

Epiphytes and hemiepiphytes have slower photosynthetic response to lightflecks than terrestrial plants: evidence from ferns and figs

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Abstract: Photosynthetic responses of 12 species including six fern species (*Neottopteris nidus*, *Microsorium punctatum*, *Pseudodrynaria coronans*, *Asplenium finlaysonianum*, *Paraleptochilus decurrens* and *Tectaria fauriei*) and seedlings of six fig species (*Ficus curtipes*, *F. gibbosa*, *F. altissima*, *F. auriculata*, *F. oligodon* and *F. hookeriana*) in different life forms to lightfleck were investigated, to test whether epiphytes and hemiepiphytes display a slower response to lightfleck and fast induction loss after a lightfleck compared with their terrestrial counterparts, and whether ferns display a slower response to lightfleck and slower induction loss compared to figs. The measurements of functional traits and physiological parameters were determined in a greenhouse of 4% full sunlight. Epiphytic ferns and hemiepiphytic figs had thicker leaves compared with their terrestrial counterparts. Compared with figs, ferns had thicker fronds, larger stomata with a low density, and lower stomatal conductance and photosynthetic capacity; ferns had lower light compensation point and dark respiration rate, conferring a positive carbon gain under low diffuse light beneath the canopy. The induction time to reach 90% maximum net photosynthetic rate (T_{90}) upon the exposure to a saturated light varied strongly among life forms. Epiphytic ferns had slower T_{90} than terrestrial ferns (19.9–26.3 vs 5.9–16.3 min, respectively), and hemiepiphytic figs had slower T_{90} than terrestrial figs (13.1–20.4 vs 5.2–7.8 min, respectively). Compared with figs, ferns showed a slower response to lightfleck. Across ferns and figs, the induction time was negatively correlated with initial stomatal conductance. No significant difference in induction loss was found between two life forms within ferns or figs, whereas ferns had a significantly slower induction loss compared with figs. These results showed that the inherent conservative water use strategy of the epiphytes and hemiepiphytes constrain their lightfleck utilization.

Key Words: *Asplenium*, epiphytes, *Ficus*, hemiepiphytes, lightflecks, *Microsorium*, *Neottopteris*, *Paraleptochilus*, photosynthetic induction, *Pseudodrynaria*, *Tectaria*, terrestrial life form

INTRODUCTION

Plants growing in a forest understorey experience extreme fluctuations in light conditions, as long periods of low diffuse light alternate with brief, unpredictable periods of high light during sunflecks. The period of high light can last for a few seconds to several minutes or even longer, and contributes 10–80% of daily photosynthetic photon flux density (PPFD) received by understorey plants (Chazdon 1988). Photosynthetic carbon gain during sunflecks contributes

substantially to carbon balance of understorey plants. Upon receiving a sunfleck, understorey leaves increase their photosynthesis from very low to high rates, which is called photosynthetic induction (Chazdon & Pearcy 1986a, Pearcy 1990). Photosynthetic induction involves the increase in the activity of Rubisco, regeneration of RuBP and stomatal opening. The biochemical activation is much quicker compared with the stomatal opening process. When the leaf is shaded after sunflecks, the fast-induction component deactivates rapidly, while the slow-induction component (i.e. stomatal closure) deactivates slowly (Percy 1990, Pons *et al.* 1992). Maintaining photosynthetic induction after lightflecks affects the responses of leaves to subsequent sunflecks.

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Apart from light instability, water limitation also constrains performance of epiphytes, as they usually occupy microhabitats that dry rapidly. Although many vascular epiphytes live in the microhabitats in the lower storeys of the forests, some members of this plant group, especially the so-called 'bark epiphytes' that completely lack canopy soil, are subject to frequent water shortage (Benzing 1990). Therefore, drought stress is a strong selection pressure for the epiphytes. Furthermore, insufficient water supply might limit stomatal conductance and further influence the use of sunflecks. Ferns, as a plant group, possess simply branched, occasionally reticulate vascular networks to irrigate fronds (henceforth leaves). Angiosperm leaves commonly utilize xylem vessels in the lower vein orders, which are absent from fern leaves (Carlquist & Schneider 2001). This great variation in vascular system between ferns and angiosperms affects the hydraulic conductance of the leaves (Sack & Frole 2006), and thus affects the performance in term of gas exchanges (Brodribb *et al.* 2007). However, whether the great variation in vascular system in leaves between ferns and angiosperms affects their lightfleck utilization is poorly understood.

