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## Research paper

# Differentiation in light energy dissipation between hemiepiphytic and non-hemiepiphytic *Ficus* species with contrasting xylem hydraulic conductivity

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Hemiepiphytic *Ficus* species (Hs) possess traits of more conservative water use compared with non-hemiepiphytic *Ficus* species (NHs) even during their terrestrial growth phase, which may result in significant differences in photosynthetic light use between these two growth forms. Stem hydraulic conductivity, leaf gas exchange and chlorophyll fluorescence were compared in adult trees of five Hs and five NHs grown in a common garden. Hs had significantly lower stem hydraulic conductivity, lower stomatal conductance and higher water use efficiency than NHs. Photorespiration played an important role in avoiding photoinhibition at high irradiance in both Hs and NHs. Under saturating irradiance levels, Hs tended to dissipate a higher proportion of excessive light energy through thermal processes than NHs, while NHs dissipated a larger proportion of electron flow than Hs through the alternative electron sinks. No significant difference in maximum net CO<sub>2</sub> assimilation rate was found between Hs and NHs. Stem xylem hydraulic conductivity was positively correlated with maximum electron transport rate and negatively correlated with the quantum yield of non-photochemical quenching across the 10 studied *Ficus* species. These findings indicate that a canopy growth habit during early life stages in Hs of *Ficus* resulted in substantial adaptive differences from congeneric NHs not only in water relations but also in photosynthetic light use and carbon economy. The evolution of epiphytic growth habit, even for only part of their life cycle, involved profound changes in a suite of inter-correlated ecophysiological traits that persist to a large extent even during the later terrestrial growth phase.

**Keywords:** chlorophyll fluorescence, non-photochemical quenching, photorespiration, photosynthesis, water use efficiency.

## Introduction

*Ficus* is the largest genus containing woody hemiepiphytes (~500 species), in which the hemiepiphytic growth habit is likely to have evolved multiple times from terrestrial lineages of *Ficus* ancestors (Berg and Corner 2005, Harrison 2005). It has been suggested that the hemiepiphytic habit evolved in response to the scarcity of light in the forest understory (Dobzhansky and Murca-Pires 1954, Ramirez 1977, Putz and

Holbrook 1986, Todzia 1986, Laman 1995, Williams-Linera and Lawton 1995). Also, by growing in the canopy young individuals of hemiepiphytes may benefit from minimizing the risk of fire, flooding, damage by terrestrial herbivores (Holbrook and Putz 1996b) and damage by falling debris. The advantages of spending the initial part of the life cycle as an epiphyte, on the other hand, can be offset by the potential limitations of low water and nutrient availability (Coxson and

## List of major symbols

$0.5v_o$	photorespiration rate calculated from Rubisco kinetics using the Farquhar and von Caemmerer model
$A_m$	leaf dry mass-based net CO <sub>2</sub> assimilation rate
$A_n$	leaf area-based net CO <sub>2</sub> assimilation rate
ETR	electron transport rate
ETR <sub>alt</sub>	electron use by alternative metabolism pathways
$g_s$	stomatal conductance
$K_l$	leaf-specific hydraulic conductivity
$K_s$	sapwood-specific hydraulic conductivity
LA/SA	leaf area to sapwood area ratio
LCP	light compensation point
LMA	leaf mass per area
PNUE	photosynthetic nitrogen use efficiency
PPFD	photosynthetic photon flux density
PPUE	photosynthetic phosphorus use efficiency
$R_d$	dark respiration rate
$R_p$	photorespiration rate estimated from the approach of Valentini et al.
WUE <sub>i</sub>	leaf intrinsic water use efficiency
$\Phi_{f,D}$	proportion of absorbed light energy dissipated through fluorescence and constitutive non-photochemical processes
$\Phi_{NPQ}$	proportion of absorbed light energy dissipated through regulated non-photochemical quenching processes
$\Phi_{PSII}$	proportion of absorbed light energy used by PSII photochemistry

Nadkarni 1995, Holbrook and Putz 1996a, 1996b, Swagel et al. 1997).

Despite the existence of an epiphytic-to-terrestrial phase transition in hemiepiphytic *Ficus* species (Hs) in terms of water availability (Holbrook and Putz 1996a, 1996b), terrestrially established Hs still retain traits that confer relatively low stem xylem water transport efficiency compared with the non-hemiepiphytic species (NHs) of the same genus (Patiño et al. 1995, Hao 2010). Due to the expected functional coordination between xylem water transport and leaf gas exchange (Brodribb and Field 2000, Melcher et al. 2001, Brodribb et al. 2002, Santiago et al. 2004, Brodribb et al. 2005, Franks 2006, Zhang and Cao 2009), Hs are expected to have lower stomatal conductance ( $g_s$ ) and higher water use efficiency than NHs, even during the terrestrial stage.

The low stomatal conductance related to conservative water use can limit the influx of CO<sub>2</sub> and thus photosynthetic carbon assimilation, resulting in an increased risk of overexcitation of photosystem II (PSII) reaction centers and thus photoinhibition when plants are exposed to excessive irradiance (Osmond 1994). This is especially the case as most *Ficus* species are light-demanding species and grow in sun-exposed sites. Therefore, mechanisms balancing the use of absorbed light for photosynthesis and the safe dissipation of potentially harmful excess light energy can be of critical importance in hemiepiphytes in overcoming potential photoinhibitory damage. Furthermore, in C<sub>3</sub> plants, such as the *Ficus* species, under

high light conditions photorespiration is considered to be an important process that can consume a considerable portion of electron flow when photosynthesis is restricted (Valentini et al. 1995, Kozaki and Takeba 1996, Muraoka et al. 2000, Franco and Lüttge 2002, Zhang et al. 2008). Besides photorespiration, alternative electron sinks, such as nitrate reduction, Mehler reaction and chlororespiration, can also be significant energy-demanding processes and may play an important role in photoprotection of photosystems under conditions of excessive light (Mehler 1951, Polle 1996, Ort and Baker 2002, Hanke et al. 2008, Peltier et al. 2010).

In the present study, we examined leaf gas exchange and chlorophyll fluorescence in response to changes in irradiance levels in five Hs and five NHs of *Ficus* with all the hemiepiphytic plants being terrestrially rooted adult trees. Two questions were addressed: (1) Do Hs and NHs of *Ficus* differ significantly in photosynthetic traits, such as net CO<sub>2</sub> assimilation rate ( $A_n$ ), efficiency of non-photochemical energy dissipation of PSII ( $\Phi_{NPQ}$ ) and photorespiration rate under conditions of excessively high irradiance? (2) Across *Ficus* species, are photosynthetic traits correlated with stem hydraulic conductivity? The use of species growing under similar environmental conditions in a common garden guaranteed that the potential variations in plant hydraulics, photochemistry and carbon assimilation can be attributable to growth form rather than environmental differences.

