

Steady and dynamic photosynthetic responses of seedlings from contrasting successional groups under low-light growth conditions

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To test the hypothesis that leaf-level photosynthetic-related traits might confer late successional a competitive advantage over early successional in low-light growth conditions, steady photosynthetic assimilation- and dynamic photosynthetic induction-related traits were examined in low-light-grown seedlings with contrasting successional status. Compared with the early successional, late successional as a group significantly exhibited lower leaf gas exchange rates. While late successional required a longer time to respond to simulated sunflecks, they had lower rates of induction losses after sunflecks. Such photosynthetic induction traits allowed late successional to more effectively utilize subsequent sunflecks. It was observed that plants with lower gas exchange rates responded more slowly to simulated sunflecks, but they had lower rates of induction losses after sunflecks. In addition, the rate of response to sunflecks was positively correlated with the rate of induction loss after sunflecks across the successional status of species. A principal components analysis (PCA) demonstrated that early and late successional were separated along the first axis of the PCA, and that early successional were grouped on the right and were associated with higher gas exchange rates, fast responses to sunflecks, and rapid rates of induction loss after sunflecks; late successional held an opposite pattern. Overall, our results suggest that smaller respiratory carbon losses and lower metabolic costs give late successional a competitive advantage in low-light growth conditions, that late successional have an advantage over early successional in utilizing sunflecks, and thus that the successional status of species are mainly associated with the leaf-level photosynthetic-related traits.

Introduction

Low-light growth conditions, such as understory habitats, commonly receive highly variable high light because the very low level of diffuse light is frequently punctuated

by bright sunflecks (Chazdon and Pearcy 1984). These bright sunflecks last for a few seconds to several minutes (Chazdon 1988, Pearcy 1990, Pfitsch and Pearcy 1989a). Previous studies have shown that sunflecks contribute 60–90% of total daily photon flux density (PFD) to

Abbreviations – A_{\max} , maximum photosynthetic assimilation rate; AQY, apparent quantum yield; $g_{s-\max}$, maximum stomatal conductance; $g_{s-\text{initial}}$, initial stomatal conductance prior to high light; IS, induction state; $IS_{10\text{min}}$, induction state after 10 min shade for fully induced leaves; LCP, light compensation point; LSP, light saturation point; PCA, principal components analysis; PFD, photon flux density; R_d , dark respiration rate; T_{50A} , time required to reach 50% of A_{\max} ; T_{90A} , time required to reach 90% of A_{\max} ; T_{50g} , time required to reach 50% of $g_{s-\max}$; T_{90g} , time required to reach 90% of $g_{s-\max}$.

understory plants, thus contributing up to 65% of total daily carbon gain (Chazdon 1988, Pfitsch and Pearcy 1989b). Undoubtedly, the capacity of leaves to make efficient use of sunflecks for photosynthesis is crucial to understory plant survival. However, not all plants can respond equally to sunflecks.

More recently, Montgomery and Givnish (2008) have proposed that the ability of plants to utilize sunflecks depends on: (1) the rate of photosynthetic induction under sunflecks, (2) the rate of induction loss after sunflecks and (3) the post-illumination carbon fixation. Summarily, a combination of biochemical and stomatal factors imposes constraints on utilization of sunflecks. Many attempts have been made to distinguish between biochemical and stomatal limitation under sunflecks (Allen and Pearcy 2000, Kirschbaum and Pearcy 1988, Pearcy and Seemann 1990, Tinoco-Ojanguren and Pearcy 1993). Overall, biochemical constraints mainly limit the utilization of sunflecks, and stomatal control of utilization of sunflecks is still being debated.

Additionally, a comparison of dynamic photosynthetic induction between species differing in life form (herbaceous vs woody species), individual habitat (understory vs open sites), and light requirement (shade-tolerant vs shade-intolerant species) has received significant attention in the past (e.g. Bai et al. 2008, Cao and Booth 2001, Chazdon and Pearcy 1986a, Fay and Knapp 1993, Han et al. 1999, Ögren and Sundin 1996, Pfitsch and Pearcy 1989a, Zhang et al. 2009, Zipperlen and Press, 1997). However, far less attention has been given to the response of contrasting successional species to dynamic high light (e.g. Küppers et al. 1996, Paliwal et al. 1994, Poorter and Oberbauer 1993, Tinoco-Ojanguren and Pearcy 1993).

Early-successional pioneer species typically photosynthesize and respire at higher rates than do late-successional canopy or understory species (Bazzaz and Carlson 1982, Bazzaz and Pickett 1980, Strauss-Debenedetti and Bazzaz 1991). However, it is the case that an early-successional species can not achieve seedling regeneration under low-light conditions, such as understory habitats, whereas a late-successional species can do. It is quite likely that early-successional species utilize steady high light at higher rate, but utilize dynamic high light (sunflecks) at lower efficiency. Understanding the dynamics of photosynthetic responses to dynamic high light is of importance in explaining ecological distribution and natural succession (Küppers and Schneider 1993). However, the question of whether leaf-level photosynthetic-related traits give late successional a competitive advantage over early successional in the low-light growth conditions has not well been addressed.

In the present study, steady-state photosynthetic assimilation- and dynamic photosynthetic induction-related traits were analyzed in low-light-grown seedlings with contrasting successional status. The objectives of this comparative study were to examine the differences between contrasting successional seedlings in the leaf-level photosynthetic-related traits, and to explore a possible relationship between steady-state photosynthetic assimilation- and dynamic photosynthetic induction-related traits across species of differing successional status. Also, we anticipated that the differences in the leaf-level photosynthetic-related traits could explain a competitive advantage or disadvantage of species with contrasting successional status in the low-light growth conditions, and thus that the different successional status of species might be associated with the different photosynthetic-related traits.

Materials and methods

Study site and species descriptions

The study was carried out at Xishuangbanna Tropical Botanical Garden (21°41'N, 101°25'E and 570 m a.s.l.), Chinese Academy of Sciences in south-west Yunnan, China. The mean annual air temperature is about 21.7°C and the annual precipitation is approximately 1560 mm in the study site. However, it has a very distinct seasonality in that more than 85% of precipitation occurs between May and October, consequently resulting in a pronounced rainy season from May to October, and a well-defined dry season from November to April. In addition, because rainfall frequently occurs from May to October, it is difficult to make consecutive measurements during this period. Therefore, all measurements in the present study were conducted at the end of the rainy season.