Hemiepiphytic plants grow as true epiphytes at their initial life stage, and then become terrestrial through aerial roots that grow from the canopy to the ground (Patiño *et al.* 1999). They make a soil connection for only a portion of their life cycle, presenting a life form between an epiphyte and a terrestrial plant. Hemiepiphytes are common in *Ficus* (Moraceae) and *Clusia* (Clusiaceae). The best known hemiepiphytes are the strangler figs. Approximately 500 fig species are classified as hemiepiphytes, commonly occurring in humid tropical regions in the world (Putz & Holbrook 1986). Like epiphytic ferns, hemiepiphytic figs are also subjected to a higher selection pressure of frequent water deficit during their initial life stage than their later ones, owing to water and minerals being less accessible for hemiepiphytic plants than for terrestrial ones. Therefore, hemiepiphytic plants may continue with a water conservation strategy even after becoming rooted in the ground, which potentially affects the efficiency of lightfleck use.

In this study, the measurements were made of photosynthetic traits, photosynthetic induction in response to simulated lightflecks, and induction loss after a lightfleck in a range of epiphytic and terrestrial ferns, and hemiepiphytic and terrestrial figs. The following two hypotheses were tested: (1) the epiphytes or hemiepiphytes display slower responses to lightflecks and faster induction loss after a lightfleck compared with their terrestrial counterparts; and (2) fern species present slower responses to a lightfleck and slower induction loss after a lightfleck compared with fig species.

METHODS

Study site and plants

This study was carried out at the Xishuangbanna Tropical Botanical Garden (21°41'N, 101°25'E, altitude 600 m), Chinese Academy of Sciences, southern Yunnan, south-west China. The mean annual temperature is 21.6 °C, and the annual precipitation is about 1560 mm. Twelve species were chosen for the study, including three epiphytic fern species (*Neottopteris nidus* (L.) J. Sm. (synonym *Asplenium nidus* L.) (Aspleniaceae), *Microsorium punctatum* (L.) Copel. (Polypodiaceae) and *Pseudodrynaria coronans* (Wall. ex Mett.) Ching (Polypodiaceae)), three terrestrial fern species (*Asplenium finlaysonianum* Wall. ex Hook. (Aspleniaceae), *Paraleptochilus decurrens* (Blume) Copel. (Polypodiaceae), and *Tectaria fauriei* Tagawa (Aspidiaceae)), three hemiepiphytic fig species (*Ficus curtipes* Corner, *Ficus gibbosa* Bl. and *Ficus altissima* Bl.), and three terrestrial fig species (*Ficus auriculata* Lour., *Ficus oligodon* Miq. and *Ficus hookeriana* Corner). Ferns were collected from a nearby nature reserve and then cultivated in a screenhouse of 4% full sunlight for adaption for 1 y. The screenhouse was constructed with neutral shade netting supplying irradiance of 4% daylight. The relative irradiance under the shade plots were estimated by integrating PPFD under the shade plots compared with that in a fully open site over a clear day in the summer. The PPFD was measured with Li-190SA quantum sensors connected to a Li-1400 data logger (LI-COR, Lincoln, NE, USA). Seeds of the six fig species were collected from mature trees planted in the botanical garden, and were germinated in plastic pots (30 cm height and internal diameter) in soils obtained from a tropical rain forest. The potted fig seedlings were also placed in the same screenhouse for 4 mo, watered as needed. When our physiological measurements were made, the ferns were about 35–80 cm high, and the fig seedlings were about 40–60 cm high. All measurements were made on the new fully developed leaves in the screenhouse at ambient temperature, with relative humidity 80–90%.

Leaf structure and chlorophyll concentration

Leaf anatomy and chlorophyll concentration (Chl) were measured on a mature leaf from each of six plants per species. Leaves were sampled and each leaf was then cut into two parts along the midrib. One half of the leaf was used to determine chlorophyll concentration with extraction by 95% ethanol (Lichtenthaler & Wellburn 1983). The area of another half was measured with a portable leaf area meter (LI-3000A, LI-COR, Lincoln, NE, USA). Leaf segments were dried at 80 °C for 48 h and then leaf mass per unit area (LMA) was calculated.

Leaf thickness (LT) was measured on hand-cut transverse sections with a light microscope. Stomatal density (SD) and guard cell length (GCL) were measured on epidermal impressions made with colourless nail polish. At least three fields of each of six leaves from six plants per species were observed.

