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Author(s): Kung-Fang Cao and E. Webber Booth
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Leaf anatomical structure and photosynthetic induction for seedlings of five dipterocarp species under contrasting light conditions in a Bornean heath forest

KUN-FANG CAO*†[1] *and* E. WEBBER BOOTH*

* *Department of Biology, Universiti Brunei Darussalam, Gadong BE1410, Brunei Darussalam*
† *Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla County, Yunnan 666303, P. R. China*
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ABSTRACT. This study compares leaf anatomy, chlorophyll content and photosynthetic induction rates for seedlings of five dipterocarp species growing both by a path and in the understorey of a Bornean heath forest. Hemispherical photographs were used to estimate the light level. Although three of the five species showed significantly higher photosynthetic capacity in high light conditions, there were no significant within-species differences in induction rates. Average induction times to reach 50% ($T_{50\%}$) and 90% ($T_{90\%}$) of maximum photosynthetic rate (A_{max}) were about 1.5 and 9 min for *Shorea pachyphylla*. In contrast, these were 18 and 37 min respectively for *Dipterocarpus borneensis*, and 12 and 25 min for *Shorea multiflora*. Intermediate values were recorded for *Hopea pentanervia* and *Cotylelobium burckii*. There was an overall weak and negative correlation of induction rate with stomatal density. Three species showed more rapid induction loss in their leaves from the path edge vs. the understorey. The results suggest that photosynthetic acclimation can influence some aspects of a leaf's dynamic response to sunflecks, such as A_{max} and induction loss, while not affecting overall induction rates. This study also shows significant differences among dipterocarp species in photosynthetic capacity, induction responses and leaf structure, and in acclimation on these traits.

KEY WORDS: Borneo, chlorophyll content, dipterocarp, kerangas, leaf anatomy, light effect, photosynthetic induction, stomatal density

INTRODUCTION

In tropical rainforest understorey, the light environment consists of low levels of diffuse irradiation, punctuated by brief sunfleck events (Chazdon & Fetcher

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[1] Corresponding address: 50 Xuefu Road, Kunming 650223, P.R. China. Email: kfcao@public.km.yn.cn

1984). Sunflecks contribute substantially to the daily photon flux received by the understorey plants. A large proportion of total daily carbon gain in understorey plants is achieved during sunfleck periods (Chazdon 1986). To use sunflecks for photosynthesis, the understorey plants must activate their photosynthetic systems quickly from a low photosynthetic rate to a high rate. The activation or induction of the photosynthetic systems involves both the relatively slow opening of stomata and more rapid light activation of photosynthetic enzymes. Induction effects can be carried over and actually enhanced by sunflecks presented in a series (Chazdon & Pearcy 1986, Poorter & Oberbauer 1993). It has been found that leaves of climax trees usually require a long time to achieve full photosynthetic induction (Chazdon & Pearcy 1986, Küppers *et al.* 1996, Kursar & Coley 1993, Poorter & Oberbauer 1993), while those of pioneer trees can be induced quickly (Poorter & Oberbauer 1993). However, the opposite trend has also been found (Valladares *et al.* 1997). Poorter & Oberbauer (1993) have shown that induction time requirement increases with increased canopy openness for seedlings of a climax tree. In contrast, Kursar & Coley (1993) have found no difference in induction time between understorey and gap-grown leaves for shade-tolerant trees. More data are needed to solve these controversies concerning plant photosynthetic responses to sunflecks.

Photosynthetic capacity of an understorey leaf also affects its efficiency to utilize sunflecks (Lei & Lechowicz 1997). For example, at a given induction state, leaves with higher photosynthetic rates should be relatively more efficient in use of sunflecks. Photosynthetic capacities of leaves are usually related to their leaf structure and chlorophyll (Chl) contents (Boardman 1977, Chazdon & Kaufmann 1993). Within species, leaves developed in high-light conditions are usually thicker, with increased mesophyll thickness and increased leaf mass in relation to area (Ashton & Berlyn 1992, Boardman 1977, Chazdon & Kaufmann 1993). A lower Chl *a:b* ratio is a common adaptation to forest shade (Björkman 1981, Boardman 1977, Lei *et al.* 1996). However, extreme shade species usually have poor plasticity in structure and physiology when facing different light conditions (Boardman 1977, Chazdon *et al.* 1996).

