Differentiation of leaf water flux and drought tolerance traits in hemiepiphytic and non-hemiepiphytic *Ficus* tree species

Guang-You Hao[1,2], Lawren Sack[3], Ai-Ying Wang[1,4], Kun-Fang Cao*[,1] and Guillermo Goldstein*[,2,5]

[1]*Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan Province 666303, China;* [2]*Department of Biology, University of Miami, Coral Gables, Florida 33124, USA;* [3]*Department of Ecology and Evolutionary Biology, University of California Los Angeles, 621 Charles E. Young Drive South, Los Angeles, California 90095, USA;* [4]*Department of Biology, Simao Teachers' College, Pu'er, Yunnan Province 665000, China; and* [5]*Laboratorio de Ecología Funcional, Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria Nuñez, Buenos Aires, Argentina*

Summary

1. Leaf structural and physiological traits are associated with growth form and habitat, but little is known of the specific traits associated with hemiepiphytes, which are an important component of many tropical forests. Given their life history that includes a drought prone epiphytic stage, hemiepiphytes should be expected to have more drought tolerance-related traits than co-occurring terrestrial species.

2. The genus *Ficus* includes woody hemiepiphytes distributed in tropical areas throughout the world. Traits related to the flux of water through the leaf and to drought adaptations were studied in five hemiephiphytic (H) and five non-hemiepiphytic (NH) *Ficus* tree species grown in a common garden to determine genetically based differences.

3. Leaves of H and NH species differed substantially in structure and physiology; on average, H species had smaller leaves with higher leaf mass per unit area, thicker epidermis, smaller vessel lumen diameters in petioles and lower petiole hydraulic conductivity. Leaf traits also indicated stronger drought tolerance in H species, including lower epidermal conductance and turgor loss point and earlier stomatal closure with desiccation than NH species. Across H and NH species, traits related to water flux capacity were negatively correlated with traits related to drought tolerance.

4. The divergences in hydraulics and water relations between growth forms for these closely related species reflected specialization according to contrasting habitat and life form. Conservative water use and increased ability of leaves to persist under severe drought would provide an advantage for H species, especially during the epiphytic phase, while the higher potential water use of NH species would be associated with higher assimilation rates and competitiveness under high water supply.

5. The results indicate a trade-off between leaf water flux capacity and leaf drought tolerance across these hemiephiphytic and non-hemiepiphytic species. Species adaptation to habitats with contrasting demands on leaf function may lead to divergence along a leaf water-flux-drought-tolerance spectrum.

Key-words: leaf hydraulics, rainforest, stomatal control, water relations

Introduction

Many classical and recent work has focused on the importance of leaf traits in plant life history, including growth form (e.g. Givnish 1987; Reich *et al.* 2004; Waite & Sack

*Correspondence author. E-mails: caokf@xtbg.ac.cn; goldstein@bio.miami.edu

2010). However, relatively few studies have focused on hemiepiphytes, which differ crucially in life history from terrestrial and epiphytic plants. Hemiepiphytes are very abundant in lowland tropical rainforests, and in lower montane and midmontane cloud forests (Putz & Holbrook 1986; Williams-Linera & Lawton 1995), and play an important role in canopy dynamics by competing with their host tree species, and stabilize mats of epiphytic organic soil that affect rainfall interception and ecosystem hydrology (Veneklaas *et al.* 1990; Williams-Linera & Lawton 1995).

This study focused on the leaf traits linked with hemiepiphytism in the genus *Ficus* (Moraceae), notable for its habitat breadth, number of species and biomass (Dobzhansky & Murca-Pires 1954; Putz & Holbrook 1986; Holbrook & Putz 1996a). Hemiepiphytism evolved at least four times in this genus (Harrison 2005) and currently, *Ficus* consists of about 500 hemiepiphytic and 300 non-hemiepiphytic species (Berg & Corner 2005).

Hemiepiphytic *Ficus* species (Fig. 1) are adapted to a water-limited epiphytic phase. Thus, for five Venezuelan *Ficus* species, the epiphytic growth phase exhibited more conservative water use and enhanced drought tolerance relative to the terrestrial phase, including stronger stomatal control and slower epidermal water loss (Holbrook & Putz 1996a,b). Studies of adult trees of hemiepiphytic (H) and non-hemiepiphytic *Ficus* species (NH) found lower stem hydraulic conductivity for the H species (Patiño, Tyree & Herre 1995; Guang-You Hao, unpublished data). Differences in stem hydraulic conductivity are probably paralleled by differences in leaf hydraulic traits. In this study, we aimed to determine the differences in leaf traits associated with water relations for *Ficus* species of the two growth forms.

The leaf is a major bottleneck in the whole-plant water flow pathway, with a hydraulic resistance that accounts on average for 30% (and up to >90%) of plant resistance (Nardini & Salleo 2000; Brodribb, Holbrook & Gutierrez 2002; Sack *et al.* 2003). Consequently, the leaf hydraulic system is a key determinant of plant hydraulic responses and water relations (Sack & Holbrook 2006; Brodribb & Cochard 2009). The leaf hydraulic conductance varies by over an order of magnitude across species and correlates with 'water flux' traits (Sack *et al.* 2003), i.e. those related to the capacity for water movement through and out of leaves, including stomatal pore area, maximum stomatal conductance and photosynthetic rate per leaf area (Aasamaa, Sober & Rahi 2001; Sack *et al.* 2003; Brodribb & Holbrook 2004; Brodribb *et al.* 2005). Leaves are also more vulnerable than stems to drought-induced cavitation; thus, species adapted to contrasting water availabilities may differ more strongly in leaf than stem hydraulic traits (Hao *et al.* 2008). We hypothesized that the H and NH life forms would be associated with strong differences in leaf water flux traits.

We examined two groups of traits, hydraulics and water relations, in five H and five NH species in a common garden to determine genetically based differences and whether these were aligned with differences in stem hydraulic conductivity and photosynthetic carbon assimilation (Patiño, Tyree & Herre 1995; Guangy-You Hao, unpublished data). Specifically, we hypothesized that H species would have leaves with lower values for water flux traits than NH species, including xylem hydraulic capacity and maximum gas exchange rates, but that they would have tighter stomatal control of water loss and a greater ability to persist under drought. We tested these hypotheses to clarify the physiological and ecological performance of species of the two growth forms.

Materials and methods

STUDY SITE AND SPECIES SAMPLING

The study was conducted in Xishuangbanna Tropical Botanical Garden (XTBG; 21° 56′ N, 101° 15′ E, 600 m altitude), Chinese Academy

Fig. 1. *Ficus concinna* of epiphytic (left) and terrestrial (right) stages strangling their host palm trees in Xishuangbanna Tropical Botanical Garden. Photos by G.-Y. Hao.

