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Leaf water use in heterobaric and homobaric leafed canopy tree species in a Malaysian tropical rain forest

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Abstract

Tropical canopy tree species can be classified into two types by their heterobaric and homobaric leaves. We studied the relation between both leaf types and their water use, together with the morphological characteristics of leaves and xylem, in 23 canopy species in a tropical rain forest. The maximum rates of photosynthesis and transpiration were significantly higher in heterobaric leaf species, which also underwent larger diurnal variations of leaf water potential compared to homobaric leaf species. The vessel diameter was significantly larger and the stomatal pore index (SPI) was significantly higher in heterobaric than that in homobaric leaf species. There was a significant positive correlation between the vessel diameter, SPI, and maximum transpiration rates in all the studied species of both leaf types. However, there was no significant difference in other properties, such as leaf water-use efficiency, leaf mass per area, leaf nitrogen content, and leaf δ^{13}C between heterobaric and homobaric leaf species. Our results indicate that leaf and xylem morphological differences between heterobaric and homobaric leaf species are closely related to leaf water-use characteristics, even in the same habitat: heterobaric leaf species achieved a high carbon gain with large water use under strong light conditions, whereas homobaric leaf species can maintain a high leaf water potential even at midday as a result of low water use in the canopy environment.

Additional key words: bundle-sheath extension; Dipterocarpaceae; gas exchange; leaf morphology; wood density.

Introduction

Plant leaves display diverse structural and physiological traits, within and among species, in order to cope with a very wide range of environmental conditions (Sack and Frole 2006, Liakoura *et al.* 2009, Brodribb *et al.* 2013). In particular, tropical rain forests have a highly complex and multilayered vertical structure (Whitmore 1998), giving rise to great variations in light availability and vapor pressure deficit (VPD) with height (Yoda 1974, Kimmins 1997, Kenzo *et al.* 2006, 2007; Zach *et al.* 2010). We can predict, as a result, that tropical trees will have large inter- and intraspecific differences in physiological capacity and structural features, and that these differences are important in determining tree life forms in tropical rain forests. Previous studies have found that tropical canopy and emergent trees achieve a high photosynthetic capacity by developing a leaf mesophyll structure that adjusts to the tropical forest canopy environment of strong irradiance and high temperature (Kenzo *et al.* 2004, 2006). Understory species with a low stomatal density and low leaf mass per area (LMA) show a low photosynthetic

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Abbreviations: BSE – bundle-sheath extension; DBH – stem diameter at breast height; D_v – vessel diameter; E_{max} – maximum transpiration rate; GCL – guard cell length; g_s – stomatal conductance at P_{max}; LMA – leaf mass per area; N_{area} – nitrogen per unit leaf area; N_{mass} – mass-based leaf nitrogen concentration; PIC – phylogenetically independent contrast; P_{max} – maximum photosynthetic rate; PNUE – the ratio of CO_2 assimilation rate to leaf organic nitrogen content; RGR – relative growth rate; SD – stomatal density; SPI – stomatal pore index; V_d – vessel density; VPD – vapor pressure deficit; W_d – wood density; WUE – intrinsic water-use efficiency; δ^{13}C – stable carbon isotope ratio; $\Delta\Psi_L$ – diurnal variation in the leaf water potential; Ψ_{mid} – leaf water potential at midday; Ψ_{pd} – leaf water potential at predawn.

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capacity, but they can adapt to the light-limited understory because they have low photosynthetic light compensation points (Yáñez-Espinosa *et al*. 2003, Kenzo *et al*. 2006).

Other anatomical traits, such as whether bundle-sheath extensions (BSE) are found in the leaf, may be further factors in determining the tree distribution in tropical rain forests. Kenzo *et al*. (2007) reported that heterobaric leaf species, which had BSE in the leaf, were distributed mainly in environments of high irradiance and drought, such as the canopy, emergent layers, and gaps in a forest; in contrast, homobaric leaf species, which had no BSE in their leaves, were found in shady and moist environments such as the forest floor. Heterobaric leaf species can undergo patchy stomatal closure under drought conditions (Hiromi *et al.* 1999, Jones 1999, Beyschlag and Eckstein 2001, West *et al*. 2005, Takanashi *et al*. 2006, Mott and Peak 2007, Kamakura *et al*. 2011), because the mesophyll of the heterobaric leaf is separated into many small bundle-sheath extension compartments by BSE (Terashima 1992). Heterobaric leaf species also show higher photosynthetic capacity per unit of leaf mass than homobaric leaf species (Liakoura *et al*. 2009). Furthermore, lack of BSE in homobaric leaves may improve their ability to exploit available sunflecks, because lateral CO_2 diffusion from shaded to illuminated areas of leaves enhances photosynthesis (Lawson and Morison 2006, Pieruschka *et al*. 2006, 2008, 2010; Morison *et al*. 2007). Homobaric leaves also increase the proportion of their leaf area that is photosynthetically active (Terashima 1992). Nevertheless, according to Kenzo *et al*. (2007), more than half of the species in the canopy layer of a tropical rain forest possess homobaric leaves despite the high irradiance and drought environment. How do heterobaric and homobaric leaf species adapt to the canopy environment of strong water stress?