Dipterocarpaceae are both ecologically and economically the most important tree family in the tropical forests of the Far East (Symington 1943, Whitmore 1984). Dipterocarps cover a wide ecological range. They are important components in forests in the lowlands and lower mountains, in heath forest on sandy soil and swamp forest. They all bear simple leaves that vary greatly in size among species (Ashton 1964), and they can vary widely in physiology and shade tolerance (Ashton 1964, Ashton & Berlyn 1992, Barker *et al.* 1997, Cao 2000, Eschenbach *et al.* 1998, Koyama 1981, Scholes *et al.* 1997; Zipperlen & Press 1996, 1997). This study characterizes the effect of light on leaf structure, chlorophyll content, and photosynthetic induction responses for seedlings of five dipterocarp species in a Bornean heath forest, and shows substantial differences among species both in these traits and in their acclimation.

METHODS

The study was conducted in a heath forest (kerangas); the Research Forest at Bukit Sawat (4°34′37″N, 114°30′11″E, 11–23 m asl) in Brunei, northern Borneo. In spite of its location in the aseasonal tropical zone, moderate droughts occur fairly frequently and prolonged droughts occur occasionally in northern Borneo (Walsh 1996). The study forest is established on albic arenosol soil on a Pleistocene terrace with white sand over 2 m in depth. Since the forest had been selectively logged in the late 1960s, its present canopy is not very dense. Important canopy tree species are *Gluta beccarii* (Engl.) Ding Hou, *Dipterocarpus borneensis* Slooten, *Shorea multiflora* (Burck) Symington, *Copaifera palustris* (Symington) de Wit and *Calophyllum ferrugineum* Ridl. (Davies & Becker 1996). A general description of Bornean heath forests can be found in Brünig (1996). Mean annual temperature is 28.1 °C (1983–1988), a value which is relatively even throughout the year (mean daily maxima = 32.0 °C, mean daily minima = 24.2 °C; Anonymous 1990). The mean annual precipitation is 2920 mm (range = 1730–4252 mm, 1958–1988).

Five dipterocarp species, as introduced below, were selected for the study. *Dipterocarpus borneensis* is the only species of the genus *Dipterocarpus* that occurs in heath forest (Ashton 1964). *Cotylelobium burckii* (Heim) Heim is a common component of heath forest. *Shorea multiflora* is an important canopy tree in both mixed dipterocarp and heath forests, and is very shade-tolerant (Turner 1990). *Shorea pachyphylla* Symington is common to both heath and peat swamp forests (Brünig 1973). *Hopea pentanervia* Wood occurs in mixed swamp forest and also in dry soils in lowland situations (Meijer & Wood 1964). Henceforth only generic names are used for the study species, except for the two *Shorea* species. For four study species, seven seedlings growing on the edge of a path within the forest and seven seedlings in the understorey were selected and marked for each. *S. pachyphylla* had only seedlings in the understorey locations. The path is mostly about 2–2.5 m wide, was used as a logging road in the 1960s and has been deserted subsequently. There were no human disturbances to plants on the edge of the path as local visitors rarely come to the site. Selected seedlings were between 0.5 and 1.3 m in height. They were healthy individuals, not sprouts, and were not overtopped by plants with heights similar to the sample plant.

The seedlings of these species have contrasting crown architectures. *S. pachyphylla* and *Cotylelobium* bear large leaves on their main stems and remain unbranched up to 1.5–2 m in height. The other three species, *Dipterocarpus*, *Hopea* and *S. multiflora*, bear relatively small leaves on plagiotropic branches (extending more or less horizontally with leaves packed in a plane) and therefore have relatively wide crowns.