Table 1. Five hemiepiphytic (H) and five non-hemiepiphytic (NH) *Ficus* tree species investigated in this study. Nomenclature follows Wu & Raven (2003)

Species name	Code	Growth form	Section	Leaf size (cm^2)	Leaf texture
Ficus benjamina Linnaeus	BE	H	Conosyce	24.2 ± 2.0	Leathery
Ficus concinna (Miquel) Miquel	CO	H	Urostigma	25.7 ± 1.6	Leathery
Ficus curtipes Corner	CU	H	Conosyce	71.3 ± 12.4	Leathery
Ficus religosa Linnaeus	RE	H	Urostigma	189.6 ± 24.6	Leathery
Ficus tinctoria Frost. f. subsp. *gibbosa* (Bl.) Corner	TI	H	Syzidium	48.3 ± 5.9	Leathery
Ficus auriculata Loureiro	AU	NH	Sycomorus	624.4 ± 75.8	Papery
Ficus esquiroliana H. Léveillé	ES	NH	Eriosycea	690.2 ± 131.1	Papery
Ficus hispida Linnaeus	HI	NH	Sycocarpus	136.4 ± 15.1	Papery
Ficus racemosa Linnaeus	RA	NH	Sycomorus	44.5 ± 4.1	Leathery
Ficus semicordata Buchanan-Hamilton ex Smith	SE	NH	Hemicardia	180.8 ± 21.1	Papery

of Sciences, Yunnan province, SW China. The climate is dominated by the southwest monsoon with well-defined alternation of wet and dry seasons. The mean annual precipitation is about 1500 mm with 80% during the May–October wet season; mean annual air temperature is 22.7 °C, with monthly means ranging from 14.8 °C in January to 25.5 °C in June. All measurements were conducted at the beginning of the wet season, May–June 2008.

Five H and five NH species that naturally occur in the region were used. The H and NH species are from three and four taxonomic sections respectively (Table 1). *Ficus tinctoria* is a hemiepiphyte that usually does not form a self-supporting trunk and falls after its host tree rots; *F. benjamina*, *F. concinna*, and *F. curtipes* are stranglers that can eventually form free-standing trunks; and *F. religosa* can form a massive trunk and canopy up to 30 m. The five NH species usually regenerate in forest margins and gaps, most commonly in secondary forests. *Ficus racemosa* can grow to 30 m and the others typically to 10 m.

Samples were taken from adult trees ranging 15–60 cm in diameter at breast height, with H species in their free-standing terrestrial growth stage. Six trees were sampled for each species. For the five dioecious species [i.e. *F. auriculata* (NH), *F. esquiroliana* (NH), *F. hispida* (NH), *F. semocordata* (NH), and *F. tinctoria* (H)], samples were taken from three male and three female individuals; no significant differences were found for any trait between individuals of different sexes (data not shown) and data were pooled for further analysis. The use of common garden plants minimized plastic adjustments to local site conditions, allowing the detection of genetically based species differences. All leaves were sampled from sun-exposed branches.

LEAF MORPHOLOGICAL AND ANATOMICAL MEASUREMENTS

Leaf area (*A*) was measured using a leaf area meter (LI-3000, LI-COR Inc., Lincoln, NE, USA) and leaf dry mass (*M*) was determined after oven-drying 48 h at 70 °C. Leaf mass per unit area (LMA) was calculated as M/A. Leaf saturated water content (SWC) and leaf lamina dry mass density (ρ_{leaf}) were measured on leaf discs rehydrated overnight as respectively (rehydrated mass–dry mass)/dry mass, and dry mass/rehydrated volume, with volume determined by water-displacement using a balance.

To determine lamina and petiole xylem traits, we made microscopic observations of cross-sections from the middle of the leaf lamina, avoiding major veins, and from the petiole immediately below the lamina insertion point. For three leaves from each of the six sampled trees of each species, measurements were made of the thickness of the lamina, adaxial epidermis, palisade mesophyll, spongy mesophyll and abaxial epidermis, and for one leaf per tree, petiole vessel lumen diameters were determined under an optical microscope (YS100, Nikon Corp., Tokyo, Japan).

We determined theoretical petiole xylem hydraulic conductivity as a proxy of leaf hydraulic conductance (K_{leaf}), which could not be quantified directly using typical techniques (e.g. Sack *et al.* 2002) because of the copious latex in these species. Leaf area-normalized petiole hydraulic conductivity was expected to be a reasonable proxy of K_{leaf} across species (Sack *et al.* 2003; Sack & Frole 2006). We measured the number of petiole vessels, and for 50 randomly chosen vessels, determined theoretical axial hydraulic conductivity, treating the vessels as ellipses:

$$K_i = \frac{\pi a^3 b^3}{64\eta(a^2 + b^2)} \qquad\qquad eqn1$$

where K_i is the theoretical axial hydraulic conductivity of an individual vessel, *a* and *b* are the long and short axes of the vessel lumen, and η the viscosity of water at 25 °C (Lewis & Boose 1995). The leaf area normalized theoretical axial hydraulic conductivity of the petiole (K_t, mmol m^{-1} s^{-1} MPa^{-1}) was then calculated as:

$$K_t = \frac{n}{50A}\sum_{1}^{50} K_i \qquad\qquad eqn2$$

where *n* is the total number of vessels in a petiole, and *A* is the lamina area (Cochard, Nardini & Coll 2004; Sack & Frole 2006).

LEAF WATER LOSS AFTER EXCISION

Measurements were made on detached leaves to determine the minimum rate of epidermal water loss after stomatal closure (Holbrook & Putz 1996b). Terminal branches were collected in the evening, immediately re-cut under water and rehydrated overnight wrapped in plastic bags to determine leaf saturated mass (SM). For each species, six leaves were excised and placed on the lab bench under dim light (ca. 3 μmol m^{-2} s^{-1} PPFD; LI-1400 data logger and quantum sensor, LI-COR Inc.), with temperature approximately 20 °C and average vapour pressure deficit 2.3 kPa (range 1.9–2.6 kPa), and leaf fresh mass (FM) for each leaf was measured periodically. Randomly paired H and NH species were measured simultaneously. At the end of the experiment, leaves were oven-dried at 70 °C for 48 h before determining dry mass (DM). Leaf relative water content [RWC = (FM−DM)/(SM−DM) × 100%] was calculated following

the dehydration process and plotted against the time interval (ΔT) from leaf excision to each FM measurement. The water loss rates between RWC of 90% and 60% for all the studied species were most stable during the dehydration process and were used to calculate mean epidermal transpiration rates (E_{min}; Muchow & Sinclair 1989; Holbrook & Putz 1996b). The time required for a saturated leaf to drop to RWC of 70% (T_{70}), a threshold for physiological damage (Lawlor & Cornic 2002) was determined from RWC vs. ΔT regressions. Epidermal conductance (g_{min}; mmol m^{-2} s^{-1}) was calculated by dividing E_{min} by the daily average value for mole fraction VPD (VPD/atmospheric pressure).

PRESSURE-VOLUME RELATIONSHIPS

Leaf pressure-volume curve parameters were quantified using the bench drying method (Tyree & Hammel 1972). For each species, a branch was collected from each of six individuals at predawn and allowed to rehydrate for 2–3 h. Leaf mass and water potential (Ψ_l, using a pressure chamber; PMS1000; Corvallis, OR, USA) were measured periodically during desiccation. At higher water potentials, latex made precise Ψ_l determination difficult, and the first measurement (> -0.3 MPa) for each leaf was not used. Leaf absolute capacitance per area (C_{leaf}; mmol m^{-2} MPa^{-1}) was determined by fitting the linear relation of $1/\Psi_l$ vs. RWC before turgor loss and was normalized by leaf area (Koide *et al.* 1991; Brodribb & Holbrook 2003):

$$C_{leaf} = \Delta RWC/\Delta\Psi_l \times (DM/LA) \times (WM/DM)/M \qquad eqn 3$$

where LA is leaf area (m^2), WM the leaf water mass at 100% RWC (WM = FM$-$DM, in g) and M the molar mass of water (g mol^{-1}).