Gas exchange

Gas exchange was measured in the morning (08h00–11h30) September–October 2006 to avoid possible midday and afternoon depression, using an infrared gas analyser (LI-6400, LI-COR, Lincoln, NE, USA). For each species, five to six fully expanded mature leaves from different plants were selected for the measurements. Photosynthetic light response curves were measured with PPFD descending from high to low light. The fern leaves were illuminated with $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD for at least 30 min, and fig species $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ for at least 20 min before measurements. CO_2 concentration inside the leaf chamber was maintained at $380 \mu\text{mol mol}^{-1}$ through the integrated CO_2 controlling system of the gas analyser. Mean relative air humidity was $80\% \pm 5\%$. According to the method described by Bassman & Zwier (1991), we calculated the photosynthetic parameters: apparent quantum yield (AQY), dark respiration rate (R_d), light compensation point (LCP), light saturation point (LSP), and maximum net photosynthetic rate (A_{max}). Intrinsic photosynthetic water use efficiency (WUE) was calculated as $A_{\text{max}}'/g_{\text{s-max}}$, where $g_{\text{s-max}}$ is the maximum stomatal conductance obtained from the light response curve. Photosynthetic induction experiments were conducted on the leaves used for photosynthetic light response curves. The sampled leaves were shaded by a one-layer screen overnight until the measurements were made the next day, preventing leaves from being photosynthetically pre-induced. During the measurements, leaves were enclosed in the leaf chamber and illuminated with low light (approximately $20 \mu\text{mol m}^{-2} \text{s}^{-1}$) for at least 30 min. Photosynthetic rate under this low light (A_d) was recorded after a steady state was reached. Afterwards, the leaf was exposed to a photosynthetically saturating PPFD determined from the light response curves, using an integrated LED light source. Net photosynthetic rate (A_n) was recorded at 2-s intervals for the first 5 min, and then every 56 s until the stable maximum assimilation rate (A_{max}) was achieved. The following parameters were determined: time to reach 50% (T_{50}) and 90% full induction (T_{90}), and the initial ($g_{\text{s-initial}}$) and maximum stomatal conductance ($g_{\text{s-max}}$). The T_{50} and T_{90} were estimated by fitting the curves with a sigmoidal equation (Zipperlen & Press 1997). The leaf was then shaded (approximately $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD) for 20 min, and then was exposed to a saturating PPFD for 60 s and the net photosynthetic rate at 60 s (A) was determined.

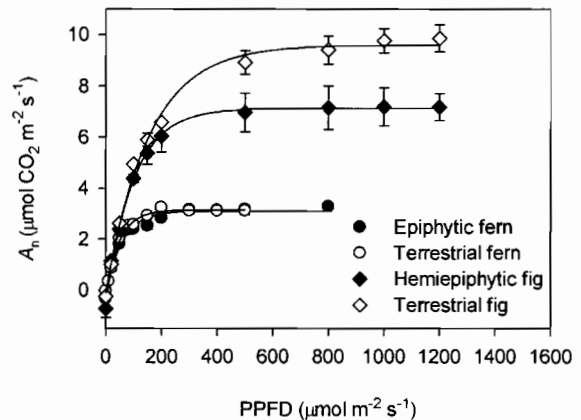


Figure 1. Photosynthetic light response curves of fully mature leaves of the four representative species studied: the epiphytic fern *Neottopteris nidus* (●), the terrestrial fern *Asplenium finlaysonianum* (○), the hemiepiphytic fig *Ficus altissima* (◆) and the terrestrial fig *Ficus oligodon* (◇). Data are mean \pm SE ($n = 6$).

The induction state (IS_{60}) after the 20-min darkness was calculated as $IS_{60} = (A - A_d) / (A_{\text{max}} - A_d)$ (Chazdon & Pearcy 1986b).

Statistical analysis

The significances of the differences in the means between two life forms within ferns or figs were assessed by Student's *t*-test. The relationship between $g_{\text{s-max}}$ and A_{max} was fitted by a linear regression, and between $g_{\text{s-initial}}$ and T_{50} or T_{90} were fitted by a double exponential decay equation.

RESULTS

Differences in leaf morphological and photosynthetic traits

The mean LMA ($t_{34} = 4.17$, $P < 0.001$), LT ($t_{34} = 2.19$, $P < 0.05$) and Chl ($t_{34} = 4.74$, $P < 0.001$) of the hemiepiphytic figs were significantly higher than those of the terrestrial figs, with no differences in mean SD and GCL between these two life forms (Table 1). Epiphytic and terrestrial ferns were similar in LMA and LT, with significantly lower Chl ($t_{34} = -6.25$, $P < 0.001$) in the former. The figs had higher LMA ($t_{70} = -6.26$, $P < 0.001$) and LT ($t_{70} = -3.40$, $P < 0.001$) but smaller and denser stomata than the ferns.

Figs varied strongly in A_{max} , $g_{\text{s-max}}$, and LSP excepting LCP, AQY and R_d (Table 2). Photosynthetic light response curves of the four representative species are shown in Figure 1. Epiphytic and terrestrial ferns were statistically different in A_{max} ($t_{34} = 4.15$, $P < 0.001$), $g_{\text{s-max}}$ ($t_{34} = -3.51$, $P < 0.01$), LCP ($t_{34} = 13.2$,

Table 1. Leaf traits of 12 species studied. Entries are mean \pm SE from six individuals of each species. LMA, leaf mass per unit area; LT, leaf thickness; SD, stomatal density; GCL, guard cell length; Chl, chlorophyll concentration. Different letters indicate significant differences in the means between two plant types within figs or ferns.