Sixteen species were selected for this study, and these species were separated into two main groups (early and late successional) according to whole plant growth performance and the occurrence of a large number of individuals of a species in the forest with respect to light availability (personal observation). In general, late successional were those species that could regenerate in the deep shade found under a closed canopy in the forest, while early successional were those species that could not regenerate under a closed canopy but required some level of disturbance to open up gaps in the canopy (Swaine and Whitmore 1988). Indeed, the grouping of species was also based on the previous studies (Cai et al. 2003a, 2003b, Guo et al. 2004, Qi et al. 2004, Zhang and Cao 2004). Successional status, family, and species nomenclature of the 16 plants are shown in Table 1. These species

Table 1. Species nomenclature, family and successional status for the studied 16 species.

Species	Family	Successional status
<i>Ficus benjamina</i> Linn.	Moraceae	Late succession
<i>Garcinia xanthochymus</i> Hook.f.ex J.Anders.	Clusiaceae	Late succession
<i>Antiaris toxicaria</i> (Pers.) Lesch.	Moraceae	Late succession
<i>Pometia tomentosa</i> (Bl.) Teysm. et Binn.	Sapindaceae	Late succession
<i>Parashorea chinensis</i> Wang Hsie	Dipterocarpaceae	Late succession
<i>Ficus tinctoria</i> Forst. f.	Moraceae	Late succession
<i>Litsea dilleniifolia</i> P. Y. Pai et P. H. Huang	Lauraceae	Late succession
<i>Celastrus monospermus</i> Roxb.	Celatraceae	Late succession
<i>Erythrina variegata</i> Linn.	Papilionaceae	Early succession
<i>Pterospermum menglunense</i> Hsue	Sterculiaceae	Early succession
<i>Bauhinia glauca</i> (Watt. ex Benth.) Benth.	Caesalpiniaceae	Early succession
<i>Mallotus esquirolii</i> Lévl.	Euphorbiaceae	Early succession
<i>Mallotus barbatus</i> (Wall.) Muell. Arg.	Euphorbiaceae	Early succession
<i>Neolamarckia cadamba</i> (Roxb.) Bosser	Rubiaceae	Early succession
<i>Syzygium szemaoense</i> Merr. et Perry	Myrtaceae	Early succession
<i>Tectona grandis</i> Linn. f.	Verbenaceae	Early succession

were identified according to the International Code of Botanical Nomenclature and the Flora of China. The species are the early successional *Erythrina variegata*, *Pterospermum menglunense*, *Bauhinia glauca*, *Mallotus esquirolii*, *Mallotus barbatus*, *Neolamarckia cadamba*, *Syzygium szemaoense* and *Tectona gradis*. The late successional consist of the upper-canopy emergents *Antiaris toxicaria*, *Pometia tomentosa* and *Parashorea chinensis*, the mid-canopy emergents *Ficus benjamina*, *Litsea dilleniifolia*, *Garcinia xanthochymus* and *Ficus tinctoria*, and *Celastrus monospermus*, a species which completes its life-cycle in the understory. The 16 species selected are all common at the study sites.

Plants and soil

Seeds of the eight early-successional species were collected from numerous mother plants. In March 2005, seeds were sown in nursery beds with 5% of full sunlight. Germination was nearly synchronous among the eight early-successional species after about three weeks. As late-successional species are generally slow-growing species, the seedlings of the eight late-successional species were directly collected from a nearby forest

where these seedlings frequently receive dynamic high light (sunflecks) and total photon exposure per day is approximately 5% of that in the large gap of the forest during the period of the rainy season (Cai et al. 2007). The mean height of these seedlings ranged from approximately 20 to 30 cm. In April 2005, the seedlings grown in nursery beds with 2–4 leaves and the seedlings directly collected from a nearby forest both were transplanted individually into white plastic pots (30 cm in diameter × 35 cm in depth). Seedlings were grown in the pots with substrates consisting of forest surface soil fully mixed with river sand 2:1 by volume. The forest soil was used to provide a substrate with a natural composition of macro- and micro-nutrients. The river sand improves the texture leading to adequate drainage. One month after transplanting, all pots received 30 g NPK slow release compound fertilizers (Osmocote, Scotts, Marysville, OH).

Experimental design

One pot containing one plant per species was randomly arranged and replicated five times, and thus the experiment involved a total of 80 plants. Seedling survival was very high, and the few that died were immediately replaced. Furthermore, the potential for shading by fast-growing species was precluded by enough space between pots, and all pots were rotated at a 20-day interval to avoid local variation in light availability. Seedlings were grown in a screened growth house where total photon exposure per day was equivalent to 5% of that in the full sunlight. This light regime was created using layers of sieve cloth on a steel frame. The daily course of incident PFD was measured with LI-190SA quantum sensors connected to an LI-1400 data logger (Li-Cor, Lincoln, NE). A typical diurnal curve of PFD for both the artificially created low light and the full sunlight was shown in

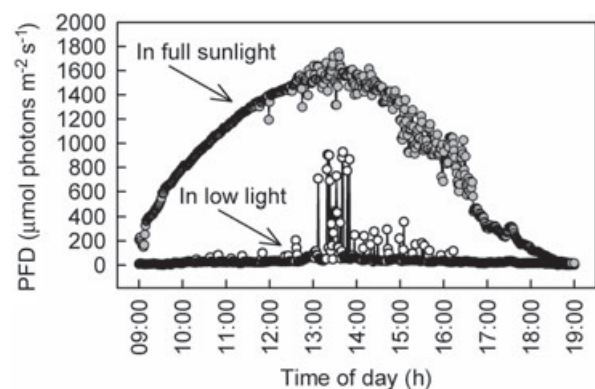


Fig. 1. Representative diurnal time courses of photon flux density (PFD) in both a screened growth house and the full sunlight on a cloudless day. Data were recorded at 1-min intervals.