STOMATAL RESPONSE TO LEAF WATER POTENTIAL

The response of stomatal conductance (g_s; measured with a portable LI-6400 photosynthetic system; LI-COR Inc.) to Ψ_l was determined *in situ* from 900 to 1600 h. Measurements were made at ambient temperature, VPD, PPFD and CO$_2$ concentration (ranging 26–38 °C, 0.6–4.5 kPa, 100–1600 μmol m^{-2} s^{-1} and 370–430 ppm respectively). After g_s measurement, leaves were removed, numbered and sealed immediately in plastic bags with wet tissue paper and kept in a cooler before Ψ_l measurement in the laboratory within 1 h (previously found not to affect Ψ_l; data not shown). To determine g_s under extreme drought, measurements were also made on excised branches (Brodribb & Holbrook 2003). The relationship between g_s and Ψ_l was fitted using a sigmoid function.

STATISTICS

One-way ANOVA was used to test differences between N and NH species means (d.f. = 1 and 8 for growth form and error terms, respectively). For correlations among species, all traits were analysed using Pearson correlations (SPSS version 15.0; SPSS, Inc., Chicago, IL, USA). We tested correlations that were hypothesized *a priori* (see 'Introduction'), and additionally we present a correlation matrix to reveal the intercorrelative structure for all tested variables, rather than to reach any conclusions about non-hypothesized relationships (Givnish, Montgomery & Goldstein 2004; Edwards 2006; Dunbar-Co, Sporck & Sack 2009). We used Bonferroni correction before 'mining' for trait correlations that were not hypothesized, given the danger of an inflated false discovery rate (Garcia 2003; Moran 2003). As a general test of the degree of inter-relationship of the measured traits, and whether this differed from what might occur due to chance, we tested whether correlations were significant in more than 5% of cases (using a proportion test; Minitab Release 15, College Park, PA, USA; Waite & Sack 2010). Linear and nonlinear regression analyses between traits were performed using SIGMAPLOT 10.0 (Systat Software, Inc., San Jose, CA, USA).

Results

Leaf characteristics differed significantly between *Ficus* species of the two growth forms. All the H species had leathery leaves while four of five NH species had papery leaves (Table 1). H species had on average 71% thicker leaves, with 120% thicker spongy mesophyll, 85% thicker upper epidermis, 159% thicker lower epidermis and 53% lower palisade/spongy ratio (see Table S1 in Supporting Informa-

Table 2. Leaf structural and physiological traits of five hemiepiphytic (H) and five non-hemiepiphytic (NH) *Ficus* species

Species	LMA* (g cm^{-2})	D_v** (μm)	K_t** (mmol m^{-1} s^{-1} MPa^{-1})	SWC^{NS} (g g^{-1})	ρ_{leaf}^{NS} (g cm^{-3})	T_{70}* (h)	g_{min}** (mmol m^{-2} s^{-1})
BE	99.2 ± 7.0	16.6 ± 0.4	0.61 ± 0.09	1.71 ± 0.09	0.35 ± 0.01	32.7 ± 11.1	0.60 ± 0.17
CO	87.3 ± 5.3	18.5 ± 0.8	0.68 ± 0.12	1.59 ± 0.04	0.37 ± 0.01	5.1 ± 0.5	3.22 ± 0.36
CU	154.7 ± 4.7	20.0 ± 1.0	0.62 ± 0.11	1.60 ± 0.07	0.34 ± 0.01	36.1 ± 3.7	0.71 ± 0.08
RE	85.2 ± 6.1	23.9 ± 2.2	0.83 ± 0.14	2.21 ± 0.24	0.45 ± 0.02	3.2 ± 0.7	4.30 ± 0.31
TI	83.1 ± 4.0	18.3 ± 0.5	0.52 ± 0.05	2.49 ± 0.11	0.27 ± 0.01	8.9 ± 2.4	1.83 ± 0.26
H mean	101.9 ± 15.1	19.5 ± 1.4	0.65 ± 0.06	1.92 ± 0.20	1.06 ± 0.08	17.2 ± 7.9	2.13 ± 0.06
AU	67.4 ± 6.6	26.9 ± 1.6	1.02 ± 0.21	1.83 ± 0.15	0.25 ± 0.01	1.9 ± 0.1	9.14 ± 0.30
ES	48.7 ± 6.7	23.1 ± 1.3	0.79 ± 0.07	2.46 ± 0.10	0.15 ± 0.01	2.6 ± 0.1	7.65 ± 0.47
HI	93.6 ± 5.3	26.5 ± 2.2	1.96 ± 0.25	2.07 ± 0.14	0.34 ± 0.01	1.6 ± 0.1	16.76 ± 1.00
RA	50.2 ± 7.1	24.8 ± 1.1	1.24 ± 0.15	2.81 ± 0.20	0.34 ± 0.01	1.3 ± 0.4	7.26 ± 1.42
SE	80.6 ± 5.3	25.0 ± 1.9	1.64 ± 0.38	1.87 ± 0.05	0.34 ± 0.01	1.0 ± 0.1	12.55 ± 0.61
NH mean	68.1 ± 9.7	25.3 ± 0.8	1.33 ± 0.24	2.21 ± 0.21	1.24 ± 0.21	1.7 ± 0.3	10.67 ± 0.22

LMA, leaf dry mass per area; D_v, average vessel lumen diameter in leaf petioles; K_t, theoretical hydraulic conductivity of petioles; SWC, leaf saturated water content; ρ_{leaf}, density of leaf lamina; T_{70}, time required for bench drying of fully saturated leaves to 70% relative water content; g_{min}, leaf epidermal conductance. Data are mean ± SE (n = 6). '**', '*'and '^{NS}' following a parameter indicate statistical difference between H and NH growth forms at $P < 0.01$, $0.01 \leq P < 0.05$, and $P \geq 0.05$ level, respectively (one-way ANOVA).

Table 3. Comparison of leaf water relation traits. π^0, osmotic potential at turgor loss point; C_{leaf}, leaf absolute capacitance; g_{max}, maximum stomatal conductance; $\Psi_{gs50\%}$, leaf water potential at 50% g_{max}; $\Psi_{gs20\%}$, leaf water potential at 20% g_{max}; $\Psi_{gs50\%}-\pi^0$, difference between $\Psi_{gs50\%}$ and π^0; $g_{s\text{-}TLP}/g_{s\text{-}Max}$, the ratio of stomatal conductance at turgor loss point to g_{max}. Error bars are not provided as species' values were derived from pressure volume curves with points pooled for all individuals, or from fitted regressions

Species	π^0* (MPa)	$C_{leaf}*$ (mmol m^{-2} MPa^{-1})	$g_{max}**$ (mol m^{-2} s^{-1})	$\Psi_{gs50\%}$ NS (MPa)	$\Psi_{gs20\%}$ NS (MPa)	$\Psi_{gs50\%}-\pi^0**$ (MPa)	$g_{s\text{-}TLP}/g_{max}**$
BE	−1.65	416.1	0.287	−1.32	−1.79	0.33	0.267
CO	−2.32	332.8	0.15	−1.97	−2.14	0.35	0.149
CU	−1.47	290.3	0.257	−1.1	−1.25	0.37	0.116
RE	−1.69	515.5	0.26	−1.51	−1.65	0.18	0.191
TI	−1.82	505.3	0.256	−1.6	−1.71	0.22	0.156
H mean	−1.79	412.0	0.242	−1.50	−1.71	0.29	0.176
AU	−0.86	532.9	0.326	−0.94	−	−0.08	0.583
ES	−1.15	517.5	0.402	−1.04	−1.42	0.11	0.378
HI	−1.23	531.5	0.281	−1.39	−1.51	−0.16	0.541
RA	−1.44	550.9	0.412	−1.48	−2.17	−0.04	0.529
SE	−1.52	666.2	0.437	−1.48	−2.1	0.04	0.462
NH mean	−1.24	559.8	0.372	−1.27	−	−0.03	0.499

'**', '*' and 'NS' following a parameter indicate statistical difference between H and NH growth forms at $P < 0.01$, $0.01 \leq P < 0.05$, and $P \geq 0.05$ level respectively (one-way ANOVA).

tion). H species had 50% larger LMA values than NH species, which resulted from their greater leaf thickness, as leaf dry mass density did not differ between growth forms (Table 2).