A prolonged El Niño associated drought occurred in northern Borneo during the period from December 1997 to middle May 1998. The dipterocarp seedlings taller than 0.5 m barely suffered from that drought, although they did greatly reduce their stomatal conductance and assimilation rates during the drought period (Cao 2000). The present study was conducted during the moist period between middle July and August 1998. The pre-dawn leaf water potentials of the dipterocarp seedlings during this period were near zero as indicated by occasional measurements using a pressure chamber.

The photosynthetic induction determinations were carried out when the soils were well watered by rain, using young, fully developed leaves located in the upper crowns of the seedlings. The seedlings were covered with two layers of neutral shading net for at least 2 h prior to the induction measurements to ensure no sunflecks affected the induction state of their leaves. Net photosynthetic rates in the low diffuse light prior to the induction were measured with a portable closed gas exchange system (LICOR 6200, Lincoln, USA). After one minute, artificial light was supplied at a saturating photosynthetic photon flux density (about 500 μmol m^{-2} per s for understorey leaves, and 800 μmol m^{-2} per s for those by the path). The light was supplied through a spot lamp (12 V, 100 W, Philips, Germany), filtered through a hot mirror (Wide Band Type 3, OCLI, UK) and powered with a battery (12 V, 17 Ah, Yuasa, UK). Gas exchange rates were recorded every 5–10 s during the first 5 min of induction and every 20–30 s thereafter. The measurement was continued until the photosynthetic rates levelled off as maximum steady-state photosynthesis (A_{max}) was reached. CO_2 concentration and air humidity in the leaf chamber were maintained as close as possible to those in ambient air by regularly flushing ambient fresh air into the leaf chamber by means of a toggle valve. In the leaf chamber, CO_2 concentration was between 330–355 ppm, relative air humidity was kept to at least 90% of the relative humidity of the ambient air. The data recorded during opening and shortly after closure of the toggle valve were discarded. Due to relatively high vapour pressure deficit of the bulk air in the leaf chamber during an induction, the calibration of the humidity sensor was unreliable. Therefore, the stomatal conductance data are not published (also cf. Kursar & Coley 1993, Poorter & Oberbauer 1993).

Once fully induced, the time-dependent course of induction loss was examined by exposing the leaf to low diffuse light under the shading cloth. During the diffuse-light period, the light was switched on for 0.5 min every 10 min and the photosynthetic rate was measured. This was repeated for about 1 h for the understorey seedlings. As the patterns of the time-dependent induction loss were found to be fairly similar within a species, only induction states after 10 and 30 min darkness were determined for the plants by the path. Five plants (one leaf per plant) from either growth conditions per species were used for the induction experiment, except for *Hopea* where its seven plants in the understorey were used. The sample sizes for induction maintenance determination were smaller in some cases (n = 3–5 per species per condition).

The leaves used for the photosynthetic induction experiment and their neighbouring two or three leaves on the same shoot were harvested, sealed in plastic bags, and immediately stored in a cold box. On the same day, in the laboratory, 1–3 of the harvested leaves per plant were cut in half longitudinally, and a part of each was stored in a freezer at −20 °C. These parts were used to extract Chl *a* and *b* (with 95% ethanol), following the method described in Johnston *et al.* (1984). The balance of the harvested leaves and leaf portions were stored in a refrigerator. Subsequently, the central parts beside the main vein of these leaves were sectioned to determine the thickness of the leaf and epidermal layers, palisade and spongy mesophyll, using a microscope binocular with 10 × and 40 × objectives. Their stomatal density and guard cell length were also examined using nail-paint prints.

Hemispherical photographs were taken on overcast days from immediately above each of the seedlings, using black-and-white film (Kodak, Tri-X, 400 ASA). The camera (Minolta X-700, MPS) with a fisheye lens (MC Fisheye Rokkor 1:4, f = 7.5 mm, Minolta) was mounted on a tripod, aligned to compass north and aimed vertically using a bubble level. With the lens focused at infinity, exposures were made at 1/125s to freeze leaf movements. Canopy openness, direct site factors (DSF), diffuse site factors (ISF) and total site factors (TSF) above the seedlings were calculated using the program WINPHOT (Tropenbos, Wageningen, the Netherlands). DSF, ISF and TSF were the fractions of direct, indirect and total potential daily photosynthetic photon flux density that penetrate to a particular site relative to the amount of radiation above the forest canopy. These indices were, however, just used as a rough estimate of potential light availability. For more precise analysis of light level using the hemispherical photographs, the photographing and processing of the photographs should be more carefully carried out, and calibration with measurement of quantum sensors is preferred (cf. Clearwater *et al.* 1999a).