Differences of internal leaf anatomy may be closely related to the architecture of water conductive pathways, such as vessels and stomata, and in turn to the water supply within a tree. It is known that BSE may be an important route for water to run from minor veins to mesophyll and/or epidermis evaporation sites in the leaf (Wylie 1952, Sack *et al*. 2005, Sack and Frole 2006, Zwieniecki *et al*. 2007, Scoffoni *et al*. 2008, Boyce *et al*. 2009, Brodribb *et al*. 2010b, McKown *et al*. 2010, Walls 2011) and thus heterobaric leaf species with BSE may allow themselves larger water supply in the leaf than homobaric leaf species without BSE under canopy conditions. To support this water demand in the leaf, heterobaric leaf species might also need a large vessel diameter and/or high stomatal density, both of which have high hydraulic efficiency and then close link to high photosynthetic capacity in the leaf (Brodribb and Field 2000, Santiago *et al*. 2004, Zhang and Cao 2009, Tanaka *et al*. 2013). In contrast, homobaric leaf species without BSE would have their mesophyll and epidermis relatively hydraulically disconnected from the xylem, which is not efficient in utilizing the hydraulic system to maximize photosynthetic activity, and would tend to close stomata well before xylem pressures reach a ctitical stage (Zwieniecki *et al*. 2007). Therefore, homobaric leaf species may tend to have a small vessel diameter and/or low stomatal density to keep their conservative water use compared with heterobaric leaf species. In this study, we hypothesize that there are different strategies for water use with different morphological characteristics of leaf and xylem, such as vessel diameter and stomatal density, between heterobaric and homobaric leaf species even in the same canopy environment. To test our hypothesis, we examined physiological and morphological parameters related to leaf water use in 23 canopy or emergent tree species, of which 15 possessed heterobaric leaves and 8 had homobaric leaves, in a Bornean tropical rain forest.

Material and methods

Study site: Our study was conducted in lowland, mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°12'N, 114°00'E, 150–250 m a.s.l.). The mean canopy height of the stands was about 40 m; some emergent trees reached 50 m. Measurements were made at a 4-ha experimental plot (200 × 200 m). An 85-m-tall canopy crane with a 75-m-long rotating jib was constructed in the center of the plot, so as to provide access to the top of the canopy (Sakai *et al*. 2002). The emergent layer in the area accessed by the canopy crane (1.77 ha) was mostly occupied by Dipterocarpaceae (72% of all the individuals), but the canopy layer was shared by various families, such as Dipterocarpaceae (38%), Anacardiaceae (15%), Burseraceae (8%), Saporaceae (6%), and Myrtaceae (5%). In our study plot, the flora composition in emergent and canopy species was in the range of typical tropical rain forests in Borneo Island including canopy species (Ashton 2005). The study area has a humid tropical climate, with weak seasonal changes in rainfall and temperature (Kumagai and Kume 2012). The mean annual rainfall and temperature at Lambir Hills National Park from 2000–2009 were approximately 2,600 mm and 25.8°C, respectively (Kume *et al*. 2011). In the canopy and emergent layers, the daily maximum temperature and photosynthetic photon flux density were sometimes above 35°C and 2,000 μmol m^{-2} s^{-1}, respectively (Hiromi *et al*. 2012).

Plant material: We selected 42 individuals of 23 species, all of which were typical canopy or emergent species in the study plot. The species selected were those which had as many individuals as possible for measurement and nearly completely exposed crowns accessible by the canopy crane. These contained 26 individuals of 15 species having heterobaric leaves, and 16 individuals of 8 species having homobaric leaves (Table 1) according to Kenzo *et al.* (2007) classification of the leaf types. Only in two species, *Artocarpus obtusus* and *Swintonia sp*., which were out of the species list of Kenzo *et al*. (2007), we classified ourselves according to their leaf types by observing leaf transverse sections. Transverse slices were prepared by using a sliding microtome and observed with or without bundle sheath extensions with an optical microscope (*BIOPHOT*, *Nikon*, Japan).