The NH species had anatomical traits indicating capacity for higher leaf water flux rates. The NH species had 30% larger vessel lumen diameters (D_v) than H species ($P < 0.01$; Table 2), although the number of vessels per petiole, normalized by leaf area, did not differ between growth forms (1.69 and 2.65 cm^{-2} respectively; $P = 0.12$). The K_t value of NH species was on average 104% higher than that of H species ($P < 0.05$, one-way ANOVA; Table 2).

The growth forms also differed strongly in maximum stomatal conductance (g_{max}) and in the response of g_s to decline of leaf water potential. NH species had higher g_{max} and higher turgor loss points (π^0) than H species (Table 3). The leaf water potential at which g_s fell to 50% and 20% of maximum values ($\Psi_{gs50\%}$ and $\Psi_{gs20\%}$) did not differ between H and NH species (Table 3). However, at turgor loss point, H species had stronger stomatal closure than NH species. In H species, g_s had been reduced nearly to its minimum value at turgor loss point (Fig. 2a–e), whereas in NH species, g_s remained around 50% of g_{max} even after turgor loss (Fig. 2f–j). Thus, in H species, $\Psi_{gs50\%}$ were 0.18 to 0.37 MPa higher than π^0, while in NH species, $\Psi_{gs50\%}$ were lower than π^0 in three of five species and in the other two species, *F. esquiroliana* and *F. racemosa*, $\Psi_{gs50\%}$ was only 0.11 and 0.04 MPa higher than π^0 respectively.

Leaves of H species were much more resistant to water loss after excision than those of NH species. NH species had on average four times higher g_{min} than H species (10.7 and 2.1 mmol m^{-2} s^{-1} respectively; Table 2). The T_{70} for H species (17.2 h) was on average ten times that for NH species (1.7 h; Table 2). For two H species (*F. benjamina* and *F. curtipes*), T_{70} was 32.7 and 36.1 h respec-

tively, several times longer than for the other species (Table 2). Several factors can affect the water loss from excised leaves and thus would influence the T_{70}; these include the length of time that the stomata remain open, their rate of closure and the rate of water loss after stomatal closure. Thus, all else being equal, a higher g_{max} should reduce T_{70}, while faster stomatal closure with leaf desiccation and a lower g_{min} should increase T_{70}. Analyses of correlations between T_{70} and these possible underlying traits showed that T_{70} was uncorrelated with g_{max} (Fig. 3a), but was negatively correlated with $g_{s\text{-}TLP}/g_{max}$ (where low values represent early effective stomatal closure during desiccation) and negatively correlated with g_{min} (Fig. 3b,c).

Traits related to xylem water supply and transpiratory demand were coordinated (Table S2). Among the 19 tested leaf traits, there were 46 significant correlations of 171 tested (27%), greater than the 5% to be expected due to chance ($P < 0.001$, proportion test), indicating a significant tendency for functional trait coordination. Thus, K_t was positively correlated with D_v, g_{max} (with the exception of outlier *F. hispida*) and $g_{s\text{-}TLP}/g_{max}$ (Fig. 4a–c). Negative correlations of leaf water flux traits and drought tolerance traits were also found across species of the two life forms. Across species, K_t and D_v were negatively correlated with T_{70}, and K_t was negatively correlated with the difference between $\Psi_{gs50\%}$ and π^0 ($\Psi_{gs50\%}-\pi^0$; Fig. 5a,b,c). These correlations indicated that leaves of species with lower hydraulic conductivity tended to desiccate more slowly after excision because of lower cuticle and stomatal leakiness and wider safety margins, such that stomata closed earlier during desiccation, even before turgor loss. The $g_{s\text{-}TLP}/g_{max}$ and π^0 were positively correlated across species with H species and NH species segregated along the regression line (Fig. 5d).