Fig. 1. Meanwhile, all seedlings were maintained under natural air temperature and relative humidity, and were well watered to keep near field capacity. In addition, weed species were removed regularly and insecticides were used if necessary. At the time of gas exchange measurements, all plants were growing vigorously and there was no evidence of root restriction by the pot.

Photosynthetic responses to steady-state light

In mid-November 2005, at the end of the rainy season, photosynthetic assimilation responses to steady-state light levels were examined with a portable photosynthesis apparatus (LI-6400, Li-Cor, Lincoln, NE). The measurement was performed on newly developed and fully expanded young leaves in the late morning, between 09:30 and 11:00. The PFD, CO₂ concentration and temperature in the broadleaf chamber (20 mm × 30 mm) were 0–1500 μmol photons m⁻² s⁻¹, 360 μmol mol⁻¹ and 25°C, respectively. The PFD was controlled by an internal LED light source (LI-6400-2B), and leaf-to-air vapor pressure deficit was less than 1.5 kPa. The leaf was enclosed in the dark chamber, and the dark respiration rate (R_d) was recorded once gas exchange rate was steady. Afterwards, photosynthetic responses to steady-state light levels were measured at 10 light intensities following the order 1000, 1500, 800, 500, 200, 150, 100, 50, 20 and 0 μmol photons m⁻² s⁻¹. Measurements were logged once gas exchange rate became stable. Maximum stomatal conductance (g_{s-max}) was obtained under the maximum PFD. The net photosynthetic assimilation rate (A) was plotted against incident PFD, and the resulting curve was fitted to a non-rectangular hyperbola (Tausz et al. 2005). The asymptotic light-saturated photosynthetic assimilation rate (A_{max}) was determined from the fitted curve. The light saturation point (LSP) was calculated as the lowest value of PFD for which photosynthesis reached 90% of A_{max}. The apparent quantum yield (AQY) and light compensation point (LCP) were estimated by the slope and x-intercept of the linear region of the light response curve, respectively.

Photosynthetic responses to simulated sunflecks

Photosynthetic responses to simulated sunflecks were also conducted in the late morning (09:30–11:00). The leaf previously used to measure photosynthesis light response curves was darkened overnight by covering the canopy of seedlings with shade cloth, preventing the leaf from being photosynthetically pre-induced. During the period of measurements, the leaf was firstly enclosed into the broadleaf chamber and illuminated with the low light (20 μmol photons m⁻¹ s⁻¹) provided

by the internal LED light source for at least 10 min. The initial photosynthetic assimilation rate (A_{initial}) and stomatal conductance (g_{s-initial}) under this low light were recorded after the readings were stable. In order to simulate sunflecks, the PFD was then increased to 800 μmol photons m⁻² s⁻¹ in one step, and gas exchange readings were recorded at 2-s intervals for the first 10 min, and subsequently at 10-s intervals until the maximum gas exchange rate was stably achieved. This photosynthetic response to simulated sunflecks was determined using the LI-6400's automatic time-lamp program. The light intensity of simulated sunflecks was set to 800 μmol photons m⁻² s⁻¹. The reason is that this light intensity was frequently experienced by the 16 species studied (see Fig. 1), and was higher than the LSP (see Table 2), thus being sufficient to induce A_{max}.

Fitting of response curves

The response of A to a sudden increase in PFD from 20 to 800 photons μmol m⁻² s⁻¹ (Fig. 3a) was described by the equation (Naumburg and Ellsworth 2000, Tausz et al. 2005): $A(t) = A_{\text{initial}} + (A_{\text{max}} - A_{\text{initial}}) \times [1 - \exp(-t/t_1)]$, where A_{initial} is the initial photosynthetic assimilation rate in the low light (20 photons μmol m⁻² s⁻¹), A_{max} is the maximum photosynthetic assimilation rate achieved in response to the simulated sunflecks, t is the time from the beginning of the simulated sunflecks and t₁ is a characteristic time constant (time until 63% of change occurs). Two parameters were then calculated using the resulting equation: the time required to reach 50% of A_{max} (T_{50A}) and 90% of A_{max} (T_{90A}). Stomatal responses to the simulated sunflecks (Fig. 3b) were best described by a logistic curve (Naumburg and Ellsworth 2000, Tausz et al. 2005): $g(t) = g_{\text{s-initial}} + (g_{\text{s-max}} - g_{\text{s-initial}}) / [1 + (t/t_1)^p]$, where g_{s-initial} is the initial stomatal conductance in the low light (20 μmol photons m⁻² s⁻¹), g_{s-max} is the maximum stomatal conductance reached during the simulated sunflecks, t is the time from the beginning of the simulated sunflecks, t₁ is a characteristic time constant and p is a parameter determining the curve shape. The time required to reach 50% of g_{s-max} (T_{50g}) and 90% of g_{s-max} (T_{90g}) were then calculated from the resulting function.

Rate of induction loss

The rate of induction loss was measured according to the method as described by Allen and Pearcy (2000) with a slight modification. In brief, the leaves were fully induced in situ with light from 12-V, 50-W quartz halogen projector lamps. We varied the distance between the lamp and the leaf to give saturating PFD

Table 2. The steady-state photosynthetic parameters in leaves of 16 plant species studied. The variables are given as mean \pm SE (n = 5 for individuals of 16 species, and n = 8 for late- or early-successional species group). Mean values were compared between late- and early-successional species (*t* tests). **P* < 0.05; ***P* < 0.01.