Non-linear curves were fitted to the time-dependent induction data. With the help of the curves and the raw photosynthetic data, the times necessary to build up 50% ($T_{50\%}$) and 90% ($T_{90\%}$) of the steady state photosynthesis were determined for each of the leaves. Leaf attributes, chlorophyll contents, Ch *a:b* ratios, A_{max}, $T_{50\%}$, $T_{90\%}$, and induction states (IS%) after 10 and 30 min darkness following the full induction reached, were compared between the two light conditions for each species, using t-test or Mann–Whitney U-test. As both $T_{50\%}$ and $T_{90\%}$ were not significantly different for any of the study species, each of them from the two conditions were combined per species and compared among species (ANOVA). The IS% values were calculated according to Chazdon & Pearcy (1986). Correlation analysis was applied to examine the relationships between A_{max}, $T_{50\%}$, DSF, ISF, thickness of leaf, palisade and spongy layers, SLA, Chl *a* and *b* concentrations, Chl *a:b* ratio and stomatal density.

RESULTS

DSF, ISF and TSF were strongly correlated with the canopy openness (r was 0.93, 0.98 and 0.93 respectively, $P < 0.001$). The mean canopy openness, DSF, ISF and DSF were 10.9% (SD = 2.6%), 0.22 (SD = 0.06), 0.17 (SD = 0.05) and 0.21 (SD = 0.06) respectively, for the understorey seedlings, and were 20.5% (SD = 9.3%), 0.43 (SD = 0.15), 0.34 (SD = 0.13) and 0.41 (SD = 0.14) for the seedlings by the path. *Shorea multiflora* seedlings were in relatively more shady conditions, e.g. mean DSF was 0.30 (SD = 0.04) for its seedlings by the path, and 0.15 (SD = 0.04) for its understorey seedlings.

The seedlings by the path had thicker leaves, thicker palisade and spongy mesophyll, greater palisade cell height/width ratios, and smaller SLA than those in the understorey for *Cotylelobium*, *Hopea* and *Dipterocarpus*, although the differences were not always significant for the last species (Table 1). Two of five *Cotylelobium* seedlings by the path had two tiers of palisade cells. Of five *Hopea* seedlings by the path, one seedling had two tiers and one seedling had three tiers of palisade cells. The second- and third-tier palisade cells were about 50–70% as long as, but 130–200% as wide as, the first-tier ones. *Dipterocarpus* and *Hopea* seedlings by the path had greater stomatal density than those in the understorey (Table 1). There were no significant differences in guard cell length between the leaves from the two distinct light conditions for any of the study species. In contrast to other species, *Shorea multiflora* did not show any significant differences in leaf structural attributes between its seedlings both by the path and in the understorey. This species had two types of stomata, large and small. Some of the small stomata were somewhat aggregated. Their guard cells were the smallest among the study species.

The understorey leaves had much higher Chl *a* and *b* concentrations in relation to weight than the leaves from the path edge for *Cotylelobium*, *Hopea* and *Shorea multiflora* (Table 1). For *Cotylelobium* and *Hopea*, understorey leaves also had significantly lower Chl *a:b* ratios than the leaves from the path edge. In contrast, Chl concentration and Chl *a:b* ratios were not significantly different between the leaves from the two contrasted conditions for *Dipterocarpus*. On the leaf-area basis, the overall mean Chl $a + b$ contents were 39.8 $\mu g\ cm^{-2}$ (SD = 10.9) for the leaves from the path edge of the four study species, and 45.3 $\mu g\ cm^{-2}$ (SD = 13.1) for the understorey leaves of the five species.