Type, species	LMA (g m^{-2})	LT (μm)	SD (no mm^{-2})	GCL (μm)	Chl ($\mu\text{g cm}^{-2}$)
Hemiepiphytic figs					
<i>Ficus curtipes</i>	53.3 \pm 1.5	215 \pm 10.8	228 \pm 12.9	13.5 \pm 1.1	55.6 \pm 4.4
<i>Ficus gibbosa</i>	40.1 \pm 1.2	175 \pm 10.9	136 \pm 11.7	19.6 \pm 1.9	55.3 \pm 2.5
<i>Ficus altissima</i>	58.5 \pm 5.6	455 \pm 8.7	205 \pm 17.7	20.0 \pm 2.0	55.0 \pm 4.4
Mean	49.7 a	260 a	187 a	17.4 a	55.4 a
Terrestrial figs					
<i>Ficus auriculata</i>	44.5 \pm 3.9	240 \pm 15.5	144 \pm 8.4	21.3 \pm 0.7	36.9 \pm 3.6
<i>Ficus oligodon</i>	30.5 \pm 3.6	167 \pm 16.2	390 \pm 45.4	13.3 \pm 1.7	38.9 \pm 3.3
<i>Ficus hookeriana</i>	32.3 \pm 1.1	159 \pm 16.5	192 \pm 25.9	12.5 \pm 1.3	49.8 \pm 1.2
Mean	35.8 b	190 b	233 a	15.7 a	41.9 b
Epiphytic ferns					
<i>Neottopteris nidus</i>	68.3 \pm 4.9	357 \pm 12.0	25.2 \pm 5.0	50.8 \pm 1.7	30.6 \pm 3.8
<i>Microsorium punctatum</i>	75.2 \pm 4.5	568 \pm 44.2	23.0 \pm 2.5	52.9 \pm 1.2	29.5 \pm 2.0
<i>Pseudodrynaria coronans</i>	77.1 \pm 1.1	186 \pm 14.0	104 \pm 5.0	34.2 \pm 1.2	27.7 \pm 2.1
Mean	73.6 a	370 a	50.6 a	46.0 a	29.4 a
Terrestrial ferns					
<i>Asplenium finlaysonianum</i>	97.8 \pm 8.1	478 \pm 13.0	21.8 \pm 3.9	66.3 \pm 3.3	49.9 \pm 3.6
<i>Paraleptochilus decurrens</i>	69.1 \pm 5.2	226 \pm 10.2	31.3 \pm 2.4	45.4 \pm 2.0	42.1 \pm 4.5
<i>Tectaria fauriei</i>	30.6 \pm 2.9	164 \pm 16.8	34.3 \pm 2.2	49.6 \pm 1.2	47.8 \pm 3.8
Mean	65.8 a	289 a	29.2 b	53.8 b	46.6 b

$P < 0.001$), and R_d ($t_{34} = -11.0$, $P < 0.001$). The figs had significantly greater A_{max} ' ($t_{70} = 11.7$, $P < 0.001$), $g_{s\text{-max}}$ ' ($t_{70} = 9.48$, $P < 0.001$), LCP ($t_{70} = 3.42$, $P < 0.01$), LSP ($t_{70} = 8.88$, $P < 0.001$), and R_d ($t_{70} = -3.35$, $P < 0.01$) than the ferns. Epiphytic ferns and hemiepiphytic figs had higher WUE than the terrestrial plants ($t_{70} = 12.7$, 3.51; $P < 0.001$, 0.01, respectively), with no difference in WUE between ferns and figs (Table 2 and Figure 2).

Induction time and induction loss

The time courses of photosynthetic induction in the four representative species of different life forms were shown in Figure 3. There was no significant difference in mean T_{50} between the epiphytic and terrestrial ferns, whereas hemiepiphytic figs had lower mean T_{50} than terrestrial figs (Table 3). The means of T_{90} in the epiphytic ferns

Table 2. Gas exchange parameters for the six fig and six fern species. Entries are mean \pm SE from six individuals of each species. A_{max} ', maximum net photosynthetic rate; $g_{s\text{-max}}$ ', maximum stomatal conductance recorded during the measurement of light response curve; WUE, water use efficiency; LCP, light compensation point; LSP, light saturation point; AQY, apparent quantum yield; R_d , dark respiration rate. Different letters indicate significant differences in the means between two plant types within figs or ferns.