Species	A_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	LSP ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	LCP ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	AQY	$g_{s-\max}$ ($\text{mmol m}^{-2} \text{s}^{-1}$)	$g_{s-\text{initial}}$ ($\text{mmol m}^{-2} \text{s}^{-1}$)
Individuals of late successional							
<i>Ficus benjamina</i>	8.11 \pm 0.03	313 \pm 15	11.75 \pm 0.20	-0.52 \pm 0.02	0.044 \pm 0.004	275 \pm 9	57.0 \pm 4.0
<i>Garcinia xanthochymus</i>	3.74 \pm 0.17	198 \pm 4	11.48 \pm 1.66	-0.63 \pm 0.15	0.053 \pm 0.004	186 \pm 8	35.1 \pm 3.8
<i>Antiaris toxicaria</i>	3.94 \pm 0.05	314 \pm 12	11.37 \pm 1.67	-0.32 \pm 0.05	0.029 \pm 0.001	163 \pm 14	62.2 \pm 4.1
<i>Pometia tomentosa</i>	4.74 \pm 0.03	363 \pm 7	12.80 \pm 1.47	-0.42 \pm 0.05	0.033 \pm 0.000	199 \pm 11	48.7 \pm 3.3
<i>Parashorea chinensis</i>	5.79 \pm 0.05	319 \pm 17	10.36 \pm 0.50	-0.41 \pm 0.03	0.040 \pm 0.003	195 \pm 10	57.8 \pm 3.5
<i>Ficus tinctoria</i>	4.04 \pm 0.08	234 \pm 34	10.17 \pm 2.16	-0.43 \pm 0.03	0.045 \pm 0.006	186 \pm 5	42.7 \pm 3.7
<i>Litsea dilleniifolia</i>	7.17 \pm 0.02	388 \pm 7	12.37 \pm 0.80	-0.54 \pm 0.04	0.042 \pm 0.001	226 \pm 9	59.0 \pm 4.0
<i>Celastrus monospermus</i>	5.40 \pm 0.03	239 \pm 3	12.74 \pm 0.68	-0.73 \pm 0.04	0.056 \pm 0.000	228 \pm 7	48.7 \pm 4.0
Individuals of early successional							
<i>Erythrina variegata</i>	15.89 \pm 0.70	592 \pm 12	16.68 \pm 0.70	-1.01 \pm 0.03	0.063 \pm 0.003	424 \pm 13	107.6 \pm 3.3
<i>Pterospermum menglunense</i>	7.96 \pm 0.13	339 \pm 20	11.20 \pm 0.32	-0.57 \pm 0.06	0.051 \pm 0.004	258 \pm 12	52.3 \pm 2.7
<i>Bauhinia glauca</i>	9.00 \pm 0.04	396 \pm 9	11.42 \pm 0.29	-0.52 \pm 0.02	0.046 \pm 0.001	263 \pm 6	64.4 \pm 4.2
<i>Mallotus esquirolii</i>	10.56 \pm 0.03	386 \pm 4	12.74 \pm 0.45	-0.72 \pm 0.04	0.057 \pm 0.000	353 \pm 8	49.4 \pm 3.3
<i>Mallotus barbatus</i>	7.83 \pm 0.05	379 \pm 14	14.00 \pm 1.01	-0.74 \pm 0.08	0.053 \pm 0.002	281 \pm 9	77.1 \pm 3.5
<i>Neolamarchia cadamba</i>	7.34 \pm 0.09	360 \pm 7	13.40 \pm 0.57	-0.76 \pm 0.06	0.058 \pm 0.002	211 \pm 12	64.1 \pm 4.5
<i>Syzygium szemaense</i>	9.67 \pm 0.08	453 \pm 12	14.55 \pm 0.49	-0.74 \pm 0.04	0.052 \pm 0.001	325 \pm 13	82.8 \pm 2.5
<i>Tectona grandis</i>	8.39 \pm 0.13	344 \pm 6	12.30 \pm 0.42	-0.80 \pm 0.07	0.064 \pm 0.003	241 \pm 10	76.6 \pm 3.5
Late-successional species group	5.37 \pm 0.56	296 \pm 23	11.63 \pm 0.35	-0.50 \pm 0.05	0.043 \pm 0.003	207 \pm 12	51.4 \pm 3.3
Early-successional species group	9.58 \pm 0.97	406 \pm 29	13.29 \pm 0.64	-0.73 \pm 0.05	0.056 \pm 0.002	294 \pm 24	71.8 \pm 6.6
F	3.74**	2.93*	2.27*	3.35**	2.26*	3.19**	2.76*

at the surface, confirming the PFD with a quantum sensor. After induction, the leaf was then sealed in the chamber under the PFD of 800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, and once a steady state was achieved, values for A_{\max} were recorded. The leaf was then removed from the chamber and covered with a dark cloth for 10 min. A few minutes before the end of this dark period, the leaf was again sealed in the cuvette while exposed to low PFD (20 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). Under this low-light condition, values for A (A_{low}) were recorded once the rate of gas exchange became stable. At the end of the 10-min shade exposure, the leaf was re-illuminated promptly by the PFD of 800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ for 90 s and gas exchange rate was continuously recorded at 2-s intervals using the automatic time-lamp program of the Li-6400. The mean value of A recorded over the last 10 s was used to calculate the photosynthetic induction state (IS) at the end of the 10-min shade exposure using the equation (Chazdon and Pearcy 1986a) $\text{IS}(\%) = 100 \times (A - A_{\text{low}}) / (A_{\max} - A_{\text{low}})$, where A is the photosynthetic assimilation rate at the end of the re-illumination, A_{low} is the photosynthetic assimilation rate recorded in the low-light conditions (20 μmol

photons $\text{m}^{-2} \text{s}^{-1}$) before the leaf was re-illuminated and A_{\max} is the maximum photosynthetic assimilation rate recorded in the fully induced leaves. $\text{IS}_{10\text{min}}$ (IS at the 10-min shade exposure) was used to evaluate the capacity of the leaf to maintain photosynthetic IS in the low-light conditions. A subtraction of $\text{IS}_{10\text{min}}$ from 100% was defined as the rate of induction loss during the period of 10-min shade exposure. Thus, the higher the value of $\text{IS}_{10\text{min}}$, the slower the induction loss in the shade environments.

Statistical analyses

The measurements of steady and dynamic photosynthetic responses were performed on five individuals per species (n = 5) in the present study. All analyses were performed with the SPSS software package (Chicago, IL), and the variables were given as means \pm SE. The comparison of photosynthetic-related traits between late and early successional species was confirmed by *t* tests with species nested within species' successional status. Pearson's correlation was made between the steady photosynthetic

assimilation- and dynamic photosynthetic induction-related traits across species' successional status. The P value of less than 0.05 could be accepted as a significant level. In order to check the significance of separating the species into two main groups according to their successional status, and to explore the existence of internal trends within early and late-successional species, we conducted a principal components analysis (PCA) of mean values of photosynthetic-related traits after they were \log_{10} -transformed.