Of the study species, *S. multiflora* had the lowest A_{max} value (Table 2). Of the understorey group, *S. pachyphylla* had the largest A_{max}. The differences in A_{max} among species for the understorey seedlings were reduced compared to those for the seedlings by the path. Three species showed significantly greater A_{max} values in the higher light condition.

A_{max} was significantly correlated with DSF ($r = 0.62$, $P < 0.05$) and ISF ($r = 0.76$, $P < 0.001$) for *H. pentanervia*, while the correlations of A_{max} with the light level indices were not significant ($P > 0.5$) for other species. However, using pooled data from the five species from both conditions, A_{max} was significantly correlated with DSF ($r = 0.56$, $P < 0.001$) and ISF ($r = 0.59$, $P < 0.001$). There were no significant correlations between A_{max} and leaf anatomical attributes or Chl concentration per unit weight for any of the study species ($P > 0.05$).

Table 1. Leaf anatomical properties, SLA (specific leaf area), and chlorophyll (Chl) content for seedlings of the five dipterocarp species both on the edge of the path and in the understorey. Entries are means, n = 5–14. Means within species within columns sharing a common letter are not significantly different (P > 0.05, t-test or Mann-Whitney U-test). nd = no data.

Species	Growth conditions	Thickness (μm)			Palisade cell height/ width	SLA (cm^2 g^{-1} DW)	Stomatal density (μm)	Guard cell length (μm)	Chl. content (mg g^{-1} FW)		Chl *a:b*
		Leaf	Palisade mesophyll	Spongy mesophyll					Chl a	Chl b	
Cotylelobium	path	234.0^{a}	75.3^{a}	126.9^{a}	7.8^{a}	82^{a}	nd	nd	1.37^{a}	0.55^{a}	2.56^{a}
burckii	understorey	204.0^{b}	48.1^{b}	118.2^{b}	5.3^{b}	100^{b}	439	15.8	1.90^{b}	0.84^{b}	2.33^{b}
Dipterocarpus	path	175.0^{a}	41.2^{a}	87.5^{a}	5.2^{a}	151^{a}	218^{a}	17.7^{a}	1.91^{a}	0.81^{a}	2.35^{a}
borneensis	understorey	160.0^{b}	35.9^{a}	81.6^{b}	3.8^{b}	168^{a}	177^{b}	16.8^{a}	2.21^{a}	0.96^{a}	2.31^{a}
Hopea	path	186.3^{a}	42.7^{a}	117.9^{a}	4.1^{a}	110^{a}	287^{a}	16.1^{a}	1.50^{a}	0.56^{a}	2.71^{a}
pentanervia	understorey	152.0^{b}	26.7^{b}	97.9^{b}	3.3^{b}	132^{b}	201^{b}	17.2^{a}	2.07^{b}	0.87^{b}	2.41^{b}
Shorea	path	191.7^{a}	29.2^{a}	133.3^{a}	3.7^{a}	144^{a}	84^{a}	5.9^{a}	1.13^{a}	0.46^{a}	2.48^{a}
multiflora	understorey	201.7^{a}	28.5^{a}	146.4^{a}	3.4^{a}	135^{a}	177^{b}	5.2^{a}	1.73^{b}	0.81^{b}	2.16^{a}
S. pachyphylla	understorey	226.4	29.7	152.5	3.2	110	293	19.7	1.10	0.48	2.25

Table 2. Maximum net photosynthetic rates (A_{max}) determined during the induction, induction times to reach 50% ($T_{50\%}$) and 90% ($T_{90\%}$) of A_{max}, and induction states after 10 and 30 min darkness following full induction reached. Entries are means ± SD; n = 5–10 for A_{max} and induction times, and n = 3–5 for induction states. Means for A_{max} and induction states within species (t-test or Mann-Whitney U-test), and means for induction times within columns among species (ANOVA) sharing the same letter, were not significantly different (P > 0.05). Data for $T_{50\%}$ were logarithmically tranformed for the significance test. nd = no data. Full names of species are in Table 1.