Field measurements: We measured leaf maximum photosynthetic (P_{max}) and transpiration (E_{max}) rates and stomatal conductance at P_{max} (g_s) at light saturation and diurnal variations of leaf water potential at the top of the sun-exposed crown of each individual. All field measurements were performed at least once for each individual from July 2007 to October 2009, on days as clear as possible, although a totally cloudless day was very rare in the area and some overcast hours were included. Some microclimate factors, including solar radiation, air temperature, and relative humidity, were measured and recorded at the top of the canopy access crane during the study period (Kumagai *et al*. 2004, Kume *et al*. 2011). Vapor pressure deficits (VPD [kPa]) were calculated from measured air temperature and relative humidity according to Buck (1981). More details about meteorological measurements can be found in Kume *et al.* (2011).

Leaf gas-exchange parameters, such as P_{max}, E_{max}, and g_s, were measured by using a portable photosynthesis apparatus (*LI-6400*, *Li-Cor*, Lincoln, NE, USA). All measurements were made from 09:00 to 11:00 h, in order to avoid the midday depression in photosynthesis and transpiration (Ishida *et al*. 1996, Kenzo *et al*. 2003). In each tree specimen, we measured fully expanded and apparently nonsenescent leaves gathered from the top of the crown. The PPFD and CO_2 concentration in the chamber were 1,500 μmol(photon) m^{-2} s^{-1} and 360 ppm, respectively. The intrinsic water-use efficiency (WUE) was defined as the ratio of P_{max} to E_{max} (Buckley *et al*. 2002). It may cause overestimation of photosynthesis due to CO_2 diffusion in the homobaric leaf without bundle sheath extension, because the leaf was partly clamped by the clamp-on leaf chamber of *LI-6400* (Pieruschka *et al*. 2006). However, Pons and Welschen (2002) showed no effect of CO_2 diffusion in the homobaric leaf on photosynthesis measurement under high light conditions (PPFD of 1,200 μmol m^{-2} s^{-1}). Therefore, we measured leaf photosynthesis under high light conditions (PPFD of 1,500 μmol m^{-2} s^{-1}) to compare the differences in physiological ability *in situ* between homobaric and heterobaric leaf species.

Leaf water potential was measured in the field with a pressure chamber (*Model 1002*, *PMS Instruments*, USA), between 06:00 and 07:00 h (predawn, Ψ_{pd}) and between 12:00 and 14:00 h (midday, Ψ_{mid}). A total of 3–5 exposed shoots were excised from each individual with pruning shears, and immediately underwent measurement. Diurnal variation in the leaf water potential ($\Delta\Psi_L$) was defined as the difference between Ψ_{mid} and Ψ_{pd}.

Leaf morphological and chemical properties: We obtained six mature leaves from the canopy surface in

Table 1. List of tree species in a Malaysian lowland tropical rainforest, showing leaf type, number of individuals (*n*), and tree height. Height is mean ± SD. Hetero – heterobaric leaf tree, Homo – homobaric leaf tree.

Family	Species	*n*	Leaf type	Height [m]
Dipterocarpaceae	*Dipterocarpus globosus*	3	Hetero	43.5 ± 3.1
	Dryobalanops aromatica	3	Hetero	44.1 ± 4.7
	Shorea beccariana	3	Hetero	49.8 ± 2.4
	Shorea bullata	1	Hetero	38.4
	Shorea crassa	3	Hetero	42.2 ± 4.4
	Shorea kunstleri	1	Hetero	40.4
	Shorea laxa	1	Hetero	39.3
	Vatica oblongifolia	1	Hetero	35.7
Fagaceae	*Lithocarpus luteus*	1	Hetero	37.6
Leguminosae	*Koompassia malaccensis*	2	Hetero	46.0
	Sindora coriacea	1	Hetero	36.2
Magnoliaceae	*Magnolia ashtonii*	1	Hetero	37.7
Moraceae	*Artocarpus obtusus*	1	Hetero	38.7
Sapotaceae	*Madhuca crassipes*	3	Hetero	35.2 ± 0.9
	Palaquium sp.	1	Hetero	36.5
Anacardiaceae	*Swintonia acuta*	3	Homo	40.1 ± 2.9
	Swintonia sp.	3	Homo	43.7 ± 3.6
Clusiaceae	*Garcinia parvifolia*	1	Homo	34.4
Ctenolophonaceae	*Ctenolophon parvifolius*	1	Homo	41.3
Loganiaceae	*Fagraea caudata*	2	Homo	35.8
Myristicaceae	*Myristica gigantea*	1	Homo	41.5
Myrtaceae	*Syzygium* sp.	3	Homo	39.3 ± 1.7
Sapotaceae	*Madhuca sessilis*	2	Homo	35.0

each studied individual. Three of these were fixed in fixation medium (FAA, 40% formaldehyde:acetic acid: 70% ethanol, 2:1:17, v/v/v) for the observation of the stomatal traits; the others were used to determine leaf dry mass, nitrogen content, and stable carbon isotope composition ($\delta^{13}C$ [‰]).