Results

It has been commonly accepted that *P. chinensis* and *S. szemaoense* are a typical late-successional species and a typical early-successional species, respectively. There were apparent differences between *P. chinensis* and *S. szemaoense* in their responses of net photosynthetic assimilation to incident PFD (Fig. 2). However, such different photosynthetic traits did not always hold true; the values of steady-state photosynthetic assimilation-related traits, such as A_{\max} , LSP, LCP, R_d , AQY, $g_{s\text{-max}}$ and $g_{s\text{-initial}}$, markedly overlapped to a certain extent between the individual of late and early successional (Table 2). When comparisons of these traits were made with species nested within species' successional status, early-successional species as a group possessed significantly higher values of A_{\max} ($F_{14} = 3.74$, $P = 0.002$), LSP ($F_{14} = 2.93$, $P = 0.011$), LCP ($F_{14} = 2.27$, $P = 0.039$), AQY ($F_{14} = 2.26$, $P = 0.040$), $g_{s\text{-max}}$ ($F_{14} = 3.19$, $P = 0.007$) and $g_{s\text{-initial}}$ ($F_{14} = 2.76$, $P = 0.015$) as well as more negative values of R_d ($t_{14} = 3.35$, $P = 0.005$) than did late-successional species.

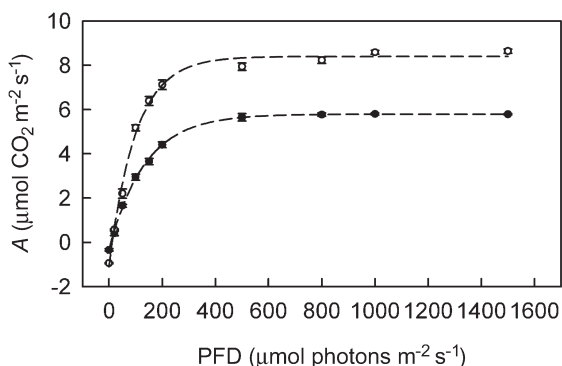


Fig. 2. The response of net photosynthetic assimilation (A) to incident PFD in fully mature leaves of two representative species studied: the late-successional species *Parashorea chinensis* (closed circles) and early-successional species *Syzygium szemaoense* (open circles). Light-response curves were fitted to a non-rectangular hyperbola, and the mean \pm se ($n = 5$) is shown for each point.

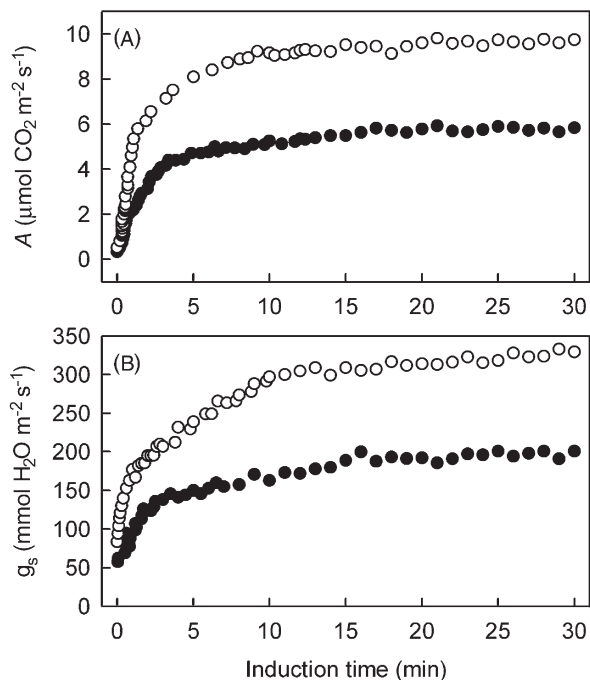


Fig. 3. Responses of net photosynthetic assimilation – A (A) – and stomatal conductance – g_s (B) – to the simulated sunflecks in two representative species studied: the late-successional species *Parashorea chinensis* (closed circles) and early-successional species *Syzygium szemaoense* (open circles). Typical data for a leaf of each species are shown. Leaves were first exposed to $20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ until steady-state rates of gas exchange were reached, and a simulated sunfleck was then imposed by increasing incident photosynthetic PFD to $800 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. The simulated sunfleck started at time 0, and, for clarity, only a part of data recorded during the simulated sunfleck is drawn.

The time to reach maximum gas exchange rate appeared to be different between the late-successional species *P. chinensis* and the early-successional species *S. szemaoense* during simulated sunflecks (Fig. 3). However, values of dynamic photosynthetic induction-related traits, such as T_{50A} , T_{90A} , T_{50g} , T_{90g} and $IS_{10\text{min}}$, also overlapped to a certain extent across species with contrasting successional status (Table 3). Comparisons with species nested within species' successional status demonstrated that late-successional species as a group apparently exhibited significantly higher values of T_{50A} ($F_{14} = 3.95$, $P = 0.001$), T_{90A} ($F_{14} = 3.61$, $P = 0.003$), T_{50g} ($F_{14} = 3.31$, $P = 0.005$), T_{90g} ($F_{14} = 3.69$, $P = 0.002$) and $IS_{10\text{min}}$ ($F_{14} = 2.54$, $P = 0.023$) than did early-successional species.

Pearson's correlation between values of steady-state photosynthetic assimilation-related traits and of dynamic photosynthetic induction-related traits were made within the 16 species studied (Table 4). Significant correlations of steady-state photosynthetic assimilation-related traits,

Table 3. Parameters of photosynthetic induction properties in leaves of the 16 species studied. The variables are given as mean \pm SE (n = 5 for individuals of 16 species, and n = 8 for late- or early-successional species). Mean values were compared between late- and early-successional species (t tests). *P < 0.05; **P < 0.01.