## Materials and methods

### Site and plant material description

The study was carried out in the Xishuangbanna Tropical Botanical Garden (XTBG) (21°56'N, 101°15'E, 600 m altitude) of the Chinese Academy of Sciences, Yunnan, SW China. The climate of Xishuangbanna is dominated by the humid southwest monsoon arising from the Indian Ocean in the rainy season from May to October and by dry winds from the southwest from November to April, and thus an alternation of wet and dry seasons with 80% of the rainfall occurring during the rainy season. Measurements were carried out on clear days in April and May 2008. During these two months, intermittent rainfall maintained adequate soil moisture and the studied plants were not drought stressed.

The 10 study species were all from the genus *Ficus* with five Hs and five NHs that are commonly found in the rainforests of Xishuangbanna. *Ficus tinctoria* Frost. f. subsp. *gibbosa* (Bl.) Corner is a hemiepiphyte that usually does not form a firm self-supporting trunk and falls down soon after the host tree rots. *Ficus benjamina* L., *Ficus concinna* (Miquel) Miquel and *Ficus curtipes* Corner are stranglers that can form free-standing trunks. *Ficus religosa* L. is a species that starts its growth on a host and later on forms a massive trunk and canopy up to 30 m tall. Among the five *Ficus* NHs (i.e., *Ficus*

*auriculata* Loureiro, *Ficus esquiroliana* H. Léveillé, *Ficus hispida* L., *Ficus racemosa* L. and *Ficus semicordata* Buchanan-Hamilton ex Smith), *Ficus racemosa* can grow up to 30 m tall and the other four species are trees of medium size usually no more than 10 m tall. All plants used were grown in XTBG with relatively open habitats and homogeneous soil. The diameter at breast height of the studied trees ranged from 15 to 60 cm, with individuals of the Hs all at the terrestrial growth stage. All sampled plants had branches reachable from the ground or by using a ladder. To reduce the confounding effects of light, only sun-exposed branches and leaves from the outer canopy were sampled for measuring hydraulic conductivity and photosynthesis.

### Stem hydraulic conductivity

Stem hydraulic conductivity was measured on three branches per tree of six to eight individuals per species. Branches were collected in the morning, re-cut immediately under water to avoid embolisms and transported to the laboratory with the cut end immersed in water and the free end tightly covered with opaque plastic bags. One ~50-cm-long stem segment without leaves and secondary twigs was cut off each branch under water for conductivity measurement. Because *Ficus* species produce latex, which can cause clogging of vessels, both ends of a segment were shaved with a sharp razor blade immediately before each measurement of flow rate. One end of the segment was then connected to a silicon tubing apparatus that was connected to a reservoir containing degassed and filtered water. The reservoir was elevated above the horizontal branch segment to give a 50-cm hydraulic head. The reservoir was large enough and thus during the measurement the change in water level was negligible. The rate of water flow through the stem segment was measured using a graduated pipette connected to the other end of the segment. The hydraulic conductivity ( $\text{kg m s}^{-1} \text{MPa}^{-1}$ ) of each segment was calculated as

$$K_h = J_v / (\Delta P / \Delta L)$$

where  $J_v$  is flow rate through the segment ( $\text{kg s}^{-1}$ ) and  $\Delta P / \Delta L$  is pressure gradient across the segment ( $\text{MPa m}^{-1}$ ). Sapwood area was determined at 1 cm from both ends of the segment using the dye staining method and the two values were averaged. Total area of leaves distal to the stem segment was measured using a LI-3000 leaf area meter (Li-Cor, Inc., Lincoln, NE, USA). Sapwood-specific hydraulic conductivity ( $K_s$ ;  $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ) was calculated as the ratio of  $K_h$  to sapwood area, and leaf-specific hydraulic conductivity ( $K_l$ ,  $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ) was calculated as the ratio of  $K_h$  to total area of leaves distal to the segment. Leaf area to sapwood area (LA/SA) was calculated as the total area of leaves distal to the segment divided by sapwood area of the segment.

### Gas exchange and fluorescence analyses

A portable LI-6400 photosynthetic system with a 6400-40 Fluorescence Chamber (Li-Cor, Inc., Lincoln, NE, USA) was used to measure net  $\text{CO}_2$  assimilation and chlorophyll fluorescence simultaneously in response to a temporal change in photosynthetic photon flux density (PPFD) in intact leaves. The night before the light response measurements were carried out, maximum chlorophyll fluorescence yield ( $F_m$ ) was measured by illuminating leaves with a pulse of saturation irradiance ( $7000 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) provided by the fluorescence chamber. Photosynthetic light response curves were obtained the following day from the same leaves used for night-time  $F_m$  measurements. All light response measurements were made between 8:00 AM and 11:30 AM (solar time) when photosynthesis was most active. Leaves were illuminated at a PPFD of  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  until a steady state of net  $\text{CO}_2$  fixation and a stable fluorescence yield were reached. The PPFD was then increased to  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  and then decreased stepwise from 2000 to  $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The leaf cuvette temperature was set at  $30^\circ\text{C}$  but the actual leaf temperatures ranged from  $28$  to  $32^\circ\text{C}$ . At each PPFD level, net  $\text{CO}_2$  assimilation rate, chlorophyll fluorescence yield under illumination ( $F_s$ ) and maximum fluorescence yield during illumination ( $F_m'$ ) were measured after a 5-min equilibration period.

The allocation of photons absorbed by PSII antennae to photosynthetic electron transport and thermal dissipation were assessed from the light response measurements. The total absorbed light energy was considered to be partitioned to four different quenching pathways, i.e., to photochemistry ( $\Phi_{\text{PSII}}$ ), regulated ( $\Phi_{\text{NPQ}}$ ) and constitutive ( $\Phi_{\text{D}}$ ) non-photochemical energy dissipation and fluorescence ( $\Phi_{\text{f}}$ ), respectively. These parameters summed up to unity when expressed in fluorescence terms (Hendrickson et al. 2004):

$$\Phi_{\text{PSII}} = 1 - \frac{F_s}{F_m'} \quad (1)$$

$$\Phi_{\text{f,D}} = \Phi_{\text{f}} + \Phi_{\text{D}} = \frac{F_s}{F_m} \quad (2)$$

$$\Phi_{\text{NPQ}} = \frac{F_s}{F_m'} - \frac{F_s}{F_m} \quad (3)$$

Electron transport rate (ETR) was calculated using the following equation (Krall and Edwards 1992):

$$\text{ETR} = 0.5\alpha_l (\text{PPFD}) (\Phi_{\text{PSII}}) \quad (4)$$

where  $\alpha_l$  is the average leaf absorptance (species means of studied species ranging from 0.909 to 0.926) of photosynthetically active radiation of the leaves measured for each species using a spectrometer (USB 4000; Ocean Optics Inc., Dunedin, FL, USA).

