345

SAS (1987) SAS/STAT Guide for Personal Computers. Version 6. SAS Institute, Cary, North Carolina

Seemann JR, Kirschbaum MUF, Sharkey TD, Pearcy RW (1988) Regulation of ribulose-1,5-bisphosphate carboxylase activity in *Alocasia macrorrhiza* in response to step changes in irradiance. Plant Physiol 88:148–152

Windsor DM (1990) Climate and moisture availability in a tropical forest, long term records for Barro Colorado Island, Panama. Smith Contrib Earth Sciences 29:1–145

Woodrow IE, Mott KA (1989) Rate limitation of non-steady-state photosynthesis by ribulose-1,5-bisphosphate carboxylase in spinach. Aust J Plant Physiol 16:487–500

Woods DB, Turner NC (1971) Stomatal response to changing light by four tree species of varying shade tolerance. New Phytol 70:77–84