To observe the stomatal traits, a replica of the abaxial surface of each collected leaf was made and observed by Suzuki's Universal Micro-Printing method, by using adhesive for the plastic model (Koike *et al.* 1998). These replicas were observed under an optical microscope (*BIOPHOT*, *Nikon*, Japan), and the length and density of stomata were measured. They were counted in three leaf areas of the microscopic field of view (0.2 × 0.3 mm) on each leaf. In species with hairy or papillate leaves, trichomes were removed from the leaves by a razor blade and their remnants were cleared off by sodium hypochlorite solution (a 50% solution of household bleach). When the leaves appeared transparent, the bleach solution was vacuumed off and they were rinsed several times in distilled water. The abaxial leaf surfaces of the cleared leaves could be directly observed under the optical microscope. The length and density of stomata were measured according to the same procedure as the Suzuki's Universal Micro-Printing method. We defined a stomatal length (guard cell length) as the distance in micrometers between the junctions of the guard cells at each end of the stoma (Xu and Zhou 2008). The stomatal pore index (SPI, a dimensionless index of stomatal pore area per lamina area), was calculated as (stomatal density) × (guard cell length)^2 on the abaxial surface of the lamina (Sack *et al.* 2003).

For measurement of leaf nitrogen and $\delta^{13}C$, the leaves were dried at 60°C for three days, and the leaf dry mass was measured. The leaves were ground to fine powder and then passed through a 250-mesh sieve (250 µm). Leaf nitrogen was measured by an NC analyzer (*SUMIGRAPH NC-95*, *Shimadzu*, Kyoto, Japan). The stable carbon isotope composition of the leaf samples was determined by using an isotope ratio mass spectrometer (*MAT252*, *Thermo Electron*, Bremen, Germany). The overall carbon isotope ratio was expressed in delta notation relative to the PD Belemnite standard: $\delta^{13}C\ [‰] = (R_{sample}/R_{standard} - 1) \times 1000$, where R_{sample} is the $^{13}C/^{12}C$ ratio of the sample, and $R_{standard}$ is the ratio of the standard (Tanaka-Oda *et al.* 2010).

Xylem structure and wood density: Using an increment borer (5.15 mm in diameter, *Haglof*, Langsele, Sweden), we obtained two wood core samples at breast height from all the individual specimens. We fixed one sample for microscopic analysis by FAA; the other was used to measure the wood density shortly after sampling. For microscopic analysis, we used a sliding microtome, and obtained segments of the radial side of the core from the outer layer of the cambium, 2–3 cm deep. This depth corresponds to the greatest sap flow velocity in the radial profile in some tropical rain forest trees (Kume *et al.* 2008). These segments were stained with a 1% fuchsin acid solution, and photographed by a digital camera (*DP12*, *Olympus*, Japan) connected to a stereomicroscope (*SZX12*, *Olympus*, Japan). Only three species, *Artocarpus obtusus*, *Koompassia malaccensis*, and *Lithocarpus luteus*, had their wood core polished by the sliding microtome, after which a transverse section of the wood core surface was directly photographed; this is because their stem was too hard for segments to be made. The images were analyzed by software (*Image J*, *National Institute of Health*, Bethesda, MD, USA) for estimation of the vessel diameter and density. A stage micrometer (resolution 10 µm) was used for scale reference. In estimating the vessel diameter, we measured at least 100 vessels per stem wood core. To determine the vessel density, an area of 15–40 mm^2 was chosen and the number of all vessels in this area was counted for each stem wood core. Stem samples for determining the wood density were oven-dried at 70°C for at least 3 d, and then weighed. The volume was calculated by measuring the diameter and the length of each core sample and assuming that the core was cylindrical (Osunkoya *et al.* 2007, Ishida *et al.* 2008).

Relative growth rate: The relative growth rates (RGR [% per year]) for stem diameter at breast height (DBH) of all the individuals were calculated as follows: $RGR = \{[\ln(DBH_{t+n}) - \ln(DBH_t)]/n\} \times 100$, where DBH_t is DBH in the year t, and it becomes DBH_n after n years (Nakagawa *et al.* 2000). DBH was calculated from tree census data; all trees in the study plot ≥ 10 cm in diameter at breast height (1.3 m above ground) were tagged and measured annually from 2000–2008 (Nakagawa *et al.* 2013).