Type, species	A_{max} ' ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	$g_{s\text{-max}}$ ' ($\text{mmol m}^{-2} \text{s}^{-1}$)	WUE ($\mu\text{mol mol}^{-1}$)	LCP ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	LSP ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	AQY ($\mu\text{mol mol}^{-1}$)	R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
Hemiepiphytic figs							
<i>Ficus curtipes</i>	8.1 \pm 0.7	69.6 \pm 6.3	123 \pm 5	6.7 \pm 1.7	520 \pm 28	0.051 \pm 0.006	0.40 \pm 0.07
<i>Ficus gibbosa</i>	6.2 \pm 0.4	116.9 \pm 17.2	54 \pm 3	7.9 \pm 1.9	589 \pm 58	0.047 \pm 0.005	0.40 \pm 0.13
<i>Ficus altissima</i>	7.1 \pm 0.7	138.5 \pm 2.0	52 \pm 1	7.1 \pm 0.9	459 \pm 39	0.065 \pm 0.007	0.57 \pm 0.21
Mean	7.1 a	111.4 a	76 a	7.3 a	523 a	0.054 a	0.49 a
Terrestrial figs							
<i>Ficus auriculata</i>	9.5 \pm 1.7	256.7 \pm 55.5	37 \pm 1	17.4 \pm 0.4	696 \pm 95	0.045 \pm 0.003	1.02 \pm 0.07
<i>Ficus oligodon</i>	9.5 \pm 0.6	214.7 \pm 19.9	44 \pm 1	4.2 \pm 1.6	718 \pm 45	0.057 \pm 0.000	0.26 \pm 0.10
<i>Ficus hookeriana</i>	9.6 \pm 1.1	164.7 \pm 13.4	58 \pm 1	2.9 \pm 0.6	639 \pm 86	0.059 \pm 0.005	0.21 \pm 0.04
Mean	9.5 b	212.0 b	47 b	7.6 a	680 b	0.054 a	0.47 a
Epiphytic ferns							
<i>Neottopteris nidus</i>	3.1 \pm 0.1	31.1 \pm 0.1	102 \pm 1	3.9 \pm 0.4	271 \pm 8	0.061 \pm 0.002	0.22 \pm 0.03
<i>Microsorium punctatum</i>	4.0 \pm 0.1	55.4 \pm 8.5	93 \pm 10	6.4 \pm 0.2	275 \pm 3	0.059 \pm 0.002	0.47 \pm 0.02
<i>Pseudodrynaria coronans</i>	6.0 \pm 0.1	69.4 \pm 6.6	93 \pm 4	5.9 \pm 0.6	439 \pm 15	0.050 \pm 0.001	0.37 \pm 0.03
Mean	4.4 a	51.9 a	96 a	5.4 a	328 a	0.057 a	0.35 a
Terrestrial ferns							
<i>Asplenium finlaysonianum</i>	3.4 \pm 0.1	78.1 \pm 10.2	46 \pm 1	2.8 \pm 0.3	313 \pm 5	0.055 \pm 0.005	0.16 \pm 0.02
<i>Paraleptochilus decurrens</i>	2.6 \pm 0.1	58.3 \pm 4.8	48 \pm 2	1.7 \pm 0.3	208 \pm 7	0.062 \pm 0.003	0.11 \pm 0.02
<i>Tectaria fauriei</i>	3.3 \pm 0.0	62.0 \pm 1.1	55 \pm 1	2.6 \pm 0.2	310 \pm 6	0.053 \pm 0.004	0.14 \pm 0.01
Mean	3.1 b	65.7 b	50 b	2.4 b	277 b	0.057 a	0.13 b

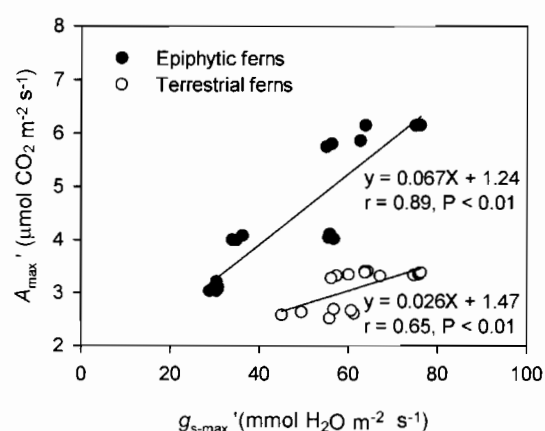


Figure 2. The relationships between maximum photosynthetic rate (A_{\max}') and maximum stomatal conductance ($g_{s-\max}'$). Each point is from one measurement of one plant per species ($n = 6$).

(19.8–26.3 min) and the hemiepiphytic figs (13.1–20.4 min) were significantly slower than that in the terrestrial ferns (5.9–16.3 min) and terrestrial figs (5.2–7.8 min), respectively. The figs had much faster induction responses compared with the ferns.