Photorespiration rate ( $R_p$ ) was first estimated following the approach of Valentini et al. (1995):

$$R_p = [\text{ETR} - 4(A_n + R_d)]/12 \quad (5)$$

where  $A_n$  is net  $\text{CO}_2$  assimilation rate under each irradiance level and  $R_d$  is respiration other than photorespiration, which is often measured in the dark or calculated from light response analysis as in the present study. This model assumes that all alternative electron sinks are negligible. However, alternative electron sinks may be significant. Thus, photorespiration rate ( $0.5v_o$ ) was also calculated from Rubisco kinetics (Farquhar and von Caemmerer 1982, Brooks and Farquhar 1985, Sharkey 1988):

$$0.5v_o = \frac{1}{2}(A_n + R_d) \left( \frac{1}{\Phi} - 0.5 \right) \quad (6)$$

$$\Phi = 2\Gamma^*/C \quad (7)$$

where  $\Phi$  is the ratio of carboxylation rate to oxygenation rate,  $\Gamma^*$  is the  $\text{CO}_2$  compensation point in the absence of respiration (von Caemmerer 2000) and  $C$  is intercellular partial pressure of  $\text{CO}_2$ . The calculation of  $\Gamma^*$  under different temperatures followed Brooks and Farquhar (1985):

$$\Gamma^* = [42.7 + 1.68(T - 25) + 0.012(T - 25)^2]P \quad (8)$$

where  $T$  is leaf temperature in degrees Celsius and  $P$  is atmospheric pressure.

We estimated the rate of electron use by the alternative metabolism pathways ( $\text{ETR}_{\text{alt}}$ ) using the following equation:

$$\text{ETR}_{\text{alt}} = \alpha_f \text{ETR} - 4(A_n + R_d) - 12 \times 0.5v_o \quad (9)$$

Light response curves were fitted by the algorithm  $Y = Y_{\text{max}} - ae^{-bx}$ , where  $Y$  is ETR or  $A_n$ ,  $x$  is PPFD and  $a \times b$  is the initial slope of the light response curve (Iqbal et al. 1996). Dark respiration ( $R_d$ ) and light compensation point (LCP) were calculated by fitting a linear regression to the relationship between  $A_n$  and PPFD at lower levels of PPFD (from 100 to  $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).

Besides light response measurements,  $A_n$  and  $g_s$  were also measured using the LI-6400 between 9:00 AM and 11:00 AM under a controlled PPFD of  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  to examine the performance of gas exchange under optimal conditions. Leaf intrinsic water use efficiency ( $\text{WUE}_i$ ) was calculated as the ratio of  $A_n$  to  $g_s$ .

### Leaf chemical analysis

Total leaf N concentration was determined with an auto Kjeldahl unit (K370; BÜCHI Labortechnik AG, Flawil, Switzerland) after samples were digested with concentrated  $\text{H}_2\text{SO}_4$ . Total leaf P concentration was analyzed using an inductively coupled

plasma atomic-emission spectrometer (IRIS Advantage-ER; Thermo Jarrell Ash Corporation, Franklin, MA, USA) after samples were digested with concentrated  $\text{HNO}_3/\text{HClO}_4$ . Leaf N and P content was also expressed on a leaf area basis ( $N_a$  and  $P_a$ ;  $\text{mol m}^{-2}$  and  $\text{mmol m}^{-2}$ ) based on leaf mass per area (LMA) measurements. The photosynthetic nitrogen use efficiency (PNUE) and photosynthetic phosphorus use efficiency (PPUE) were calculated by dividing  $A_n$  by  $N_a$  and  $P_a$ , respectively.

## Results

Hemiepiphytic *Ficus* species had significantly lower sapwood-specific ( $1.85$  vs.  $7.27 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ ) and leaf-specific ( $1.84$  vs.  $10.51 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ ) hydraulic conductivity than their congeneric NHs (Figure 1a and b). The leaf area to sapwood area ratio did not show significant differences between species of the two growth forms ( $127.6$  vs.  $117.0 \text{ cm}^2 \text{ mm}^{-1}$ ; Figure 1c).

Under optimal field conditions (mid-morning; PPFD  $900$ – $1300 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ), Hs had significantly lower  $g_s$  than NHs but similar  $A_n$  values (Table 1). Hemiepiphytic *Ficus* species showed significantly higher  $\text{WUE}_i$  and dark respiration rates compared with NHs (Tables 1 and 2). Consistent with the similar mid-morning measurement of  $A_n$  across all species, the maximum  $\text{CO}_2$  assimilation rate calculated from light response curves was also not significantly different between the two growth forms; however, maximum ETR values were lower for Hs (Tables 1 and 2). Hemiepiphytic *Ficus* species had significantly higher LMA and consequently lower leaf dry mass based maximum net  $\text{CO}_2$  assimilation rate ( $A_m$ ) than NHs (Table 1).

The two growth forms showed different patterns in the partitioning of light energy among the three dissipation components, namely  $\Phi_{f,D}$ ,  $\Phi_{\text{NPQ}}$  and  $\Phi_{\text{PSII}}$  (Figure 2a and b). The  $\Phi_{f,D}$  values were very constant ( $\sim 0.2$ ) irrespective of the changing irradiance and not significantly different between growth forms (Figure 2a and b). Unlike  $\Phi_{f,D}$ ,  $\Phi_{\text{PSII}}$  and  $\Phi_{\text{NPQ}}$  were significantly different between the two growth forms under higher irradiance levels (except  $\Phi_{\text{NPQ}}$  at  $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD), with Hs having higher  $\Phi_{\text{NPQ}}$  but lower  $\Phi_{\text{PSII}}$  ( $P < 0.05$ ,  $t$ -test; Figure 2c and d). Notably, although the differences in  $\Phi_{\text{PSII}}$  between Hs and NHs were relatively small ( $\leq 0.05$ ), it resulted in relatively large differences in ETR considering the fact that only a small fraction of light energy is used for photochemistry under higher irradiance ( $< 0.3$  when PPFD  $> 1000$ ; Figures 2c and 3b).