Statistical analysis: After we checked the normality of all the parameters studied by *Shapiro-Wilk*'s test, one-way analysis of variance (*ANOVA*) and *Kruskal-Wallis* test were used to compare differences in each parameter studied between heterobaric and homobaric leaf species. Phylogenetically independent contrasts (PIC) were calculated by using the *APE* package for the *R* environment (Paradis *et al.* 2004). A phylogenetic tree was first constructed by using *PHYLOMATIC* (ver. 3) (Webb *et al.* 2008). Phylogenetic relationship of species belonging to Dipterocarpaceae was determined to dissolve polytomy of the phylogenetic tree according to Tsumura *et al.* (2011). Branch lengths of the phylogenetic tree were assigned by using the *BLADJ* function of *PHYLOCOM* (Webb *et al.* 2008). The correlation between the parameters was tested to consider the effect of phylogenetic bias on the studied species by *Pearson*'s cross-species and phylogenetically independent contrasts correlation test. Principal component analysis was made to assess the relationships of measured plant structural and functional traits between heterobaric and homobaric leaf species. For all statistical analyses, we used the *R version 2.15.1* (*The R Foundation for Statistical Computing*, Vienna, Austria).

Results

Diurnal patterns of microclimate change: The value of solar radiation began to increase in the early morning and rose rapidly from about 08:00 to 11:00 h, reaching a peak of approximately 800 W m^{-2} at 12:00 h, then dropping sharply (Fig. 1). The maximum solar radiation sometimes exceeded 900 W m^{-2}. The air temperature began to rise after sunrise, reaching about 30°C by 13:00 h and plateauing until 16:00 h, after which it gradually fell to a minimum of approximately 23°C just before dawn. VPD increased during the morning, reaching a peak of approximately 1.5 kPa between 13:00 and 15:00 h, after which it gradually decreased until just before dawn (Fig. 1).

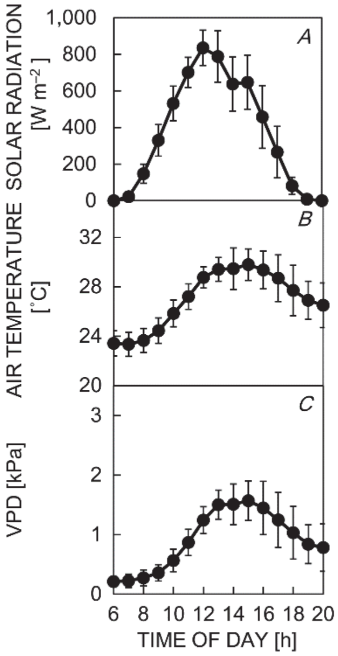

Fig. 1. Diurnal changes in solar radiation (*A*), air temperature (*B*), and vapor pressure deficit (VPD) (*C*) recorded at the top of the crane by the meteorological stations in Lambir Hills National Park.

Relation between leaf types and leaf physiological and growth traits: P_{max}, E_{max}, and g_s were significantly higher in heterobaric than in homobaric leaf species (Table 2; Fig. 1S, *supplement available online*). There were large interspecific variations in each trait among all the species studied, even under the same canopy conditions (Table 1S, *supplement available online*). There was no significant difference in water-use efficiency (WUE) between homobaric and heterobaric leaf species (Table 2). The Ψ_{mid} was significantly lower in heterobaric than that in homobaric leaf species, although there was no significant difference in Ψ_{pd} between the two types. Diurnal variation of leaf water potential ($\Delta\Psi_L$) was significantly larger in heterobaric than that in homobaric leaf species. The relative diameter growth rate (RGR) was significantly higher in heterobaric than in homobaric leaf species.

Relation between leaf types and chemical and morphological properties: Heterobaric and homobaric leaf species were similar to each other in leaf photosynthetic nitrogen use efficiency (PNUE, the ratio of CO_2 assimilation rate to leaf organic nitrogen content) and leaf chemical parameters, such as nitrogen content per unit of leaf area (N_{area}), mass-based leaf nitrogen concentration (N_{mass}), and $\delta^{13}C$ (Tables 1S, 2). Interspecific variations in N_{area}, N_{mass}, and PNUE were large and the differences were approximately three times across all the species studied. Of leaf morphological properties, stomatal density, guard cell length, SPI, and LMA showed higher values in heterobaric leaf species than in homobaric leaf species, although the difference between heterobaric and homobaric leaf species was significant only in SPI (Tables 1S, 2). There was no difference in wood and vessel density, although heterobaric leaf species had significantly larger vessel diameter than homobaric leaf species (Table 2).