The hemiepiphytic figs had much lower $g_{s-\text{initial}}$ compared to their terrestrial counterparts. Similarly, the epiphytic ferns had lower $g_{s-\text{initial}}$ than their terrestrial counterparts. $g_{s-\text{initial}}$ and T_{50} or T_{90} were negatively correlated when pooling data for 12 studied species. After $g_{s-\text{initial}}$ exceeded the threshold of $50 \text{ mmol m}^{-2} \text{ s}^{-1}$, it had no effect on T_{50} (Figure 4a). This was not so between T_{90} and $g_{s-\text{initial}}$ (Figure 4b). Although ferns had slow induction response, they tended to maintain higher photosynthetic

induction state than the fig seedlings after full induction (Table 3).

DISCUSSION

By comparing leaf morphological traits and photosynthetic light induction responses across epiphytic ferns, hemiepiphytic figs, and their terrestrial counterparts, this study provided evidence of a trade-off between conserving water and maximizing carbon gain of these relatively less-investigated plant groups. Water conservation is more important for epiphytic and hemiepiphytic plants. Ferns and figs presented significant differences in stomatal regulation and photosynthetic light induction characteristics, probably resulting from the difference in their vascular system and hence hydraulic conductance.

Difference in leaf morphology between plant groups

Epiphytic ferns and hemiepiphytic figs had thicker leaves than their terrestrial counterparts (Table 1), consistent with previous studies (Holbrook & Putz 1996, Watkins *et al.* 2007). Thick and dense leaves favour epiphytes to adapt to drought-prone epiphytic habitats, reducing transpiration and increasing water use efficiency (Gratani & Bombelli 2001). The ferns had larger and sparser stomata than figs (Table 1), consistent with other studies (Hietz & Briones 1998, Holbrook & Putz 1996). Ferns have low stomatal conductance and consequently low photosynthetic capacity in this study, as in other reports (Brodrribb & Holbrook 2004, Brodrribb *et al.* 2005), which

Table 3. Photosynthetic induction parameters in six fig and six fern species. Data are means \pm SE of time required to reach 50% (T_{50}) and 90% of maximum net photosynthetic rate (T_{90}), induction state (IS_{60}) measured after 20 min of dark-adaption following the full induction, initial stomatal conductance ($g_{s-\text{initial}}$) and maximum stomatal conductance ($g_{s-\max}$). The group means in one column with the same letter are not significantly different for either figs or ferns, respectively ($P > 0.05$).

Type, species	T_{50} (min)	T_{90} (min)	IS_{60} (%)	$g_{s-\text{initial}}$ ($\text{mmol m}^{-2} \text{ s}^{-1}$)	$g_{s-\max}$ ($\text{mmol m}^{-2} \text{ s}^{-1}$)
Hemiepiphytic figs					
<i>Ficus curtipes</i>	5.6 ± 0.6	13.1 ± 0.8	42.5 ± 6.6	5.9 ± 1.7	66.5 ± 4.5
<i>Ficus gibbosa</i>	9.7 ± 2.6	20.4 ± 0.5	52.1 ± 2.6	20.8 ± 2.5	118.4 ± 4.5
<i>Ficus altissima</i>	7.3 ± 0.2	13.8 ± 0.8	48.4 ± 3.3	7.5 ± 0.1	125.3 ± 4.4
Mean	7.5 a	15.8 a	47.7 a	11.4 a	103.4 a
Terrestrial figs					
<i>Ficus auriculata</i>	0.7 ± 0.1	5.2 ± 0.9	49.3 ± 4.2	181.2 ± 38.3	269.6 ± 3.6
<i>Ficus oligodon</i>	1.2 ± 0.2	7.6 ± 3.4	46.8 ± 7.9	142.7 ± 20.8	211.8 ± 12.3
<i>Ficus hookeriana</i>	1.4 ± 0.3	7.8 ± 1.5	43.8 ± 4.4	105.6 ± 15.0	165.7 ± 2.4
Mean	1.1 b	6.9 b	46.6 a	143.2 b	215.7 b
Epiphytic ferns					
<i>Neottopteris nidus</i>	5.3 ± 0.4	26.3 ± 0.9	54.5 ± 2.3	6.8 ± 0.1	30.1 ± 0.1
<i>Microsorium punctatum</i>	1.1 ± 0.3	19.9 ± 0.2	61.1 ± 1.6	33.5 ± 5.6	57.3 ± 4.5
<i>Pseudodrynaria coronans</i>	0.9 ± 0.1	22.3 ± 1.5	53.3 ± 2.8	27.1 ± 3.4	67.4 ± 5.6
Mean	2.4 a	22.8 a	56.3 a	22.5 a	52.6 a
Terrestrial ferns					
<i>Asplenium finlaysonianum</i>	0.6 ± 0.13	5.9 ± 0.1	58.8 ± 4.0	62.2 ± 6.6	76.2 ± 9.2
<i>Paraleptochilus decurrens</i>	1.2 ± 0.1	15.9 ± 1.6	45.2 ± 4.0	33.7 ± 3.1	60.3 ± 4.8
<i>Tectaria fauriei</i>	4.8 ± 0.5	16.3 ± 0.6	67.7 ± 3.0	25.0 ± 0.3	62.5 ± 2.1
Mean	2.2 a	12.7 b	57.2 a	40.3 b	66.3 b