Species	T _{50A} (s)	T _{90A} (min)	T _{50g} (s)	T _{90g} (min)	IS _{10min} (%)
Individuals of late successional					
<i>Ficus benjamina</i>	102.2 \pm 3.5	11.51 \pm 0.56	131.1 \pm 5.5	14.35 \pm 0.94	66.1 \pm 3.3
<i>Garcinia xanthochymus</i>	101.2 \pm 3.7	13.50 \pm 0.42	140.5 \pm 7.6	16.80 \pm 0.77	77.4 \pm 3.0
<i>Antiaris toxicaria</i>	115.8 \pm 3.0	12.28 \pm 0.51	127.9 \pm 5.5	18.41 \pm 0.58	84.9 \pm 3.1
<i>Pometia tomentosa</i>	100.2 \pm 3.4	10.18 \pm 0.57	137.3 \pm 6.6	16.11 \pm 0.81	76.7 \pm 2.7
<i>Parashorea chinensis</i>	98.0 \pm 3.0	11.85 \pm 0.28	114.6 \pm 2.8	14.73 \pm 0.68	80.6 \pm 3.0
<i>Ficus tinctoria</i>	95.6 \pm 3.2	12.16 \pm 0.37	147.9 \pm 6.5	15.50 \pm 0.74	70.8 \pm 2.6
<i>Litsea dilleniifolia</i>	81.5 \pm 3.7	10.97 \pm 0.51	125.5 \pm 5.4	13.52 \pm 0.67	74.9 \pm 2.8
<i>Celastrus monospermus</i>	85.4 \pm 2.5	9.67 \pm 0.56	133.2 \pm 7.4	16.54 \pm 0.71	84.9 \pm 3.3
Individuals of early successional					
<i>Erythrina variegata</i>	58.2 \pm 3.4	5.95 \pm 0.32	75.5 \pm 3.9	8.78 \pm 0.93	43.7 \pm 2.2
<i>Pterospermum menglunense</i>	77.8 \pm 3.1	9.61 \pm 0.28	123.6 \pm 4.5	15.37 \pm 0.64	69.0 \pm 2.7
<i>Bauhinia glauca</i>	72.7 \pm 3.9	8.90 \pm 0.42	113.4 \pm 6.1	12.58 \pm 0.65	74.5 \pm 2.5
<i>Mallotus esquirolii</i>	70.3 \pm 4.3	9.47 \pm 0.49	97.2 \pm 5.3	11.59 \pm 0.68	69.7 \pm 3.0
<i>Mallotus barbatus</i>	90.6 \pm 3.0	10.46 \pm 0.30	113.4 \pm 5.7	12.39 \pm 0.72	72.6 \pm 2.1
<i>Neolamarchia cadamba</i>	94.6 \pm 3.3	10.83 \pm 0.41	134.5 \pm 6.3	14.91 \pm 0.51	73.8 \pm 3.0
<i>Syzygium szemaense</i>	62.9 \pm 3.3	7.74 \pm 0.46	100.6 \pm 5.3	9.59 \pm 0.61	53.3 \pm 2.6
<i>Tectona grandis</i>	67.2 \pm 3.8	8.90 \pm 0.47	108.1 \pm 3.3	11.92 \pm 0.82	67.2 \pm 3.0
Late-successional species group	97.5 \pm 3.7	11.51 \pm 0.43	132.3 \pm 3.6	15.75 \pm 0.55	77.0 \pm 2.3
Early-successionals species group	74.3 \pm 4.5	8.98 \pm 0.55	108.3 \pm 6.3	12.14 \pm 0.80	65.5 \pm 3.9
F	3.95**	3.61**	3.31**	3.69**	2.54*

Table 4. Pearson's correlation coefficients between traits of steady-state photosynthetic assimilation and of dynamic photosynthetic induction. *P < 0.05; **P < 0.01.

	T _{50A}	T _{90A}	T _{50g}	T _{90g}	IS _{10min}
A _{max}	-0.808**	-0.855**	-0.894**	-0.884**	-0.834**
LSP	-0.668**	-0.828**	-0.843**	-0.811**	-0.755**
LCP	-0.561*	-0.744**	-0.665**	-0.683**	-0.688**
R _d	0.723**	0.692**	0.637**	0.701**	0.647**
AQY	-0.612*	-0.545*	-0.558*	-0.541*	-0.550*
g _{s-max}	-0.784**	-0.819**	-0.862**	-0.870**	-0.828**
g _{s-initial}	-0.587*	-0.761**	-0.801**	-0.763**	-0.725**

such as A_{max}, LSP, LCP, AQY, g_{s-max}, g_{s-initial} and R_d, with dynamic photosynthetic induction-related traits (e.g. T_{50A}, T_{90A}, T_{50g}, T_{90g} and IS_{10min}) were found within the 16 species studied.

Multivariate comparisons of species were carried out with mean values of leaf-level photosynthetic-related traits. Early- and late-successional species were apparently separated along the first axis of the PCA (Fig. 4). The first two axes of the PCA explained 88.8% of the total variation of the 12 leaf traits (Table 5). Early-successional species was grouped on the right and was associated with higher gas exchange rate (e.g. higher R_d, A_{max} and LCP), a fast response to sunflecks (e.g. shorter T_{50A} and T_{50g}), and a higher rate of induction loss after sunflecks (e.g. lower IS_{10min}); late-successional species held an opposite pattern. Additionally, in PCA

Table 5. Factor loadings and the explained percentage of variance of the first two principal components.

Variable	Component 1	Component 2
A _{max}	0.972	0.139
LSP	0.895	-0.245
LCP	0.659	-0.091
R _d	0.800	0.132
AQY	0.166	-0.255
g _{s-max}	0.830	0.531
g _{s-initial}	0.798	-0.554
T _{50A}	-0.960	-0.092
T _{90A}	-0.946	0.027
T _{50g}	-0.941	0.132
T _{90g}	-0.968	-0.015
IS ₁₀	-0.909	0.062
% of variance	81.2	7.60
Cumulative %	81.2	88.8

analysis, we observed that there were significantly positive correlations between IS_{10min} and T_{50A}, T_{90A}, T_{50g} and T_{90g} across species' successional status (data not shown). Such positive correlations distinctly imply that plants responding more quickly to simulated sunflecks have a higher rate of induction loss after sunflecks.