Hemiepiphytic
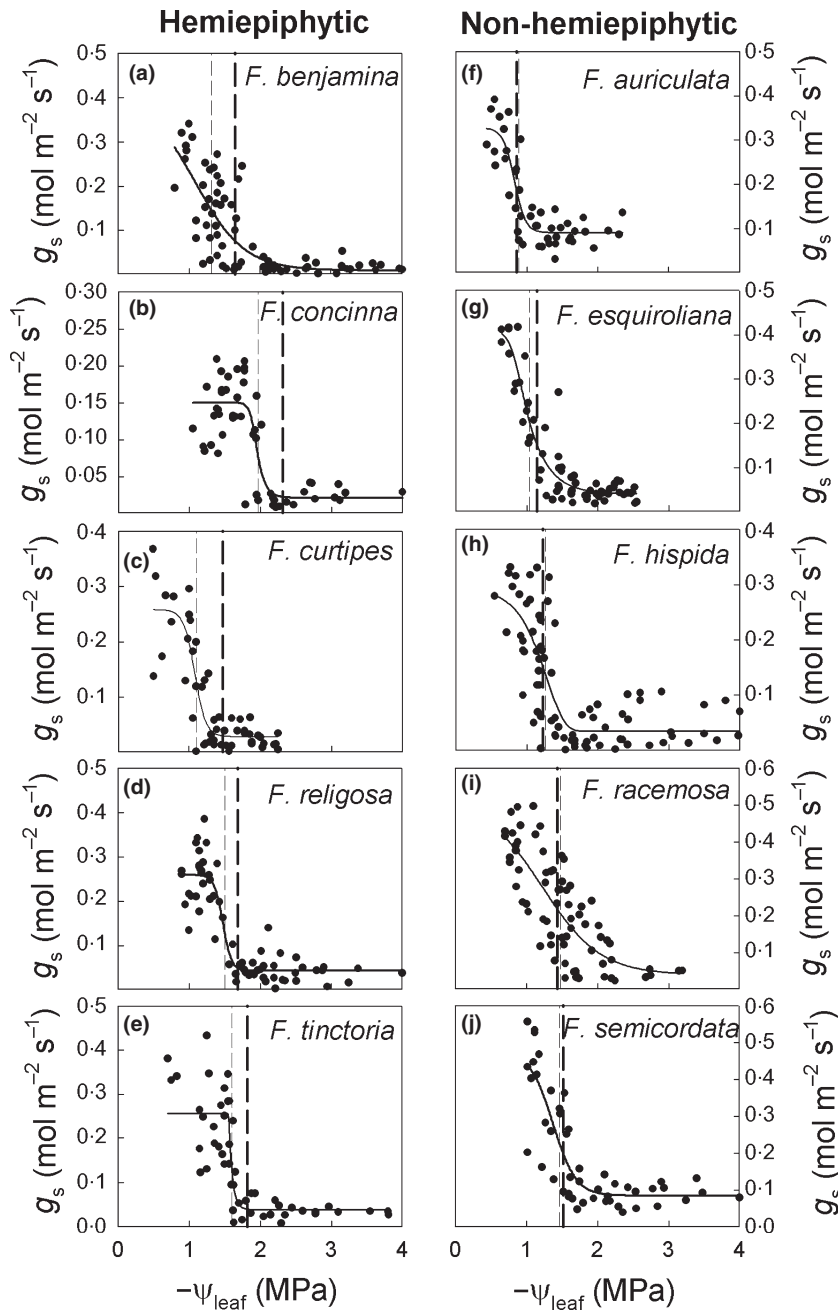
Non-hemiepiphytic

Fig. 2. Stomatal conductance (g_s) in response to declining leaf water potential (Ψ_l) in five hemiepiphytic (a to e) and five non-hemiepiphytic (f to j) *Ficus* species. A sigmoid function was fitted to the data (y = a/(1 + exp(−(x−x$_0$)/b))). Vertical dashed lines show Ψ_l at 50% of maximum g_s and the heavy dashed lines show Ψ_l at turgor loss.

Discussion

### TRAITS LINKED WITH MAXIMUM WATER FLUX THROUGH THE LEAF

We found strong differences between H and NH species, such that H species had lower values for leaf water flux-related traits. These findings parallel the earlier finding that hemiepiphytes tend to have lower hydraulic conductivity in stems (Patiño, Tyree & Herre 1995; Zotz, Patiño & Tyree 1997). The higher D_v, K_t, g_{max}, C_{leaf} and $g_{s\text{-}TLP}/g_{max}$ all support NH having higher leaf water flux rates than H species, which would support higher gas exchange and, for a given level of leaf allocation, higher relative growth rates (Sack & Holbrook 2006). Indeed, our greenhouse growth experiment

showed seedlings of NH species to have higher growth rates than H species (Guang-You Hao, unpublished data).

The lower values for flux-related traits in H species are consistent with a lower requirement for water per unit leaf area. Indeed, just as H species had lower g_{max} compared with NH species (Table 3), midmorning measurements of gas exchange showed that H species had lower g_s and higher intrinsic water use efficiencies (net CO_2 assimilation/g_s) than NH species (Guang-You Hao, unpublished data). Higher C_{leaf} in NH species may be important for buffering higher rates of water flux to minimize transient fluctuations in mesophyll water potential, as reported for temperate woody species (Sack *et al.* 2003) and as has been indicated also as a function for capacitance in wood (Meinzer *et al.* 2009). The correlation between C_{leaf} and K_t (see Table S2) may explain
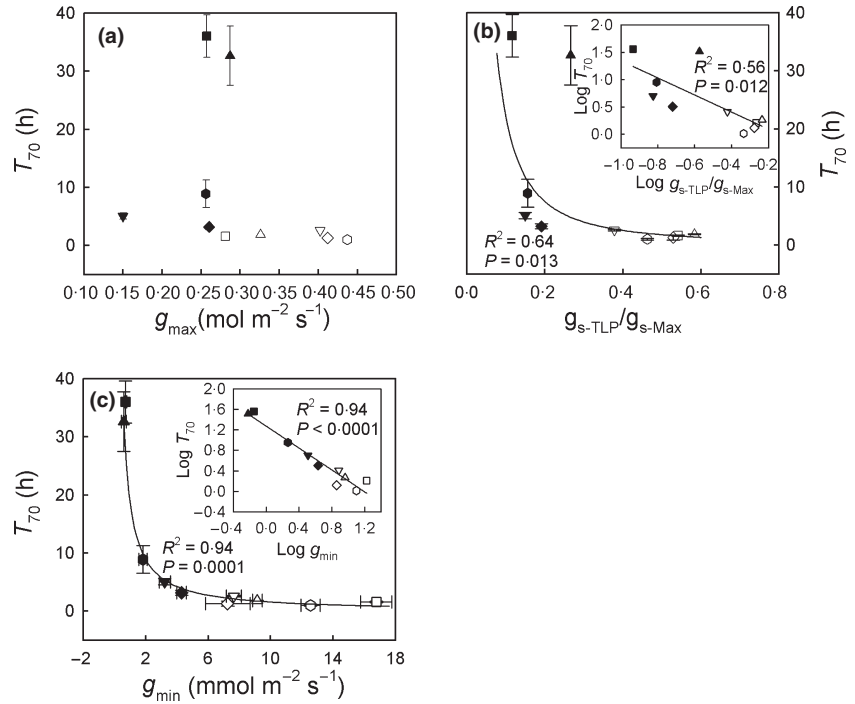
Fig. 3. Correlations between time required for a saturated leaf to decline to a relative water content of 70% (T_{70}) and (a) maximum stomatal conductance (g_{max}), (b) ratio of stomatal conductance at turgor loss point to g_{max} ($g_{s\text{-}TLP}/g_{max}$), (c) leaf epidermal conductance (g_{min}) across five hemiepiphytic (H; filled symbols) and five non-hemiepiphytic (NH; open symbols) *Ficus* species. Data in plots b and c were fitted with power functions ($y = ax^b$) and the insets show linear regressions fitted to log$_{10}$-transformed data. *Ficus benjamina* (▲), *F. concinna* (▼), *F. curtipes* (■), *F. religosa* (◆), *F. tinctoria* (⬟), *F. auriculata* (△), *F. esquiroliana* (▽), *F. hispida* (□), *F. racemosa* (◇), *F. semicordata* (◖).
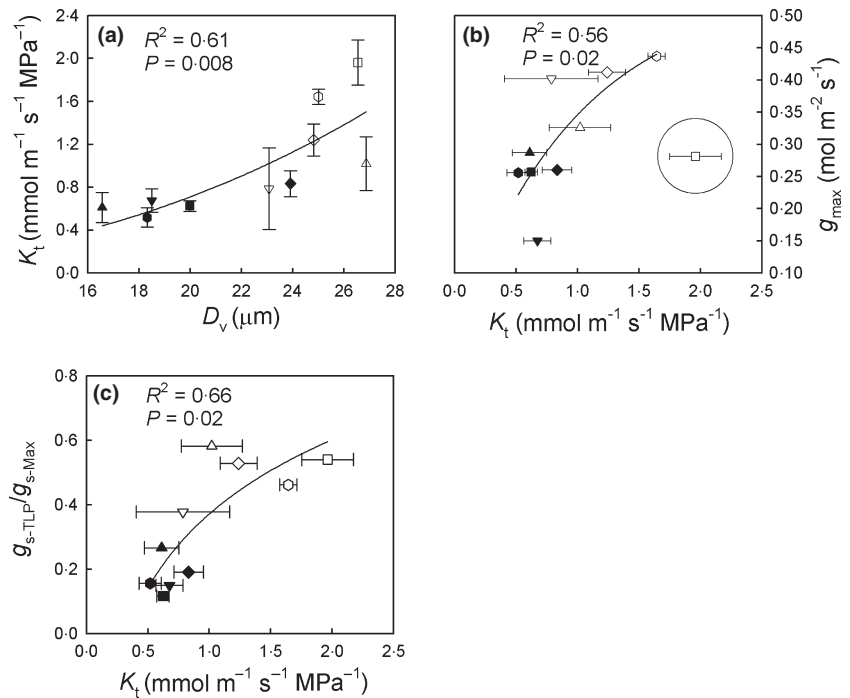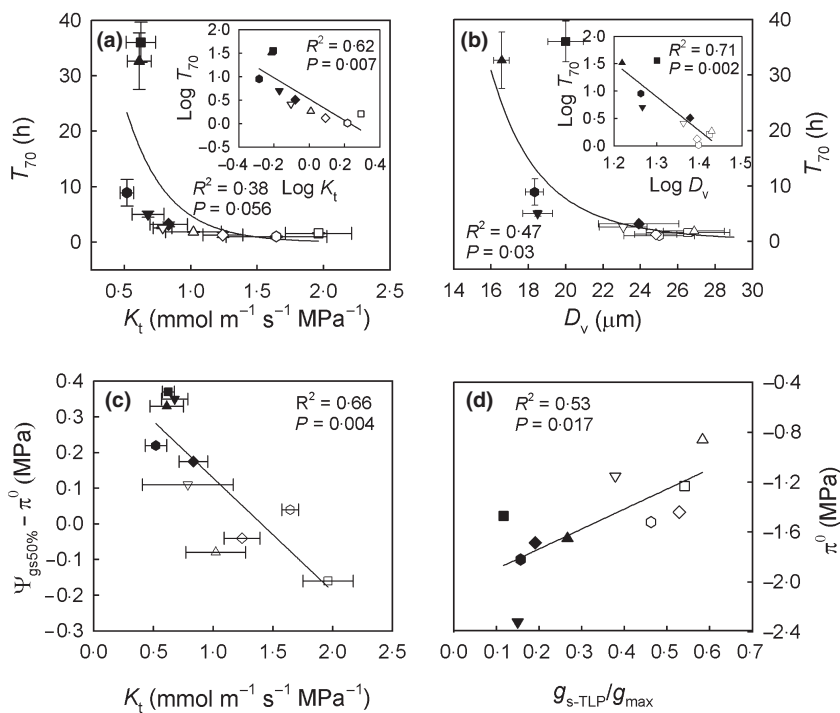