Correlation between parameters: In all the species studied, E_{max}, P_{max}, and g_s increased significantly with SPI (Fig. 2*A*–*C*,*E*,*F*), both for cross-species means and PIC, but correlation between E_{max} and SPI became nearly significant when analyzed by using phylogenetically independent contrasts (Fig. 2*D*). Vessel diameter was also significantly correlated with SPI, both for cross-species means and PIC (Fig. 3*A*,*C*). E_{max} increased significantly with vessel diameter (Fig. 3*B*,*D*) and with $\Delta\Psi_L$ (Fig. 4), both for cross-species means and PIC. There was no significant correlation between $\Delta\Psi_L$ and vessel diameter, both for cross-species means and PIC (Table 2S, *supplement available online*).

Discussion

Heterobaric and homobaric leaf species clearly possessed different physiological traits closely related with water conductive pathways, such as vessel diameter and SPI, regardless of phylogenetic effect, even when growing under the same canopy conditions.

The two leaf types differed significantly in P_{max} and E_{max}; values were higher in heterobaric than in homobaric species. BSE of heterobaric leaf species comprise transparent tissue, guiding visible light to the internal layers of mesophyll (Karabourniotis *et al.* 2000, Nikolopoulos *et al.* 2002). BSE also act as an efficient water pathway from minor veins to mesophyll and/or epidermic evaporation sites (Wylie 1952, Sack *et al.* 2005, Sack and Frole 2006, Zwieniecki *et al.* 2007, Scoffoni *et al.* 2008, Boyce *et al.*

Table 2. Comparison of functional and structural traits in heterobaric and homobaric leaves. Significant correlations are shown in *bold type*. Traits are mean ± SD. E_{max} – maximum transpiration rate; g_s – maximum stomatal conductance; LMA – leaf mass per area; N_{area} – nitrogen per unit of leaf area; N_{mass} – mass-based leaf nitrogen concentration; P_{max} – maximum photosynthetic rate; PNUE – photosynthetic nitrogen-use efficiency; RGR –relative growth rate; WUE – intrinsic water-use efficiency; $\delta^{13}C$ – stable carbon isotope ratio; $\Delta\Psi_L$ – diurnal leaf water potential; Ψ_{mid} – leaf water potential at midday; Ψ_{pd} – leaf water potential at predawn.

Trait	Heterobaric	Homobaric	*P*
$\Delta\Psi_L$ [MPa]	1.30 ± 0.30	0.90 ± 0.17	**0.002**
E_{max} [mmol m^{-2} s^{-1}]	5.34 ± 0.96	4.01 ± 0.66	**0.002**
g_s [mmol m^{-2} s^{-1}]	0.38 ± 0.10	0.28 ± 0.07	**0.025**
Guard cell length [µm]	23.26 ± 4.41	20.42 ± 5.02	0.175
LMA [g m^{-2}]	154.5 ± 37.16	143.6 ± 52.60	0.565
Mean annual diameter RGR [% y^{-1}]	0.81 ± 0.45	0.49 ± 0.34	**0.049**
N_{area} [g m^{-2}]	2.54 ± 0.73	2.26 ± 0.26	0.287
N_{mass} [mg g^{-1}]	17.02 ± 5.32	17.29 ± 5.57	0.949
P_{max} [µmol m^{-2} s^{-1}]	12.94 ± 2.35	10.43 ± 1.81	**0.016**
PNUE [mmol g^{-1} s^{-1}]	5.36 ± 1.20	4.64 ± 0.62	0.128
Stomatal density [No. mm^{-2}]	537.54 ± 198.30	421.57 ± 270.80	0.252
Stomatal pore index [x10^{-2}]	27.73 ± 9.77	15.71 ± 7.59	**0.007**
Vessel density [No. mm^{-2}]	5.89 ± 3.32	6.14 ± 2.78	0.857
Vessel diameter [µm]	180.00 ± 59.15	134.33 ± 18.85	**0.013**
Wood density [g cm^{-3}]	0.68 ± 0.16	0.70 ± 0.04	0.679
WUE [µmol mmol^{-1}]	2.45 ± 0.37	2.69 ± 0.74	0.409
$\delta^{13}C$ [‰]	−29.41 ± 1.31	−28.78 ± 0.99	0.245
Ψ_{mid} [MPa]	−1.69 ± 0.31	−1.31 ± 0.15	**0.004**
Ψ_{pd} [MPa]	−0.39 ± 0.05	−0.41 ± 0.06	0.321