The two growth forms exhibited similar maximum net  $\text{CO}_2$  assimilation rates ( $A_{\text{max}}$ ), which were attained at similar PPFD levels on the light response curves (Figure 3a; Table 2). On the other hand, ETR was significantly lower in Hs at saturating PPFD levels (Figure 3b). Based on the model of Valentini et al.,  $R_p$  was significantly lower in Hs than NHs (Figure 3c). However,

when calculated using the Farquhar and von Caemmerer model, photorespiration rate was not significantly different between the two growth forms (Figure 4a). In all the species,  $0.5v_o$  (photorespiration calculated using the Farquhar and von Caemmerer model) was substantially lower than  $R_p$  (photorespiration calculated using the Valentini et al. model), which may be attributable mainly to the existence of a relatively large alternative electron sink in these species (Figure 4b). Especially, NHs exhibited higher levels of alternative electron use than Hs.

Across the 10 studied species, significant correlations between xylem hydraulic conductivity and leaf functional traits

were observed. Leaf area-specific hydraulic conductivity ( $K_l$ ) was negatively correlated with  $\Phi_{NPQ}$  but was positively correlated with maximum electron transport rate ( $ETR_{max}$ ; Figure 5a and b). In addition,  $K_l$  was negatively related to LMA and positively related to  $g_s$  (Figure 5c and d). Hs had significantly higher concentrations of leaf N but similar leaf P compared with NHs when measured on leaf dry mass basis (Table 3). Photosynthetic N and P use efficiency were significantly lower in Hs (Table 3) and both were negatively correlated with water use efficiency across the 10 studied species ( $P = 0.04$  and  $0.11$ , respectively, linear regression with log-transformed data; Figure 6a and b), although the correlation between PPUE and  $WUE_i$  was only marginally significant.

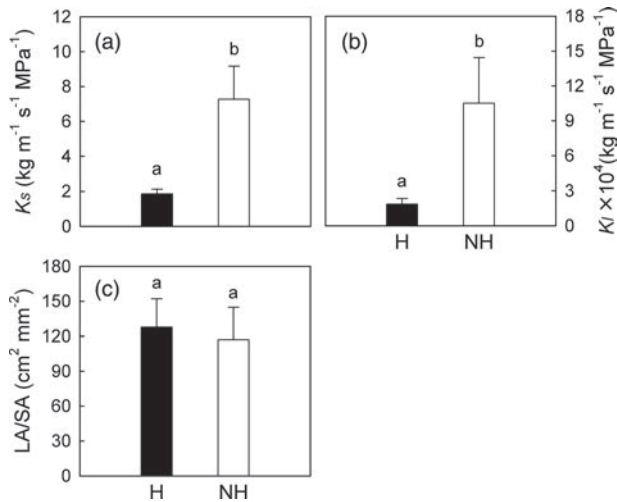


Figure 1. Average values of sapwood-specific hydraulic conductivity ( $K_s$ ; a), leaf-specific hydraulic conductivity ( $K_l$ ; b) and leaf area to sapwood area ratio (LA/SA; c) in Hs and NHs of *Ficus*. Error bars show standard errors ( $n = 6-8$ ). Significant differences between growth forms are indicated by different letters.

## Discussion

Consistent with our hypothesis, Hs and NHs of *Ficus* with contrastingly different xylem hydraulic conductivity exhibited significant differences in photochemistry and gas exchange. These differences include quenching of excited light energy through photochemical and non-photochemical pathways (i.e., among  $\Phi_{fD}$ ,  $\Phi_{NPQ}$  and  $\Phi_{PSII}$ ), PNUE and PPUE,  $g_s$  and  $WUE_i$ . More importantly, these photosynthetic traits were consistently correlated with leaf-specific hydraulic conductivity across all the studied species. Analysis in photochemistry across a group of species with a relatively large range of hydraulic conductivity further expanded our understanding of hydraulic–photosynthetic coordination beyond the knowledge about the general influence of xylem hydraulic conductivity on photosynthetic capacity (Brodribb and Field 2000, Melcher et al. 2001, Brodribb et al. 2002, Santiago et al. 2004, Brodribb et al. 2005, Franks 2006, Campanello et al. 2008, Zhang and Cao 2009).

Table 1. Leaf mass per area (LMA) and photosynthetic traits of five Hs and five NHs of *Ficus*. Light-saturated net  $CO_2$  assimilation rate on area ( $A_n$ ) and mass ( $A_m$ ) basis, stomatal conductance ( $g_s$ ), intercellular  $CO_2$  concentration ( $C_i$ ) and intrinsic leaf water use efficiency ( $WUE_i$ ) measured at mid-morning. Data are mean values  $\pm$  SE ( $n = 5-6$ ). ‘\*\*\*’ and ‘\*\*’ imply significant differences between the two growth forms at  $P < 0.01$  and  $0.05$  level ( $t$ -test), respectively.