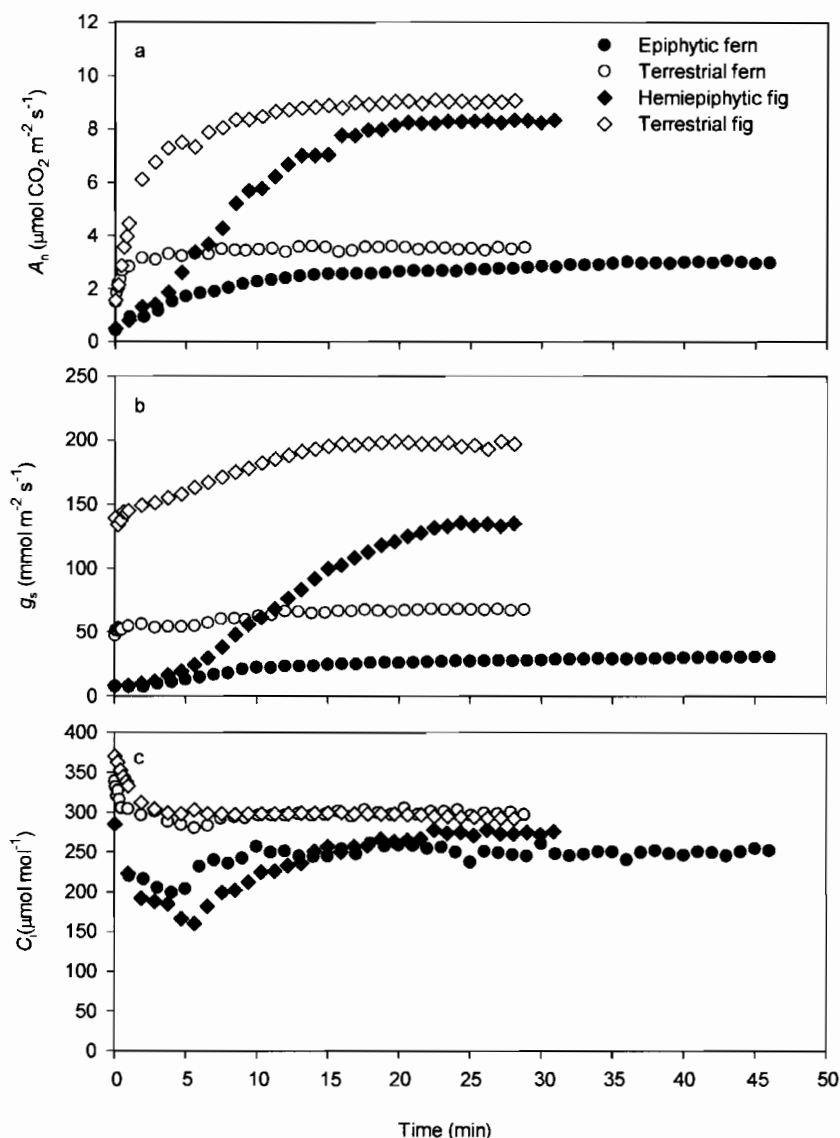


Figure 3. The response of net photosynthesis (A_n ; a), stomatal conductance (g_s ; b) and intercellular CO_2 concentration (C_i ; c) to a simulated lightfleck in the four representative species: the epiphytic fern *Neottopteris nidus* (●), the terrestrial fern *Asplenium finlaysonianum* (○), the hemiepiphytic fig *Ficus altissima* (◆) and the terrestrial fig *Ficus oligodon* (◇). Typical data for a leaf are shown. Leaves were first exposed to $20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ until rates of gas exchange were steady; a simulated lightfleck was then imposed by increasing irradiance to the saturated light. The simulated lightfleck started at time 0.

could result from the vascular system of ferns not being well developed to allow fast transpiration through dense stomata. However, low density of stomata might be favourable for epiphytic ferns to reduce transpirational water loss (Cao 2000). Under low-light condition, ferns had lower LCP and R_d than the figs, conferring a positive carbon gain.