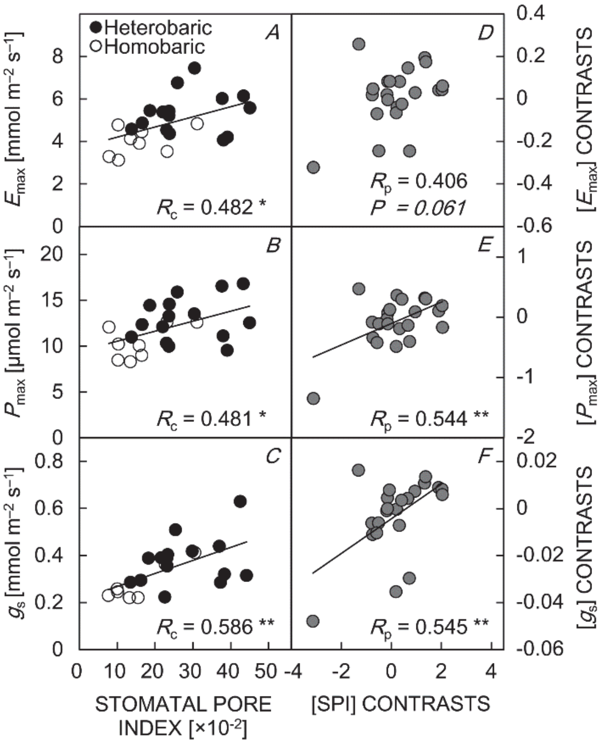

Fig. 2. Relation between SPI and maximum transpiration rate (E_{max}) (*A,D*), maximum photosynthetic rate (P_{max}) (*B,E*), and stomatal conductance at P_{max} (g_s) (*C,F*). *Black* and *white circles* represent heterobaric and homobaric leaf species, respectively. *Pearson*'s cross-species (R_c) and phylogenetically independent contrast (R_p) correlation coefficients are shown. $^*P<0.05$; $^{**}P<0.01$.

2009, Brodribb *et al.* 2010b, McKown *et al.* 2010, Walls 2011). Recent reports have found that heterobaric leaf species achieve a larger water flow, with a lower leaf hydraulic resistance than homobaric leaf species under the conditions of high irradiance (Scoffoni *et al.* 2008) and reduced humidity (Buckley *et al.* 2011). Heterobaric leaf species may therefore develop higher photosynthetic and transpiration capability than homobaric species, by exploiting anatomical leaf traits suitable for light harvesting and water transport in the tropical canopy environment of high light intensity and drought. Despite existing significant differences in gas-exchange capacity between two leaf types, there was no significant difference in WUE and leaf $\delta^{13}C$, which reflects long-term leaf photosynthetic water-use efficiency, between heterobaric and homobaric leaf species. There are many reports that heterobaric leaf species plastically increase the density of BSE in the leaf with increasing light intensity and/or drought stress (Crocker 1919, Wylie 1951, Roth 1984, Koike *et al.* 1997, Nikolopoulos *et al.* 2002, Kenzo *et al.* 2007) and as a result they increase WUE in the leaf (Lynch *et al.* 2012). Such an effective water use in heterobaric leaf species might allow them to achieve similar values of WUE and leaf $\delta^{13}C$ to those in homobaric leaf species in the same canopy environment.

The difference in water demand between homobaric and heterobaric leaf species is strongly correlated with their water conductive pathway parameters, such as SPI and vessel diameter. In our study, the two leaf types differed significantly in SPI. Several studies have previously found that SPI is a determinant of maximum stomatal

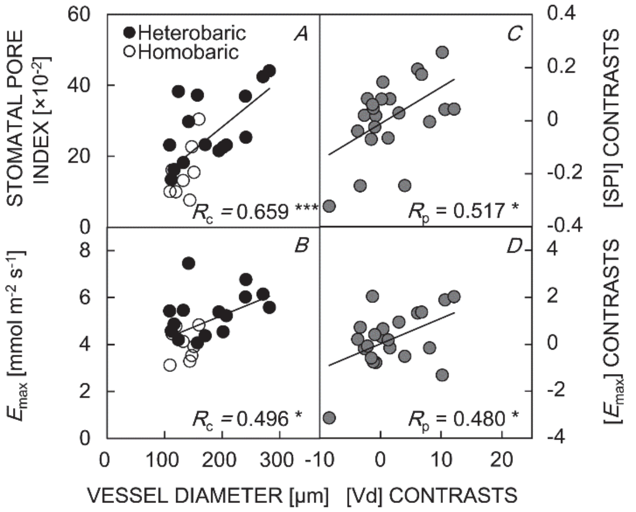

Fig. 3. Relation between vessel diameter and stomatal pore index (SPI) (*A*,*C*) and maximum transpiration rate ($E_{\max}$) (*B*,*D*). *Black* and *white circles* represent heterobaric and homobaric leaf species, respectively. *Pearson*'s cross-species (R_c) and phylogenetically independent contrast (R_p) correlation coefficients are shown. $^{*}P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$.