Species (code)	LMA* ( $g\ m^{-2}$ )	$A_n$ ( $\mu mol\ m^{-2}\ s^{-1}$ )	$A_m$ * ( $\mu mol\ g^{-1}\ s^{-1}$ )	$g_s$ ** ( $mol\ m^{-2}\ s^{-1}$ )	$C_i$ ** ( $\mu mol\ mol^{-1}$ )	$WUE_i$ ** ( $\mu mol\ mol^{-1}$ )
<i>F. benjamina</i> (BE)	99.2 $\pm$ 7.0	11.30 $\pm$ 1.48	0.114 $\pm$ 0.015	0.255 $\pm$ 0.031	295.1 $\pm$ 7.0	44.7 $\pm$ 3.9
<i>F. concinna</i> (CO)	87.3 $\pm$ 5.3	11.75 $\pm$ 1.23	0.135 $\pm$ 0.014	0.263 $\pm$ 0.041	306.2 $\pm$ 4.4	46.2 $\pm$ 3.4
<i>F. curtipes</i> (CU)	154.7 $\pm$ 4.7	15.35 $\pm$ 0.74	0.099 $\pm$ 0.005	0.332 $\pm$ 0.024	283.6 $\pm$ 3.1	46.9 $\pm$ 4.0
<i>F. religosa</i> (RE)	85.2 $\pm$ 6.1	15.26 $\pm$ 0.68	0.179 $\pm$ 0.008	0.442 $\pm$ 0.028	292.0 $\pm$ 8.4	34.7 $\pm$ 1.3
<i>F. tinctoria</i> (TI)	83.1 $\pm$ 4.0	14.48 $\pm$ 0.32	0.174 $\pm$ 0.004	0.281 $\pm$ 0.025	282.2 $\pm$ 8.6	52.7 $\pm$ 4.2
Hs	101.9 $\pm$ 15.1	13.63 $\pm$ 0.98	0.140 $\pm$ 0.018	0.315 $\pm$ 0.039	291.8 $\pm$ 4.9	45.0 $\pm$ 3.3
<i>F. auriculata</i> (AU)	67.4 $\pm$ 6.6	16.01 $\pm$ 0.93	0.238 $\pm$ 0.014	0.462 $\pm$ 0.037	300.0 $\pm$ 4.6	34.8 $\pm$ 1.3
<i>F. esquiroliana</i> (ES)	48.7 $\pm$ 6.7	12.52 $\pm$ 0.61	0.257 $\pm$ 0.013	0.433 $\pm$ 0.063	301.3 $\pm$ 11.4	30.0 $\pm$ 3.4
<i>F. hispida</i> (HI)	93.6 $\pm$ 5.3	13.09 $\pm$ 0.59	0.140 $\pm$ 0.006	0.366 $\pm$ 0.019	301.5 $\pm$ 1.6	35.9 $\pm$ 1.4
<i>F. racemosa</i> (RA)	50.2 $\pm$ 7.1	16.57 $\pm$ 0.63	0.330 $\pm$ 0.013	0.477 $\pm$ 0.041	306.1 $\pm$ 2.7	35.2 $\pm$ 1.8
<i>F. semicordata</i> (SE)	80.6 $\pm$ 5.3	12.64 $\pm$ 0.81	0.157 $\pm$ 0.010	0.368 $\pm$ 0.053	312.5 $\pm$ 7.4	35.5 $\pm$ 4.1
NHs	68.1 $\pm$ 9.7	14.16 $\pm$ 0.98	0.224 $\pm$ 0.039	0.421 $\pm$ 0.026	304.3 $\pm$ 2.58	34.3 $\pm$ 1.2

Table 2. Dark respiration rate ( $R_d$ ), photosynthetic LCP, PPFD at 90% of maximum net assimilation rate and electron transport rate (PPFD<sub>90%A</sub> and PPFD<sub>90%ETR</sub>), maximum net CO<sub>2</sub> assimilation rate ( $A_{max}$ ) and maximum relative electron transport rate (ETR<sub>max</sub>) calculated from photosynthetic light response curves. Data are mean values  $\pm$  SE ( $n = 5-6$ ). Abbreviations are as defined in Table 1. ‘\*’ implies significant differences in a measured trait between the two growth forms at  $P < 0.05$  level ( $t$ -test).

Code	$R_d^*$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	LCP ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	PPFD <sub>90%A</sub> ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	PPFD <sub>90%ETR</sub> ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$A_{max}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	ETR <sub>max</sub> * ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
BE	1.45 $\pm$ 0.21	26.5 $\pm$ 4.0	633 $\pm$ 49	635 $\pm$ 31	12.84 $\pm$ 1.08	136.9 $\pm$ 11.1
CO	2.04 $\pm$ 0.41	37.3 $\pm$ 6.5	984 $\pm$ 182	853 $\pm$ 68	15.36 $\pm$ 3.21	168.0 $\pm$ 19.2
CU	2.63 $\pm$ 0.84	54.9 $\pm$ 19.7	1230 $\pm$ 170	799 $\pm$ 47	16.56 $\pm$ 1.72	162.8 $\pm$ 11.6
RE	1.12 $\pm$ 0.04	21.2 $\pm$ 0.7	956 $\pm$ 156	695 $\pm$ 69	15.46 $\pm$ 1.32	130.9 $\pm$ 13.7
TI	1.47 $\pm$ 0.41	31.8 $\pm$ 10.5	823 $\pm$ 115	1069 $\pm$ 26	13.02 $\pm$ 2.89	135.3 $\pm$ 22.4
Hs	1.74 $\pm$ 0.30	34.1 $\pm$ 6.5	925 $\pm$ 110	810 $\pm$ 84	14.65 $\pm$ 0.82	146.8 $\pm$ 8.6
AU	1.22 $\pm$ 0.06	27.6 $\pm$ 3.7	627 $\pm$ 42	736 $\pm$ 71	12.87 $\pm$ 1.54	165.2 $\pm$ 17.8
ES	0.76 $\pm$ 0.26	18.0 $\pm$ 6.4	698 $\pm$ 71	844 $\pm$ 6	12.61 $\pm$ 1.06	152.3 $\pm$ 3.6
HI	0.85 $\pm$ 0.08	22.1 $\pm$ 2.9	803 $\pm$ 32	939 $\pm$ 88	13.05 $\pm$ 1.34	198.9 $\pm$ 20.3
RA	1.14 $\pm$ 0.11	24.1 $\pm$ 3.1	884 $\pm$ 71	954 $\pm$ 82	19.02 $\pm$ 2.12	193.1 $\pm$ 18.6
SE	1.40 $\pm$ 1.00	28.4 $\pm$ 0.9	760 $\pm$ 101	896 $\pm$ 57	15.65 $\pm$ 3.45	175.4 $\pm$ 21.5
NHs	1.08 $\pm$ 0.13	24.0 $\pm$ 2.1	754 $\pm$ 49	874 $\pm$ 44	14.64 $\pm$ 1.37	177.0 $\pm$ 9.6

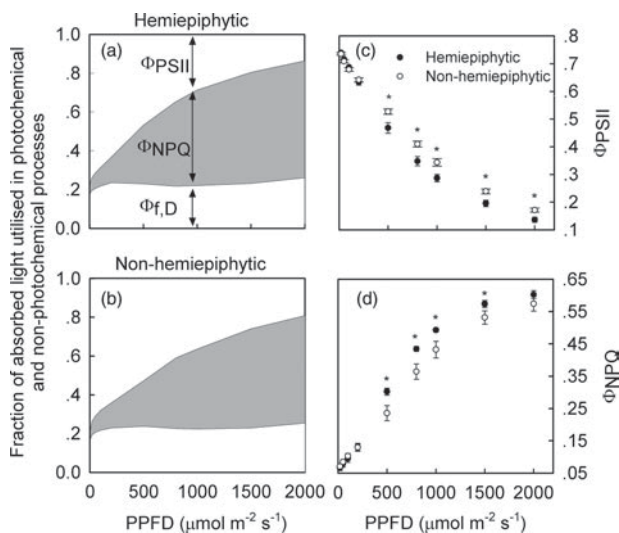


Figure 2. Estimated fraction of absorbed PPFD consumed via photochemistry ( $\Phi_{PSII}$ ),  $\Delta\text{pH}$ - and xanthophyll-regulated thermal dissipation ( $\Phi_{NPQ}$ ), and the sum of fluorescence and constitutive thermal dissipation ( $\Phi_{f,D}$ ) in Hs (a) and NHs (b) of *Ficus* at different instantaneous PPFDs from 0 to 2000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . In panels (c) and (d), average values of  $\Phi_{PSII}$  and  $\Phi_{NPQ}$  were compared between hemiepiphytic and non-hemiepiphytic growth forms under different irradiance levels. ‘\*’ marked significant differences between growth forms under a specific irradiance level ( $P < 0.05$ ,  $t$ -test).