Species	A_{max} (μmol m^{-2} s^{-1})		Induction time (min.)		Induction state (%)			
	Path	Understorey	$T_{50\%}$	$T_{90\%}$	10 min in dark		30 min in dark	
					Path	Understorey	Path	Understorey
C. burckii	8.7 ± 1.9^{a}	4.9 ± 0.7^{b}	6.7 ± 3.3^{a}	16.9 ± 4.4^{ac}	39.2 ± 20.6^{a}	55.5 ± 12.8^{b}	20.6 ± 8.8^{a}	24.0 ± 3.3^{a}
D. borneensis	7.3 ± 1.3^{a}	4.8 ± 0.7^{b}	18.1 ± 4.0^{b}	37.4 ± 6.8^{b}	44.1 ± 1.5^{a}	69.8 ± 6.8^{b}	29.0 ± 11.3^{a}	51.4 ± 9.3^{b}
H. pentanervia	6.3 ± 2.0^{a}	4.5 ± 0.9^{b}	3.1 ± 2.9^{c}	25.0 ± 12.5^{c}	58.1 ± 11.7^{a}	71.7 ± 10.6^{b}	36.2 ± 9.7^{a}	56.0 ± 15.5^{b}
S. multiflora	4.5 ± 0.9^{a}	3.4 ± 0.6^{a}	12.3 ± 5.3^{ab}	25.3 ± 7.3^{c}	66.9 ± 7.1^{a}	78.3 ± 7.3^{a}	47.7 ± 3.3^{a}	49.3 ± 2.1^{a}
S. pachyphylla	nd	5.4 ± 1.2	1.4 ± 0.4^{c}	9.1 ± 5.4^{a}	nd	76.8 ± 11.9	nd	48.6 ± 9.4

In general, there were not significant within-species differences in induction times, either as $T_{50\%}$ or $T_{90\%}$, between the seedlings in the two contrasted light conditions ($P > 0.05$). Three different patterns of time-dependent photosynthetic induction were found within the five species. *S. pachyphylla* displayed rapid induction (Figure 1, Table 2). On average, its $T_{50\%}$ was about 1.5 min, and $T_{90\%}$ about 9 min. *Hopea* showed fast initial induction but was slow to complete. In contrast, *Dipterocarpus* and *Shorea multiflora* displayed an overall gradual and slow induction. The mean $T_{50\%}$ and $T_{90\%}$ for *Dipterocarpus* were 18 and 37 min, respectively, and 12 and 25 min for *S. multiflora*. *Hopea* and *Cotylelobium* had intermediate values. Some *Hopea* and *Dipterocarpus* seedlings also showed quite rapid induction.

$T_{50\%}$ for *Dipterocarpus* was significantly negatively correlated with DSF ($r = -0.66$, $P < 0.05$), Chl *a* concentration per unit weight ($r = 0.70$, $P < 0.05$), and SLA ($r = 0.77$, $P < 0.01$). $T_{50\%}$ for *S. multiflora* was significantly negatively correlated with A_{max} ($r = -0.70$, $P < 0.05$), but positively correlated with thickness of leaf ($r = 0.69$, $P < 0.05$) and spongy mesophyll ($r = 0.76$, $P < 0.01$). Using pooled data from the five species, excluding obvious outliers, there were weak negative correlation of $T_{50\%}$ ($r = -0.46$, $P < 0.001$) and $T_{90\%}$ ($r = -0.40$,