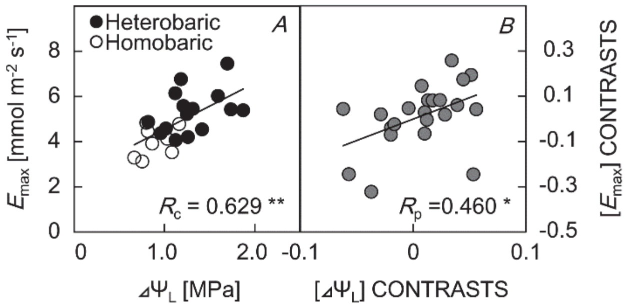

Fig. 4. Relation between maximum transpiration rate ($E_{\max}$) and diurnal variations of leaf water potential ($\Delta\Psi_L$). *Black* and *white circles* represent heterobaric and homobaric leaf species. *Pearson*'s cross-species (R_c) and phylogenetically independent contrast (R_p) correlation coefficients are shown. $^{*}P<0.05$; $^{**}P<0.01$.

conductance (Nobel 1999) and reflects the transpirational demand related to a range of environmental factors (Nardini *et al.* 2005, Sack *et al.* 2005, Brodribb and Jordan 2011). Also in vessel diameter in the stem, heterobaric- and homobaric-leafed species differed significantly in the canopy species studied, and it was correlated with SPI and the maximum transpiration ratio regardless of phylogenetic effect. Since it is known that there is a significant correlation between the vessel sizes in the stem and the twig in the same tree species (Anfodillo *et al.* 2006, Lintunen and Kalliokoski 2010, McCulloh *et al.* 2010, Schuldt *et al.* 2013) including mid-story and canopy tree species in aseasonal tropical rainforests in Southeast Asia (Zach *et al.* 2010), the vessel diameter in the stem may be hydraulically linked closely to leaf transpirational demand in the twig. Therefore, heterobaric leaf species with higher SPI might be able to maintain a higher leaf physiological capacity and thus a faster growth rate than homobaric leaf species.

Differences in the leaf and xylem structures of tropical tree species might be crucial for determining plant distribution in tropical rain forests. Heterobaric leaf species dominate the emergent layer (96%), but homobaric leaf species are nearly equal in distribution (57%) to heterobaric leaf species (43%) in the canopy layer (Kenzo *et al.* 2007), which receives high solar irradiance equal to the emergent layer in tropical rain forests (Yoda 1974, Kenzo *et al.* 2006). It is well known that vessel cavitation impairs water conduction and increases midday water stress in leaves in a high water stress environment (Tyree and Dixon 1986, Brodribb *et al.* 2010a). Previous studies showed that trees with large vessel diameter were enabled to respond to larger water demand, but at the same time they were more vulnerable to cavitation than those with the smaller vessel diameter (Wheeler *et al.* 2005, Hacke *et al.* 2006, Cai and Tyree 2010, Christman *et al.* 2012). Moreover, it also accelerates the cavitation risk; a more negative xylem water potential provides a larger driving force for water transport (Manzoni *et al.* 2013). Heterobaric leaf species therefore may suffer from increased susceptibility to cavitation during the midday and drought period (Martínez-Vilalta *et al.* 2002, Hiromi *et al.* 2012). On the other hand, homobaric leaf species had the smaller vessel diameter, lower SPI, and lower transpiration rates and $\Delta\Psi_L$ than heterobaric ones even in the same canopy environment, thus, the former might maintain their physiological capacity as a result of reduced cavitation risk. They might therefore be distributed evenly over the canopy layer, though a low photosynthetic rate may also limit their growth rate even under bright canopy conditions.

Conclusions: We found distinct strategies for adaptation to the canopy environment in heterobaric and homobaric leaf species in a tropical rain forest in Southeast Asia. Among canopy species, the difference between the two leaf types was closely related to the vessel diameter, stomatal traits, and water-use characteristics. Heterobaric leaf species develop a high photosynthetic and transpiration capability by having high SPI and the large vessel diameter suited to efficient water transport and carbon gain under bright canopy conditions. Homobaric leaf species, with the low SPI and small vessel diameter, adopt a more conservative strategy to cope with diurnal water stress, maintaining a favorable water status for the whole day. An increase in the severity and frequency of drought is predicted by models of global climate change (Corlett and Lafrankie 1998, Christensen *et al.* 2007, Overpeck and Cole 2007, Wright 2010), with implications for the dynamics of tropical rain forests (Bebber 2002, Engelbrecht *et al.* 2007). Our results may suggest that different strategies for leaf water use between heterobaric and homobaric leaf species in the same habitat might be closely related to sensitivity and resistance to unusual severe drought events, *e.g.*, associated with El Niño. Further studies of drought tolerances of different leaf types should provide a better understanding of the response of tropical canopy and emergent trees to severe drought events caused by future climate change.

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