Discussion

Early successional species generally possessed higher A_{max} compared to late successional species (Table 2). From a successional point of view, early successional species commonly

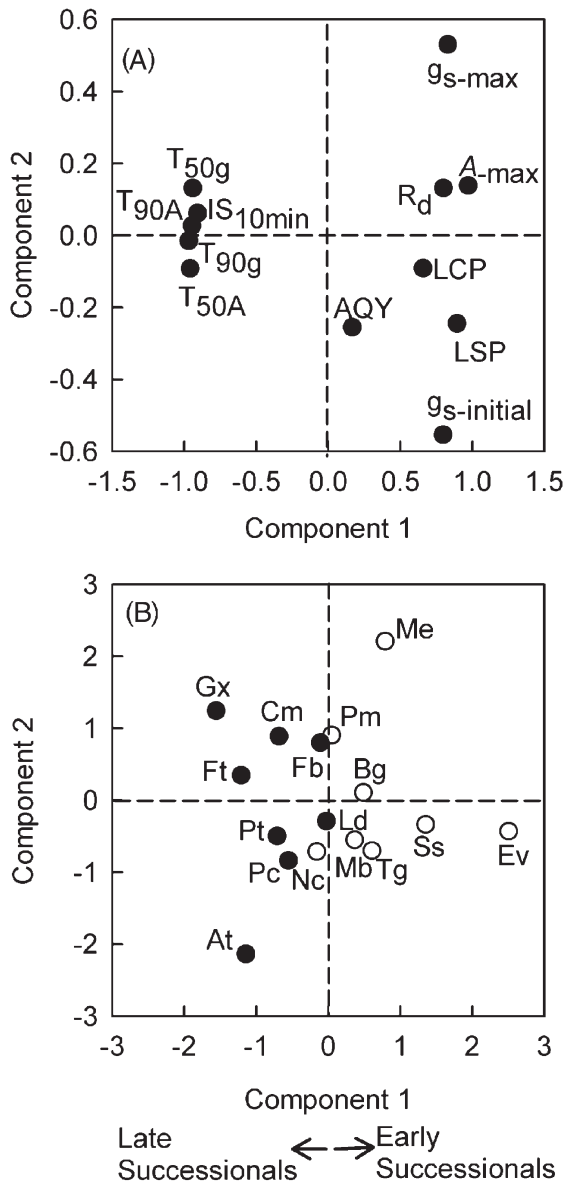


Fig. 4. A principal component analysis for (A) 12 photosynthetic-related traits and (B) the eight early-successional species (open circles) and eight late-successional species (closed circles) for the first two axes. Percentage of variation explained by the first two components: 1, 83%; 2, 8%. See an explanation of trait abbreviations in Tables 2 and 3. Species indicated by codes: Fb, *Ficus benjamina*; Gx, *Garcinia xanthochymus*; At, *Antiaris toxicaria*; Pt, *Pometia tomentosa*; Pc, *Parashorea chinensis*; Ft, *Ficus tinctoria*; Ld, *Litsea dilleniifolia*; Cm, *Celastrus monospermus*; Ev, *Erythrina variegata*; Pm, *Pterospermum menglunense*; Bg, *Bauhinia glauca*; Me, *Mallotus esquirolii*; Mb, *Mallotus barbatus*; Nc, *Neolamarchia cadamba*; Ss, *Syzygium szemaoense* and Tg, *Tectona grandis*.

inhabit open sites and late successional low-light environments (e.g. understory habitat). Higher A_{max} values allow early successional to effectively utilize high light

in open sites and to achieve a larger amount of carbon gain. Lower A_{max} in late successional can be interpreted as an adaptive feature of species common in the low-light conditions. Numerous comparative studies on species of contrasting successional status have documented that early successional inherently exhibited higher A_{max} compared to late successional even independent of light regimes (Bazzaz 1979, Bazzaz and Carlson 1982, Bazzaz and Pickett 1980, Oberbauer and Strain 1984, Strauss-Debenedetti and Bazzaz 1991). Thus, not surprisingly, early successional are able to maintain more sun-leaf characteristics; while late successional more shade-leaf characteristics in the low-light growth conditions in the current study. However, higher A_{max} cannot necessarily give early successional a competitive advantage over late successional in the light-limited conditions, because the light intensity recorded for most time in one day would have been far below the LSP in early successional (Fig. 1, Table 2), indicating that the full photosynthetic potential of early successional cannot be realized in the low-light conditions. There has been evidence that the maintenance of positive net carbon balance is likely achieved through minimizing energy expenditure rather than maximizing energy gain rates as the latter is constrained in the low-light conditions (Grime and Jeffery 1965, Reich et al. 2003). Thus, it may be accepted that more respiratory carbon loss than photosynthetic carbon uptake has a major influence on the leaf carbon balance in the low-light conditions in that metabolic costs are incurred both day and night and regardless of irradiance, as suggested by Givnish (1988). A great deal of research has found that late successional inherently possess lower R_d (Grime 1965, Loach 1967, Read and Hill 1985, Reich et al. 1998), being consistent with the result obtained in the present study. It is likely that late successional achieve a relatively greater positive net carbon gain under the low-light conditions because of their lower respiratory carbon losses (Table 2). Stem or root respiration has not been taken into account, but it is commonly argued that leaf respiration rates dominate whole plant respiratory carbon losses in small seedlings (Lehto and Grace 1994). Overall, a smaller respiratory carbon loss gives late successional a competitive advantage over early successional in the low-light conditions.

Besides lower respiration rates, late successional generally exhibited both lower LCP and lower LSP (Table 2). Lower LCP and lower LSP both are considered beneficial in low-light conditions (Boardman 1977) because there is insufficient light below the LCP to maintain a positive and adequate carbon balance. Thus, it is undoubted that late successional will be better able to tolerate low light as they will less frequently experience leaf-level carbon

deficits in the low-light conditions. Similarly, several earlier studies have found both lower LCP and lower LSP in late successional than early successional when both were grown in a comparable shade (Fetcher et al. 1983, Mulkey 1986, Sims and Pearcy 1989). Therefore, our results, combined with the previously reported results, strongly imply that, besides a minimization of carbon losses, a competitive advantage of late successional grown in the low-light conditions might also be attributed to the photosynthetic traits that minimize carbon deficits.