Fig. 4. (a) Relationship between average vessel lumen diameter in leaf petiole (D_v) and petiole theoretical hydraulic conductivity (K_t); (b) relationship between K_t and maximum stomatal conductance (g_{max}); (c) relationship between K_t and ratio of stomatal conductance at turgor loss point to g_{max} ($g_{s\text{-}TLP}/g_{max}$) across five hemiepiphytic (H; filled symbols) and five non-hemiepiphytic (NH; open symbols) *Ficus* species. Data were fitted using power functions ($y = ax^b$ for a and b; $y = -y_0 + ax^b$ for c). In plot b, outlier *F. hispida* was excluded from the regression (the circled symbol). Symbols are as defined in Fig. 3.

the finding that excised leaves of higher leaf hydraulic conductance close their stomata relatively slowly (Aasamaa & Sober 2001; Sack *et al.* 2003). In our study too, NH species had higher C_{leaf} and weaker stomatal control of water loss during leaf desiccation than H species.

The differences between H and NH species extend the finding that species adapted to different environments tend to differ in a cluster of flux-related traits (Sack *et al.* 2003; Sack, Tyree & Holbrook 2005; Dunbar-Co, Sporck & Sack 2009). These traits probably contribute to NH species having greater water and nutrient transport efficiencies and a higher potential growth capacity per investment in leaf mass (Sack & Holbrook 2006; Brodribb, Field & Jordan 2007). Thus, the differences in leaf flux-related traits between H and NH species may underlie the NH species' having higher photosynthetic capacity per investment in leaf dry mass (Guang-You Hao, unpublished).

Fig. 5. (a) Correlations between the time required for a saturated leaf to decline to a relative water content of 70% (T_{70}) and theoretical petiole hydraulic conductivity (K_t); (b) between T_{70} and average vessel lumen diameter (D_v) in petiole xylem; (c) between the difference in leaf water potential from 50% of maximum stomatal conductance to turgor loss point ($\Psi_{gs50\%} - \pi^0$) and K_t; (d) between the ratio of stomatal conductance at turgor loss point to maximum stomatal conductance ($g_{s\text{-TLP}}/g_{max}$) and turgor loss point (π^0) across five hemiepiphytic (H; filled symbols) and five non-hemiepiphytic (NH; open symbols) *Ficus* species. Data in plots a and b were fitted with power functions ($y = ax^b$); the insets show linear regressions fitted to $\log_{10}$-transformed data. Data in plots c and d were fitted with a linear regression. Symbols are as defined in (Fig. 3).

TRAITS CONFERRING DROUGHT TOLERANCE

We found H species to possess traits linked with greater drought tolerance than NH species. H species had higher LMA (Table 2), typical of adaptation to drier environments (Hoffmann *et al.* 2005; Hao *et al.* 2008; Poorter *et al.* 2009), as well as thicker epidermises (Table S1). The densely arranged multi-layered epidermal cells in H species, while not contributing to a higher C_{leaf}, may play a role in localized water transfer or may slow the rate of water loss from inner mesophyll cells.

The H species reduced their g_s to minimum values at π^0 (Fig. 2a–e), while all the NH species kept g_s at relatively high values even when Ψ_l dropped below π^0 (Fig. 2f–j). Such a narrow 'safety margin' between stomatal closure and turgor loss point can benefit plants by allowing the maintenance of gas exchange and thus optimizing return on xylem investment (Brodribb & Holbrook 2004). In contrast, the effective stomatal closure in H species is consistent with a conservative water use that would reduce the risk of catastrophic hydraulic failure under drought stress (Brodribb & Holbrook 2004).

The H species did not only exhibit earlier stomatal closure in response to leaf desiccation, but they were also more efficient in preventing water losses after stomata had closed. This mechanism may confer a greater ability to persist during severe drought. The strong correlations of T_{70} with both $g_{s\text{-TLP}}/g_{s\text{-Max}}$ and g_{min} across species (Fig. 3b,c) indicated that leaf desiccation avoidance was determined by both the stomatal response to water deficits and water retention after stomata closure, which relates to the resistance to water loss of cuticle and closed stomata (Muchow & Sinclair 1989; Holbrook & Putz 1996b). Notably, the H

species had more negative π^0, consistent with greater drought tolerance, but their C_{leaf} was also lower (Table 3). Consequently, the product of the two parameters ($\pi^0 \times C_{leaf}$), which represents the amount of water released per unit area between saturation and turgor loss point, did not differ statistically between the two groups ($P = 0.81$, one-way ANOVA; mean values were -735 and -703 mmol m^{-2} respectively). Thus, the absolute amount of stored water per leaf area does not contribute to the greater drought tolerance of H species. However, because of their tighter stomatal control and lower cuticular conductance, H species are probably better able to preserve turgor and hydration during drought. These findings are consistent with field observations of frequent wilting and dieback for NH, but not H species during the peak of dry seasons.