### Non-photochemical quenching, carbon assimilation and photorespiration

An important mechanism of photoprotection is non-photochemical quenching of excited energy that takes place in the light-harvesting complexes of PSII that reduces the supply of energy to photochemical processes by diverging part of the excitation energy through thermal dissipation. This is achieved by a high trans-thylakoidal pH gradient ( $\Delta\text{pH}$ ) and the reversible de-epoxidation of the components of the xanthophyll cycle

(Osmond 1994, Gilmore 1997). In the studied *Ficus* species, energy that is dissipated via  $\Delta\text{pH}$  and xanthophyll-mediated processes ranged from 20 to 60% of the total light energy absorbed by PSII antennae as the instantaneous PPFD received by leaves varied between 500 and 2000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . On average, Hs had substantially higher  $\Phi_{NPQ}$  than NHs (Figure 2d), leading to significantly lower ETR<sub>max</sub> in Hs (Figure 3b).

Despite a significantly lower ETR in Hs,  $A_{max}$  was similar to that of NHs (Figure 3a). For a given  $\Phi_{PSII}$  or ETR<sub>max</sub>, leaves can have different  $A_{max}$  depending on the partitioning of photosynthetic electron flow between carbon assimilation, photorespiration and other alternative pathways of electron use. For example, in the uppermost-canopy leaves of four dipterocarp species Zhang et al. (2008) found high levels of ETR throughout the day but the net CO<sub>2</sub> assimilation rate exhibited sustained depression from mid-morning onward, which was largely due to increased photorespiration rates under conditions such as high vapor pressure deficit, high leaf temperature and excessive light. Photorespiration is an important energy sink in C<sub>3</sub> plants (Heber et al. 1996), which is involved in protecting PSII from potentially damaging effects of photoinhibition when plants are exposed to excessive light (e.g., Franco and Lüttge 2002, Zhang et al. 2008). Under higher instantaneous PPFDs, photorespiration increased substantially and became an important electron sink in both Hs and NHs, and the magnitude of photorespiration was similar between the two growth forms. Higher ETR at saturating irradiance levels in NHs did not result in higher net carbon assimilation rates than that of Hs, but rather a higher proportion of electron flow was diverged to alternative electron sinks in NHs. Our results also indicated that alternative electron flow may be large under high irradiance and cannot be assumed to be zero as in the Valentini et al. model (1995). Thus for these *Ficus* species, computation from the Farquhar and von Caemmerer method is more proper in modeling photorespiration.

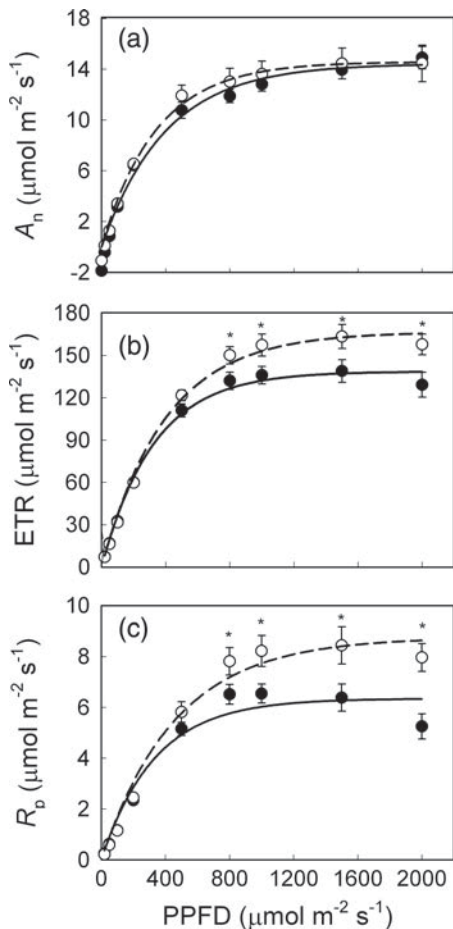


Figure 3. Response of net CO<sub>2</sub> assimilation rate ( $A_n$ ; a), ETR (b) and photorespiration rate calculated using the Valentini et al. model ( $R_p$ ; c) to different PPFD in Hs (filled circles) and NHs (open circles) of *Ficus*. Each point is the mean of five hemiepiphytic or non-hemiepiphytic species (error bars show standard errors). ‘\*’ marked significant differences between growth forms under a specific irradiance level ( $P < 0.05$ ,  $t$ -test). Curves were fitted using the algorithm  $Y = Y_{\text{max}} - ae^{-bx}$  with mean values of the five species within each growth form.

### Links between photosynthesis and hydraulics

Photosynthetic traits correlated with  $K_i$  in a consistent manner across the 10 *Ficus* species.  $\text{ETR}_{\text{max}}$  was positively correlated with  $K_i$ , which is consistent with positive correlations found between xylem hydraulic conductivity and photosynthetic capacity measured as ETR or  $\Phi_{\text{PSII}}$  in other species (e.g., Brodribb and Field 2000, Brodribb et al. 2002, Campanello et al. 2008). The correlation between photochemistry and CO<sub>2</sub> assimilation and hydraulic conductivity may not be direct but rather linked via a suite of other leaf traits, such as LMA and  $g_s$ , which are affected strongly by plant hydraulics. Plants adapted to drought-prone environments tend to produce leaves with higher LMA, which is associated with a larger water storage capacitance, a slower rate of water loss under drought

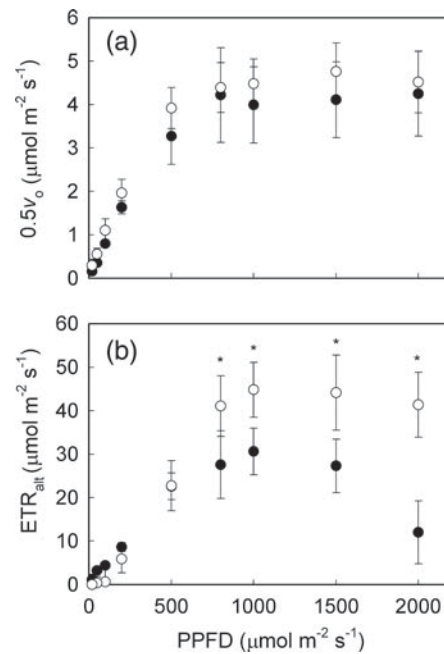


Figure 4. Photorespiration rate calculated using the Farquhar and von Caemmerer model ( $0.5V_p$ ; a) and electron use in alternative pathways ( $\text{ETR}_{\text{alt}}$ ; b) in response to PPFD in Hs (filled circles) and NHs (open circles) of *Ficus*. ‘\*’ marked significant differences between growth forms under a specific irradiance level ( $P < 0.05$ ,  $t$ -test).