Anyhow, higher gas exchange rates should not be considered to be advantageous to early successional in the low-light growth conditions, because the low light level cannot support the high metabolic cost of maintaining high photosynthetic performance (Björkman 1981, Givnish 1988). Especially, plants naturally grown in the low-light conditions frequently receive dynamic high light (e.g. sunflecks), and not steady high light. Thus, the capacity of leaves to utilize sunflecks is a key determinant of plant survival in the low-light conditions. Unexpectedly, the values of T_{50A} , T_{90A} , T_{50g} and T_{90g} were significantly lower in early successional in our experiments, indicating that early successional respond more quickly to simulated sunflecks; nevertheless, late successional had a lower rate of induction loss after sunflecks (Table 3). These do not fully agree with the previously reported results that understory plants should undergo physiological induction and open their stomata rapidly in response to sunflecks, and slowly lose induction and close stomata afterwards as compared to sun-adapted species (Bai et al. 2008, Cai et al. 2005, Chazdon and Pearcy 1986a, 1986b, Poorter and Oberbauer 1993, Tinoco-Ojanguren and Pearcy 1995, Valladares et al. 1997). It has been generally believed that photosynthetic induction dynamics in response to sunflecks vary with plant light growth conditions (Pfitsch and Pearcy 1989a, Rijkers et al. 2000, Tinoco-Ojanguren and Pearcy 1992). Accordingly, the reason for different photosynthetic responses to sunfleck events may be light-specific or species-specific.

Interestingly, plants that exhibited higher gas exchange rates are just plants that responded more quickly to sunflecks and had a higher rate of induction loss after sunflecks (Table 4). Similarly, it has been documented that plants with higher gas exchange rates showed shorter T_{90A} during sunflecks and maintained lower photosynthetic IS after sunflecks (Bai et al. 2008). More recently, Zhang et al. (2009) have found that the value of $g_{s-initial}$ of shade-adapted plants was negatively related to the value of T_{90A} and T_{50A} , as also suggested by Naumburg and Ellsworth (2000). These results suggest that plants with higher gas exchange rates more readily overcome the limiting factors during sunflecks,

and more rapidly deactivate the limiting components after sunflecks.

Also, in the PCA analysis, we found that plants that respond more quickly to sunflecks had a higher rate of induction loss after sunflecks (Fig. 4). Plants with such photosynthetic induction-related traits were just early-successional species in the present study. Despite a fast response to sunflecks, however, this alone cannot necessarily lead to a competitive advantage of early successional over late successional in the low-light growth conditions. While early successional respond more quickly to sunflecks, they rapidly lose photosynthetic IS after sunflecks and have to respond repeatedly to subsequent sunflecks, and consequently may maintain lower photosynthetic IS throughout the day. Conversely, late successional respond more slowly to sunflecks, but they have a lower rate of induction loss after sunflecks, and thus they may always maintain higher photosynthetic IS because of a cumulative effect. Therefore, compared with the capacity of leaves to respond to sunflecks, the capacity of leaves to maintain photosynthetic IS after sunflecks is a more important factor for positive carbon gains in the low-light growth conditions. Actually, there has been evidence that the positive carbon balance is determined not by the time required to respond to sunflecks, but by the photosynthetic IS before an occurrence of subsequent sunflecks (Chazdon and Pearcy 1986a, Pfitsch and Pearcy 1989b). The time required to respond to sunflecks was relatively longer, but late successional maintained higher photosynthetic IS after sunflecks (Table 3), thus allowing them a more efficient utilization of subsequent sunflecks than early successional. These results therefore indicate that late successional possess a competitive advantage over early successional in utilizing dynamic high light in the low-light growth conditions.

Our results raised such a question of why plants that respond more quickly to sunflecks have a higher rate of induction loss after sunflecks. The time course of photosynthetic induction is determined by two main phases: (1) a rapidly induced phase that is associated with the regeneration of ribulose-1,5-bisphosphate (RuBP) and the buildup of Calvin–Benson cycle metabolites (Sassenrath-Cole and Pearcy 1992) and (2) a slower increase in photosynthetic assimilation because of light regulation of Rubisco and light-driven stomatal opening (Pearcy 1990). The loss of photosynthetic IS results from the deactivation of enzymes in the Calvin–Benson cycle, stomatal closing, and depletion of high-energy metabolite pools needed for the Calvin–Benson cycle (Horton and Neufeld 1998). It has early been reported that RuBP regeneration activates rapidly during sunflecks and deactivates rapidly after sunflecks; Rubisco activation during sunflecks and deactivation after sunflecks is

a slower process, and stomatal opening during sunflecks and closing after sunflecks proceed slowly (Pearcy 1990, Pons et al. 1992, Sassenrath-Cole and Pearcy 1994). This apparently indicates that the more easily the limiting components are activated during sunflecks, the more easily they are deactivated after sunflecks, and thus the harder it is for leaves to maintain photosynthetic IS afterwards.

Additionally, our results evidently demonstrated that species' successional status was closely associated with the leaf-level photosynthetic-related traits (Fig. 4, Table 5). Early-successional species were associated with higher gas exchange rates, which enable them to effectively utilize steady high light in early-successional habitats. Conversely, late-successional species were coupled with lower gas exchange rates and a lower rate of induction loss after sunflecks, which allow them to minimize respiratory carbon losses and to make an efficient use of dynamic high light in late-successional habitats. Indeed, early- and late-successional species were scattered and intermingled to a certain extent in the principal component plot of mean values (Fig. 4), and moreover the values of photosynthetic-related traits also overlapped substantially for some individuals of early and late-successional species (Tables 2 and 3). These indicate that species' successional status is not solely determined by the leaf-level photosynthetic-related traits alone.

In conclusion, smaller respiratory carbon losses and lower metabolic costs confer late successional a competitive advantage, while higher gas exchange rates are considered to be disadvantageous to early successional in the low-light growth conditions in that the low light level cannot support the metabolic cost of maintaining high photosynthetic performance. Also, we found that late successional have an advantage over early successional in utilizing dynamic high light (sunflecks) in the low light growth conditions, and that species' successional status are mainly associated with the leaf-level photosynthetic-related traits.

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