IMPORTANCE OF TRAIT DIFFERENCES BETWEEN H AND NH SPECIES

The H and NH growth forms differed strongly in leaf traits influencing water transport and use. The NH species had higher xylem water transport capacity, associated with their larger vessels and these species also showed weaker stomatal control of water loss. In contrast, H species had lower xylem water transport capacity, but tighter stomatal control and greater ability of leaves to persist under drought. Thus, across species traits related to leaf water flux were negatively correlated with those of drought tolerance. Our finding of a negative relationship of maximum flux-related traits and drought tolerance traits for H and NH species seems analogous to the trade-off between hydraulic conductivity and xylem cavitation resistance in stems (Martinez-Vilalta *et al.* 2002). Such a

trade-off may affect the distribution of species: species distributed in relatively wet environments are usually more vulnerable to xylem embolism than species adapted to dry environments (Maherali, Pockman & Jackson 2004). The existence of a trade-off between the ability to cope with water stress and the ability to grow at high rates under more favourable water conditions can partially explain why drought-tolerant plant species are displaced from mesic and humid habitats (Orians & Solbrig 1977). The higher growth rates of plants dominating more humid environments compared with species subject to frequent drought may be partially explained by their higher hydraulic conductivity that affects the uptake of water from the soil, higher stomatal conductance and higher CO_2 assimilation rates (Salleo *et al.* 2000; Santiago *et al.* 2004). However, we note that the negative correlation across species between hydraulic conductivity and xylem cavitation resistance is not always found (Bhaskar, Valiente-Banuet & Ackerly 2007; Chen *et al.* 2009), and thus is not necessarily intrinsic or necessary, but may typically arise because of contrasting selection scenarios. For instance, there may be selection of high water flux and low drought tolerance in moist environments, where high assimilation rates would repay the investment in constructing xylem of high conductivity. On the other hand, there may be selection for low water flux and high drought tolerance in chronically dry environments, where investment in high conductivity would not be repaid. Such co-selection of traits may also explain the clustering of flux-related traits and drought-tolerance traits in H and NH species, and their negative correlation with each other. We note that a negative correlation of flux traits and drought tolerance traits was not found across phylogenetically diverse species (Sack *et al.* 2003), and thus may not necessarily arise from any intrinsic genetic or structural trade-off. The negative correlation of these traits would arise within a single genus because of contrasting adaptation, given that high flux and low drought tolerance is advantageous for NH species, and low flux and high drought tolerance is advantageous for H species.

In H species, an epiphytic growth stage that is frequently exposed to water deficits is associated with xylem composed of smaller vessels, with lower hydraulic transport efficiency, which persists even in the terrestrial growth stage. The divergences in hydraulics between H and NH species are analogous to the differences between xeric and humid-grown species (Bhaskar, Valiente-Banuet & Ackerly 2007), indicating that species within a single genus, which co-exist in the same community, can diverge significantly in numerous aspects of leaf structure and function, according to their micro-habitat in the regeneration phase. Having the epiphytic growth habit at the beginning of their life history enables H species to regenerate successfully in the canopy of dense forests with extremely shaded understory (Harrison *et al.* 2003). In contrast, the regeneration of NH species in dense rainforests depends on the formation of high irradiance forest gaps; for these species, a higher xylem water transport efficiency would enable higher rates of carbon assimilation and growth rates and thus greater competitiveness in resource acquisition, given a reliable water supply and high irradiance (Brodribb, Holbrook & Gutierrez 2002; Santiago *et al.* 2004; Brodribb *et al.* 2005; Zhang & Cao 2009).

Conclusions

The two growth forms of *Ficus* are consistent with the generalized contrasting types of plant water use according to Passioura (1982). The H species have leaf traits conferring conservative water use, of particular advantage to plants growing under dry environmental conditions, whereas the NH species show leaf traits conferring prodigal water use that would be advantageous under competitive situations (Heilmeier *et al.* 2002). The patterns identified in this study indicated that the existence of an epiphytic habit during the juvenile stage in H species involved a suite of leaf water flux and drought tolerance traits of functional importance, contrasting with those of congeneric NH species, which persist to a large degree in the terrestrially rooted adults.

Acknowledgements

References

Aasamaa, K. & Sober, A. (2001) Hydraulic conductance and stomatal sensitivity to changes of leaf water status in six deciduous tree species. *Biologia Plantarum*, **44**, 65–73.

Aasamaa, K., Sober, A. & Rahi, M. (2001) Leaf anatomical characteristics associated with root hydraulic conductance, stomatal conductance and stomatal sensitivity to changes of leaf water status in temperate deciduous trees. *Australian Journal of Plant Physiology*, **28**, 765–774.

Berg, C.C. & Corner, E.J.H. (2005) Moraceae — *Ficus. Flora Malesiana Series I (Seed Plants)* (ed. H.P. Nooteboom), pp. 1–625, volume 17, part 2. National Herbarium of the Netherlands, Leiden.

Bhaskar, R., Valiente-Banuet, A. & Ackerly, D.D. (2007) Evolution of hydraulic traits in closely related species pairs from mediterranean and nonmediterranean environments of North America. *New Phytologist*, **176**, 718–726.

Brodribb, T.J. & Cochard, H. (2009) Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiology*, **149**, 575–584.

Brodribb, T.J., Field, T.S. & Jordan, G.J. (2007) Leaf maximum photosynthetic rate and venation are linked by hydraulics. *Plant Physiology*, **144**, 1890–1898.

Brodribb, T.J. & Holbrook, N.M. (2003) Stomatal closure during leaf dehydration, correlations with other leaf physiological traits. *Plant Physiology*, **132**, 2166–2173.

Brodribb, T.J. & Holbrook, N.M. (2004) Stomatal protection against hydraulic failure: a comparison of coexisting ferns and angiosperms. *New Phytologist*, **162**, 663–670.

Brodribb, T.J., Holbrook, N.M. & Gutierrez, M.V. (2002) Hydraulic and photosynthetic coordination in seasonally dry tropical forest trees. *Plant, Cell and Environment*, **25**, 1435–1444.

Brodribb, T.J., Holbrook, N.M., Zwieniecki, M.A. & Palma, B. (2005) Leaf hydraulic capacity in ferns, conifers and angiosperms: impacts on photosynthetic maxima. *New Phytologist*, **165**, 839–846.

Chen, J.-W., Zhang, Q., Li, X.-S. & Cao, K.-F. (2009) Independence of stem and leaf hydraulic traits in six Euphorbiaceae tree species with contrasting leaf phenology. *Planta*, **230**, 459–468.

Cochard, H., Nardini, A. & Coll, L. (2004) Hydraulic architecture of leaf blades: where is the main resistance? *Plant, Cell and Environment*, **27**, 1257–1267.

Dobzhansky, T. & Murca-Pires, B.J. (1954) Strangler trees. *Scientific American*, **190**, 78–80.

Dunbar-Co, S., Sporck, M.J. & Sack, L. (2009) Leaf trait diversification and design in seven rare taxa of the Hawaiian *Plantago* radiation. *International Journal of Plant Sciences*, **170**, 61–75.

Edwards, E.J. (2006) Correlated evolution of stem and leaf hydraulic traits in *Pereskia* (Cactaceae). *New Phytologist*, **172**, 479–489.

Garcia, L.V. (2003) Controlling the false discovery rate in ecological research. *Trends in Ecology and Evolution*, **18**, 553–554.

Givnish, T.J. (1987) Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist*, **106** (Suppl.), 131–160.