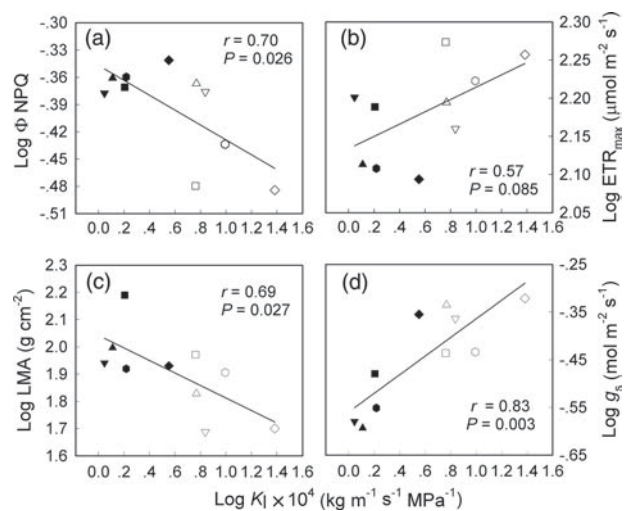


Figure 5. Relationship between leaf-specific hydraulic conductivity ( $K_i$ ) and efficiency of PSII thermal dissipation ( $\Phi_{\text{NPQ}}$ ; a), maximum electron transport rate ( $\text{ETR}_{\text{max}}$ ; b), leaf dry mass per area (LMA; c) and maximum stomatal conductance ( $g_s$ ; d).  $\Phi_{\text{NPQ}}$  values measured under a PPFD of  $800 \mu\text{mol m}^{-2} \text{s}^{-1}$  were used as representative values. Data were  $\log_{10}$ -transformed to improve normality and homoscedasticity. *Ficus benjamina* (filled triangle up), *F. concinna* (filled triangle down), *F. curtipes* (filled square), *F. religosa* (filled diamond), *F. tinctoria* (filled hexagon), *F. auriculata* (open triangle up), *F. esquiroliana* (open triangle down), *F. hispida* (open square), *F. racemosa* (open diamond), *F. semicordata* (open hexagon).

Table 3. Leaf N and P percentage content (N and P), leaf N and P content on area basis ( $N_a$  and  $P_a$ ), and PNUE and PPUE. Data are mean values  $\pm$  SE ( $n = 5$ ). Abbreviations are as defined in Table 1. '\*\*\*' and '\*\*' imply significant differences between the two growth forms at a  $P < 0.01$  and  $0.05$  level ( $t$ -test), respectively.

Code	N* (%)	P (%)	$N_a^{**}$ (mol m <sup>-2</sup> )	$P_a^*$ (mmol m <sup>-2</sup> )	PNUE* ( $\mu\text{mol CO}_2 \text{ s}^{-1} \text{ mol}^{-1} \text{ N}$ )	PPUE* ( $\text{mmol CO}_2 \text{ s}^{-1} \text{ mol}^{-1} \text{ P}$ )
BE	2.05 $\pm$ 0.10	0.111 $\pm$ 0.003	0.145 $\pm$ 0.007	3.56 $\pm$ 0.09	77.7 $\pm$ 10.2	3.17 $\pm$ 0.47
CO	2.53 $\pm$ 0.16	0.148 $\pm$ 0.008	0.158 $\pm$ 0.010	4.18 $\pm$ 0.21	74.4 $\pm$ 7.8	2.81 $\pm$ 0.29
CU	1.46 $\pm$ 0.08	0.083 $\pm$ 0.004	0.161 $\pm$ 0.009	4.16 $\pm$ 0.22	95.4 $\pm$ 4.6	3.70 $\pm$ 0.18
RE	2.44 $\pm$ 0.08	0.190 $\pm$ 0.015	0.148 $\pm$ 0.005	5.23 $\pm$ 0.42	102.8 $\pm$ 4.6	2.92 $\pm$ 0.13
TI	2.61 $\pm$ 0.13	0.235 $\pm$ 0.012	0.155 $\pm$ 0.008	6.30 $\pm$ 0.33	93.5 $\pm$ 2.0	2.30 $\pm$ 0.05
Hs	2.22 $\pm$ 0.24	0.154 $\pm$ 0.030	0.153 $\pm$ 0.003	4.69 $\pm$ 0.54	88.7 $\pm$ 6.1	2.98 $\pm$ 0.25
AU	1.86 $\pm$ 0.10	0.132 $\pm$ 0.012	0.089 $\pm$ 0.005	2.87 $\pm$ 0.26	179.1 $\pm$ 10.4	5.57 $\pm$ 0.32
ES	1.79 $\pm$ 0.14	0.200 $\pm$ 0.003	0.062 $\pm$ 0.005	3.14 $\pm$ 0.20	201.0 $\pm$ 9.8	3.99 $\pm$ 0.20
HI	2.11 $\pm$ 0.09	0.151 $\pm$ 0.013	0.141 $\pm$ 0.006	4.55 $\pm$ 0.38	92.9 $\pm$ 4.2	2.88 $\pm$ 0.13
RA	1.41 $\pm$ 0.06	0.144 $\pm$ 0.005	0.051 $\pm$ 0.002	2.33 $\pm$ 0.08	327.0 $\pm$ 12.5	7.12 $\pm$ 0.27
SE	1.78 $\pm$ 0.22	0.136 $\pm$ 0.007	0.102 $\pm$ 0.013	3.54 $\pm$ 0.19	123.6 $\pm$ 7.9	3.57 $\pm$ 0.23
NHs	1.79 $\pm$ 0.12	0.152 $\pm$ 0.013	0.089 $\pm$ 0.018	3.28 $\pm$ 0.42	184.7 $\pm$ 45.2	4.63 $\pm$ 0.86