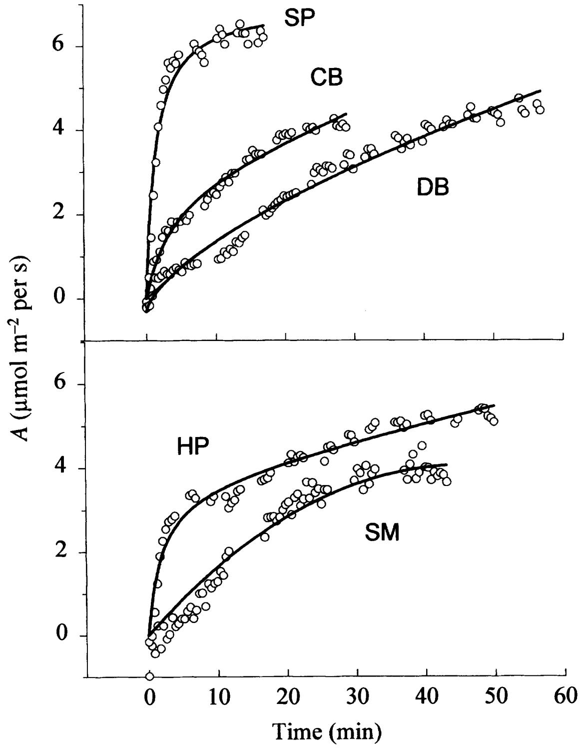

Figure 1. Representatives of time-dependent photosynthetic induction responses to a constant saturated light for an understorey leaf of each of the study species: *Cotylelobium burckii* (CB), *Dipterocarpus borneensis* (DB), *Hopea pentanervia* (HP), *Shorea multiflora* (SM), and *Shorea pachyphylla* (SP).

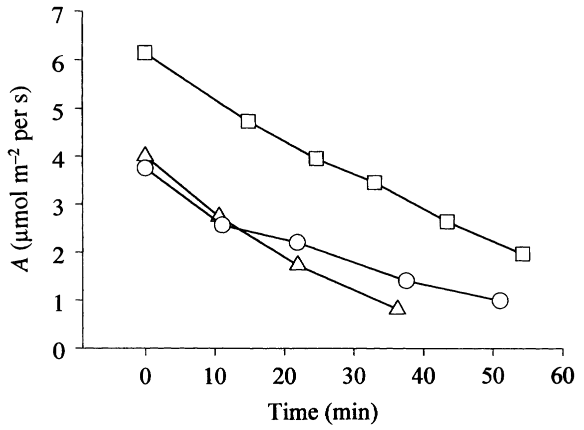

Figure 2. Representative curves of time-dependent photosynthetic induction loss under darkness for an understorey leaf of *Cotylelobium burckii* (triangles), *Dipterocarpus borneensis* (circles) and *Shorea pachyphylla* (squares).

$P < 0.01$) with stomatal density. Thus, among species, leaves with denser stomata tended to be induced quicker.

Once the leaves were fully induced, all species needed about 60 min or longer of darkness to lose induction completely (Figure 2, Table 2). The IS% values after 10 min darkness for the leaves from the path edge were significantly smaller (quicker induction loss) than those for the understorey leaves for three study species (*S. pachyphylla*, *Cotylelobium* and *Dipterocarpus*, Table 2). The IS% values after 30 min darkness for the leaves from the path edge were significantly smaller than those from the understorey only for *Dipterocarpus* and *Hopea*. Among species, *Cotylelobium* showed the quickest induction loss.

DISCUSSION

Most of the study species demonstrated substantial plasticity in leaf structure, Chl concentration, and photosynthetic capacities in relation to light conditions (Tables 1 and 2). Leaf structural and Chl concentration differentiation between sun and shade leaves are well known (Ashton & Berlyn 1992, Boardman 1977, Chazdon *et al.* 1996). Higher Chl *b* proportion relative to Chl *a* is believed to be an adaptation to enhance the absorption of the limited red light in forest shade and to maintain the energy balance between the two photosynthetic systems (Boardman 1977). Photosynthetic acclimation to different light conditions have been also reported for other dipterocarp species (Ashton & Berlyn 1992, Barker *et al.* 1997, Clearwater *et al.* 1999b, Zipperlen & Press 1996). In contrast, *Shorea multiflora* lacked plasticity in leaf structure and photosynthesis when growing in different light conditions. This species is known to be very shade-tolerant (Turner 1990). This supports the idea that extreme shade species are relatively less flexible in structure and physiology compared to light-demanding species (Björkman 1981, Boardman 1977, Chazdon *et al.* 1996).

The Chl contents per unit leaf area found in this study (mean = 39.8 μg cm^{-2} for the leaves of all species by the path) were within the range for extreme shade species in tropical America (mean = 42 μg cm^{-2}, Lee *et al.* 1990). It is not surprising that the Chl concentration per unit weight in our tropical evergreen trees (Table 1) was lower than those for temperate deciduous trees (e.g. Lei *et al.* 1996) because the former are likely to be composed of a higher proportion of construction material.