Givnish, T.J., Montgomery, R.A. & Goldstein, G. (2004) Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points. *American Journal of Botany*, **91**, 228–246.

Hao, G.-Y., Hoffmann, W.A., Scholz, F.G., Bucci, S.J., Meinzer, F.C., Franco, A.C., Cao, K.-F. & Goldstein, G. (2008) Stem and leaf hydraulics of congeneric tree species from adjacent tropical savanna and forest ecosystems. *Oecologia*, **155**, 405–415.

Harrison, R.D. (2005) Figs and the diversity of tropical rainforests. *BioScience*, **55**, 1053–1064.

Harrison, R.D., Hamid, A.A., Kenta, T., Lafrankie, J., Lee, H.-S., Nagamasu, H., Nakashizuka, T. & Palmiotto, P. (2003) The diversity of hemi-epiphytic figs (*Ficus*, Moraceae) in a Bornean lowland rain forest. *Biological Journal of Linnean Society*, **78**, 439–455.

Heilmeier, H., Wartinger, A., Erhard, M., Zimmermann, R., Horn, R. & Schulze, E.-D. (2002) Soil drought increases leaf and whole-plant water use of *Prunus dulcis* grown in the Negev Desert. *Oecologia*, **130**, 329–336.

Hoffmann, W.A., Franco, A.C., Moreira, M.Z. & Haridasan, M. (2005) Specific leaf area explains differences in leaf traits between congeneric savanna and forest trees. *Functional Ecology*, **19**, 932–940.

Holbrook, N.M. & Putz, F.E. (1996a) Water relations of epiphytic and terrestrially-rooted strangler figs in a Venezuelan palm savanna. *Oecologia*, **106**, 424–431.

Holbrook, N.M. & Putz, F.E. (1996b) From epiphyte to tree: differences in leaf structure and leaf water relations associated with the transition in growth form in eight species of hemiepiphytes. *Plant, Cell and Environment*, **19**, 631–642.

Koide, R.T., Robichaux, R.H., Morse, S.R. & Smith, C.M. (1991) Plant water status, hydraulic resistance and capacitance. *Plant Physiological Ecology* (eds R.W. Pearcy, J. Ehleringer, H.A. Mooney & P.W. Rundel). pp. 161–183, Chapman and Hall, New York.

Lawlor, D.W. & Cornic, G. (2002) Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant, Cell and Enviormnent*, **25**, 275–295.

Lewis, A.M. & Boose, E.R. (1995) Estimating volume flow rates through xylem conduits. *American Journal of Botany*, **82**, 1112–1116.

Maherali, H., Pockman, W.T. & Jackson, R.B. (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology*, **85**, 2184–2199.

Martinez-Vilalta, J., Prat, E., Oliveras, I. & Josep, P. (2002) Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia*, **133**, 19–29.

Meinzer, F.C., Johnson, D.M., Lachenbruch, B., McCulloh, K.A. & Woodruff, D.R. (2009) Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology*, **23**, 922–930.

Moran, M.D. (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos*, **100**, 403–405.

Muchow, R.C. & Sinclair, T.R. (1989) Epidermal conductance, stomatal density and stomatal size among genotypes of *Sorghum bicolour* (L.) Moench. *Plant, Cell and Environment*, **12**, 425–432.

Nardini, A. & Salleo, S. (2000) Limitation of stomatal conductance by hydraulic traits: sensing or preventing xylem cavitation? *Trees*, **15**, 14–24.

Orians, G. & Solbrig, O. (1977) A cost-income model of leaves and roots with special reference to arid and semiarid areas. *American Naturalist*, **111**, 677–690.

Passioura, J. (1982) *Water in the Soil-Plant-Atmosphere Continuum*. Springer, New York.

Patiño, S., Tyree, M.T. & Herre, E.A. (1995) Comparison of hydraulic architecture of woody plants of differing phylogeny and growth form with special reference to free-standing and hemi-epiphytic *Ficus* species from Panama. *New Phytologist*, **129**, 125–134.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist*, **182**, 565–588.

Putz, F.E. & Holbrook, N.M. (1986) Notes on the natural history of hemiepiphytes. *Selbyana*, **9**, 61–69.

Reich, P.B., Tilman, D., Naeem, S., Ellsworth, D.S., Knops, J., Craine, J., Wedin, D. & Trost, J. (2004) Species and functional group diversity independently influence biomass accumulation and its response to CO_2 and N. *Proceedings of the National Academy of Sciences*, **101**, 10101–10106.

Sack, L. & Frole, K. (2006) Leaf structural diversity is related to hydraulic capacity in tropical rainforest trees. *Ecology*, **87**, 483–491.

Sack, L. & Holbrook, N.M. (2006) Leaf hydraulics. *Annual Review of Plant Biology*, **57**, 361–381.

Sack, L., Tyree, M.T. & Holbrook, N.M. (2005) Leaf hydraulic architecture correlates with regeneration irradiance in tropical rainforest trees. *New Phytologist*, **167**, 403–413.

Sack, L., Melcher, P.J., Zwieniecki, M.A. & Holbrook, N.M. (2002) The hydraulic conductance of the angiosperm leaf lamina: a comparison of three measurement methods. *Journal of Experimental Botany*, **53**, 2177–2184.

Sack, L., Cowan, P.D., Jaikumar, N. & Holbrook, N.M. (2003) The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. *Plant, Cell and Environment*, **26**, 1343–1356.

Salleo, S., Nardini, A., Pitt, F. & Gullo, M.A.L. (2000) Xylem cavitation and hydraulic control of stomatal conductance in *Laurel* (*Laurus nobilis* L.). *Plant, Cell and Environment*, **23**, 71–79.

Santiago, L.S., Goldstein, G., Meinzer, F.C., Fisher, J.B., Machado, K., Woodruff, D. & Jones, T. (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia*, **140**, 543–550.

Tyree, M.T. & Hammel, H.T. (1972) The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *Journal of Experimental Botany*, **23**, 267–282.

Veneklaas, E.J., Zagt, R.J., Van Leerdam, A., Van Ek, R., Broekhoven, A.J. & Van Genderen, M. (1990) Hydrological properties of the epiphyte mass of a montane tropical rain forest, Colombia. *Vegetatio*, **89**, 183–192.

Waite, M. & Sack, L. (2010) How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. *New Phytologist*, **185**, 156–172.

Williams-Linera, G. & Lawton, R. (1995) The ecology of hemiepiphytes in forest canopies. *Forest Canopies* (eds M.D. Lowman & N.M. Nadkarni). pp. 255–282, Academic Press, San Diego.

Wu, C.-Y. & Raven, P.H. (2003) *Ficus*. Flora of China (eds C.-Y. Wu & P.H. Raven), vol **5**, pp. 37–71. Science Press and Missouri Botanical Garden Press, Beijing and St Louis.

Zhang, J.-L. & Cao, K.-F. (2009) Stem hydraulics mediates leaf water status, carbon gain, nutrient use efficiencies and plant growth rates across dipterocarp species. *Functional Ecology*, **23**, 658–667.

Zotz, G., Patiño, S. & Tyree, T.T. (1997) Water relations and hydraulic architecture of woody hemiepiphytes. *Journal of Experimental Botany*, **48**, 1825–1833.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Thickness of leaf lamina tissues in transverse sections.

Table S2. Pearson correlation coefficient (r) for leaf trait relationships for 10 *Ficus* species.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.