Difference in photosynthetic induction time between plant groups

Epiphytes are prone to frequent water deficits, and their water use strategies are conservative. We hypothesized

that the conservative water use strategy would influence their performance of lightfleck utilizations. Our results showed that the photosynthetic induction upon receiving lightflecks was slower in the epiphytic ferns and the hemiepiphytic figs compared with their terrestrial counterparts, and the induction time was negatively correlated with initial stomatal conductance, consistent with other studies (Bai *et al.* 2008, Valladares *et al.* 1997). Because the time course of photosynthetic induction after 1 or 2 min is predominantly determined by stomatal conductance and Rubisco activation (Kirschbaum & Pearcy 1988, Pons *et al.* 1992), inter- and intra-specific differences in induction time are likely caused by differences in the dynamic responses of the slow-inducing

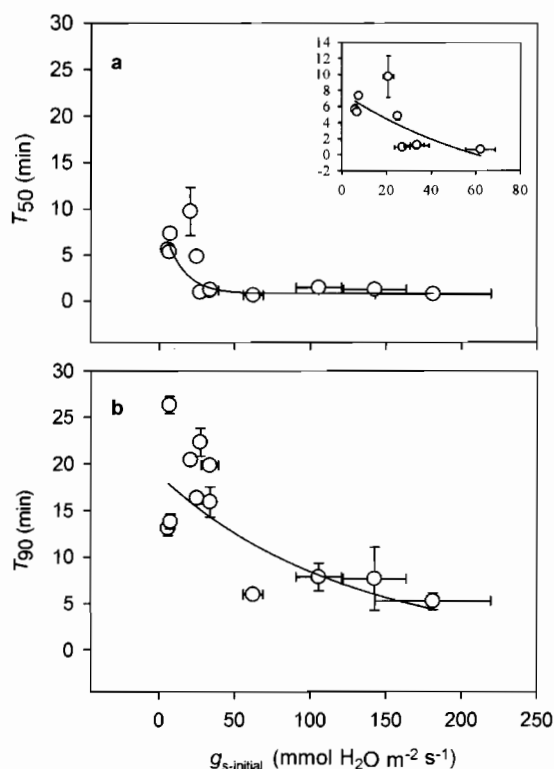


Figure 4. The relationships between time required to reach 50% (T_{50}) (a) or 90% (T_{90}) (b) of the maximum net photosynthetic rate and the initial stomatal conductance under the low light ($g_{s-initial}$) in the 12 species studied. The inset represents the relationship between T_{50} and $g_{s-initial}$ when $g_{s-initial}$ is below 70 mmol H_2O m^{-2} s^{-1} .

component, stomatal opening. We found that epiphytes (or hemiepiphytes) had significantly lower $g_{s-initial}$ compared with their terrestrial counterparts under low light in the present study, which should account for the significant difference in the photosynthetic induction time between the groups in view of the relationships between T_{90} and $g_{s-initial}$ (Figure 4). Carbon assimilation of epiphytic or hemiepiphytic plants is constrained by slow photosynthetic induction and low stomatal conductance, which reduce water loss and the risk of water deficits. As growing in the habitats with frequent water shortage, conserving water for survival is far more important for the epiphytic or hemiepiphytic plants than maximizing carbon assimilation to enhance growth.

Ferns showed slower responses to lightfleck and induction loss after a lightfleck compared with figs, probably due to higher water diffusive resistance and lower water transport capacity, and consequently slower stomatal opening and closing reactions in the leaf of ferns (Aasamaa *et al.* 2001, Brodribb *et al.* 2005, Sack & Holbrook 2006). The range of stomatal movement in ferns is much lower than that in most terrestrial understorey herbs, shrubs and tree saplings (Allen & Pearcy 2000, Chazdon & Pearcy 1986a, Pfitsch & Pearcy

1989, Valladares *et al.* 1997). Kaiser & Kappen (2000) suggested that the fine-tuning of stomatal conductance may require slow opening and closing reactions to avoid overshooting. This mechanism may also explain why our second expectation, a faster induction loss in ferns, was rejected. Lower rates of induction have also been reported for the epiphytic orchid *Aspasia principissa* (Zotz & Mikona 2003). T_{90} in three epiphytic ferns and three hemiepiphytic figs in this study is slower than most understorey shrubs, herbs and saplings reported in the literature (< 10 min; Kursar & Coley 1993, Ögren & Sundin 1996, Rijkers *et al.* 2000, Roden & Pearcy 1993, Tang *et al.* 1994).

The epiphytes are not only adapted to drier conditions but also to the lower air CO_2 concentration, as they usually grow higher up on the trunks and branches above the forest floor than the juveniles of their terrestrial counterparts. It is well known that there is a strong gradient in CO_2 concentration in forest understoreys that persists through much of the morning. High CO_2 concentration is known to increase intercellular CO_2 concentration and to reduce the time required for photosynthetic induction, and thereby to increase carbon gain during sunflecks (Leakey *et al.* 2005). This increases the difference in both photosynthetic induction time and stomatal response to sunflecks between the epiphytic or hemiepiphytic and terrestrial plants under experimental conditions of this study.

In conclusion, the epiphytic ferns and hemiepiphytic figs exhibited water-conservation leaf structures, and much slower photosynthetic induction in response to lightflecks than their terrestrial counterparts. These differences in lightfleck use as well as other leaf functional traits may drive the coexistence of ferns and figs with different life forms in a tropical rain-forest community.

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