A high interspecific variation in the induction times was found in the present study (Figure 1, Table 2). Two species, *Shorea multiflora* and *Dipterocarpus*, showed very slow induction. Slow photosynthetic induction has also been found for other dipterocarp trees in eastern Borneo (Zipperlen & Press 1997), and for rainforest plants elsewhere (Chazdon & Pearcy 1986, Küppers *et al.* 1996, Valladares *et al.* 1997). In contrast, there was one species, *Shorea pachyphylla*, that displayed very fast induction (Figure 1, Table 2). Its induction times were similar to those for seedlings of a pioneer rain-forest tree (Poorter & Oberbauer 1993) and for tropical trees with short-lived leaves (Kursar & Coley 1993). *Cotylelobium* also showed relatively fast induction. The leaves of our dipterocarp seedlings probably have long lifetimes, especially those of *S. pachyphylla* and *Cotylelobium* as evidenced by their persistence on the lower stem parts of the 1–2-m-high seedlings. Both *S. pachyphylla* and *Cotylelobium* are probably able to use sunflecks more efficiently than the other study species, at least at the leaf level, based on their faster induction as well as higher photosynthetic rates (Figure 1, Table 2, cf. Lei & Lechowicz 1997). The seedlings of both *S. pachyphylla* and *Cotylelobium*, however, bear large leaves without side shoots. They therefore have limited capacities to capture a broad horizontal array of light resources in the forest understorey (cf. Zipperlen & Press 1996). Efficient utilization of sunflecks for photosynthesis should therefore be essential for their survival in the understorey.

Our finding of general lack of significant differences in induction times between the seedlings by the path and in the understorey is in agreement with the findings of Kursar & Coley (1993) for rain forest trees in Panama, and Zipperlen & Press (1997) for *Dryobalanops lanceolata* Burck in Sabah, north-eastern Borneo. Understorey plants are subjected to dynamic light, while the plants by the path in our case or in gaps are subjected to more constant light. Therefore, the photosynthetic systems and stomatal flexibility of understorey plants are adapted to dynamic light conditions. Induction experiments using constant light might not adequately simulate the situations under which the understorey plants are induced. This may artificially reduce the differences in induction times between gap and understorey plants.

Nevertheless, there was a significant negative correlation between $T_{50\%}$ and DSF for *Dipterocarpus*, i.e. the leaves in more shady locations were induced more rapidly. This is consistent with reports for a climax species in Costa Rica (Poorter & Oberbauer 1993) and for tropical rain forest trees in southern India (Küppers *et al.* 1996).

Interestingly, our data showed that leaves with higher stomatal density tended to be induced more quickly. Both *S. pachyphylla* and *Cotylelobium* had relatively higher stomatal density than the other species and displayed faster induction. Rapid initial induction response may be due to less stomatal limitation. Dense stomata could facilitate gas exchange between leaf and ambient air.

Our finding of slow induction loss for all of the study species (Figure 2, Table 2) is consistent with results from other studies (Chazdon & Pearcy 1986, Poorter & Oberbauer 1993). Further, the maintenance of photosynthetic induction at a higher state for a longer time in the understorey leaves compared to the well-lit leaves appears to be a general trend (Table 2, Küppers *et al.* 1996, Poorter & Oberbauer 1993, Zipperlen & Press 1997). The slow induction loss should be of significance for forest understorey plants in utilizing sunflecks in series (Chazdon & Fetcher 1984).

In conclusion, although three of the five species showed significantly higher photosynthetic rates in the higher light condition, there were no significant within-species differences in photosynthetic induction rates. Three species showed more rapid induction loss in the leaves from the path edge vs. the understorey. The results suggest that photosynthetic acclimation can influence some aspects of a leaf's dynamic response to sunflecks, such as A_{max} and induction loss, while not affecting overall induction rates. The study also showed significant differences among species in both induction responses and in acclimation of photosynthetic capacity and leaf structure.

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