conditions and greater drought tolerance (Bucci et al. 2004, Hoffmann et al. 2005, Hao et al. 2008, 2010). On the other hand, higher LMA involves longer distances and larger resistances for CO<sub>2</sub> diffusion from stomata to chloroplasts (Parkhurst 1994), which may negatively affect photosynthesis. Under adequate soil water supply, high stem hydraulic conductivity allows fast water transport to leaves to compensate for transpirational water loss and consequently helps to maintain higher leaf water potential and higher maximum  $g_s$  (Meinzer et al. 1995, Sperry 2000, Meinzer 2003, Ackerly 2004, Santiago et al. 2004, Zhang and Cao 2009). Higher  $g_s$  in turn results in higher intercellular CO<sub>2</sub> concentration ( $C_i$ ), which is a function of photosynthetic assimilation rate (Farquhar et al. 1980). This intrinsic  $g_s$ - $C_i$ -assimilation linkage offered a theoretical basis for understanding hydraulic-photosynthetic coordination (Katul et al. 2003).

In the present study, differences in partitioning electron flow between carbon assimilation and other electron use pathways, such as photorespiration and other alternative electron sinks, made the correlations between xylem hydraulic conductivity and photosynthesis more complicated. The positive correlation between  $K_1$  and  $\text{ETR}_{\text{max}}$  across species did not result in a positive correlation between  $K_1$  and maximum CO<sub>2</sub> assimilation rate across the *Ficus* species, which is likely attributable to larger alternative electron sinks in species with higher ETR. Despite the light response measurements showing similar  $A_{\text{max}}$  between the two *Ficus* growth forms, diurnal measurements of gas exchange on saplings showed that NHs have a much longer daytime active photosynthetic period than Hs (Hao 2010). Longer active daytime photosynthesis in NHs may require these species to have higher rates of alternative electron use, such as nitrogen assimilation, and thus resulted in a comparable maximum CO<sub>2</sub> assimilation rate to Hs despite significantly higher ETR.

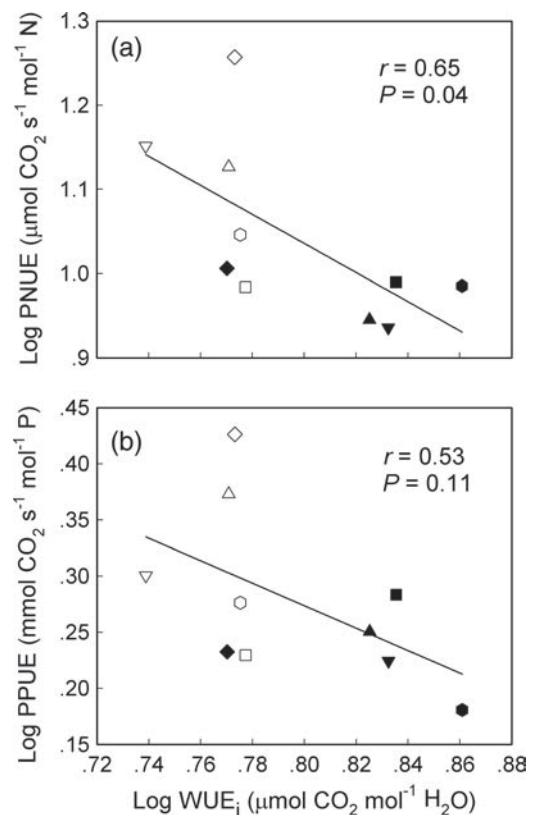


Figure 6. Relationship between PNUE (a) and PPUE (b) and WUE<sub>i</sub>. Data were log<sub>10</sub>-transformed to improve normality and homoscedasticity. Symbols are as defined in Figure 5.

### Trade-offs between WUE and photosynthetic nutrient use efficiency

To overcome the conflicts between water conservation and uptake of CO<sub>2</sub>, some woody hemiepiphytic plants, such as



species in the genus *Clusia* (Clusiaceae), evolved a facultative Crassulacean acid metabolism (CAM) to cope with the conflict between water conservation and efficient CO<sub>2</sub> uptake for photosynthesis (Ting et al. 1987, Borland et al. 1992). During their epiphytic phase, these species have facultative CAM metabolism and consequently open stomata at night to fix exogenous CO<sub>2</sub> while reducing water loss by closing stomata during the daytime. However, in Hs of *Ficus*, which maintain C<sub>3</sub> metabolism during all life stages (Ting et al. 1987), the tighter stomatal control over water loss protects plants from dropping their water potentials to critical values during drought periods and hence avoid catastrophic hydraulic failure (Brodribb and Holbrook 2004, Hao et al. 2010).

On the other hand, tight stomatal control has a carbon cost because low  $g_s$  unavoidably limits the influx of CO<sub>2</sub> and thus photosynthetic carbon assimilation. Photosynthetic N and P use efficiency were significantly lower in Hs than in NHs (Table 3). A trade-off between photosynthetic water use efficiency and nutrient use efficiency appears to exist across all the studied *Ficus* species (Figure 6a and b). Such a trade-off has also been found in other groups of species and may imply a commonly existing adaptive conflict between leaf water conservation and effective photosynthetic carbon assimilation (Field et al. 1983, Santiago et al. 2004, Zhang and Cao 2009). The trade-off is likely mediated by differences among species in stomatal regulation and light energy utilization and dissipation, such as in photorespiration and non-photochemical quenching. However, Hs tend to produce leaves with higher LMA, which are more persistent under drought (Hao et al. 2010), indicating higher investment in non-photosynthetic leaf structures and longer leaf life spans. Thus, by producing more persistent leaves with potentially longer leaf life spans, Hs compensate their lower photosynthetic nutrient use efficiency with a longer period of carbon fixation, which helps to maintain balances between water conservation and plant carbon economy.

## Conclusions

Under high light, non-photochemical energy quenching and the safe partitioning of excessive electron flows through photorespiration and other alternative pathways are important photoprotective mechanisms involved in both growth forms of *Ficus* species. Under conditions of excessive light, Hs on average dissipated a larger proportion of absorbed energy through non-photochemical pathways than NHs, while NHs dissipated a larger proportion of electrons than Hs through the alternative electron sinks. Differences in the efficiency of long-distance water transport and stomatal control of water use are involved in the underlying mechanisms explaining these differences in photosynthetic traits across the studied *Ficus* species. The relatively large variation in functional traits both within and

between growth forms and trade-offs among functional traits may have contributed to niche differentiation and species co-existence in this super-diverse genus in tropical rainforests.

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