

Stem hydraulic traits and leaf water-stress tolerance are co-ordinated with the leaf phenology of angiosperm trees in an Asian tropical dry karst forest

Pei-Li Fu^{1,2}, Yan-Juan Jiang^{1,2}, Ai-Ying Wang³, Tim J. Brodribb⁴, Jiao-Lin Zhang¹, Shi-Dan Zhu^{1,5} and Kun-Fang Cao^{1,*}

¹Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan Province 666303, China, ²Graduate University of Chinese Academy of Sciences, 19A Yuquan Road, Beijing 100049, China, ³Department of Biology, Simao Teachers' College, Pu'er, Yunnan Province 665000, China, ⁴School of Plant Science, University of Tasmania, Private Bag 55, Hobart 7001, Australia and ⁵South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

*For correspondence. E-mail caokf@xtbg.ac.cn

Received: 15 January 2012 Returned for revision: 22 February 2012 Accepted: 7 March 2012

- **Background and Aims** The co-occurring of evergreen and deciduous angiosperm trees in Asian tropical dry forests on karst substrates suggests the existence of different water-use strategies among species. In this study it is hypothesized that the co-occurring evergreen and deciduous trees differ in stem hydraulic traits and leaf water relationships, and there will be correlated evolution in drought tolerance between leaves and stems.
- **Methods** A comparison was made of stem hydraulic conductivity, vulnerability curves, wood anatomy, leaf life span, leaf pressure–volume characteristics and photosynthetic capacity of six evergreen and six deciduous tree species co-occurring in a tropical dry karst forest in south-west China. The correlated evolution of leaf and stem traits was examined using both traditional and phylogenetic independent contrasts correlations.
- **Key Results** It was found that the deciduous trees had higher stem hydraulic efficiency, greater hydraulically weighted vessel diameter (D_h) and higher mass-based photosynthetic rate (A_m); while the evergreen species had greater xylem-cavitation resistance, lower leaf turgor-loss point water potential (π_0) and higher bulk modulus of elasticity. There were evolutionary correlations between leaf life span and stem hydraulic efficiency, A_m , and dry season π_0 . Xylem-cavitation resistance was evolutionarily correlated with stem hydraulic efficiency, D_h , as well as dry season π_0 . Both wood density and leaf density were closely correlated with leaf water-stress tolerance and A_m .
- **Conclusions** The results reveal the clear distinctions in stem hydraulic traits and leaf water-stress tolerance between the co-occurring evergreen and deciduous angiosperm trees in an Asian dry karst forest. A novel pattern was demonstrated linking leaf longevity with stem hydraulic efficiency and leaf water-stress tolerance. The results show the correlated evolution in drought tolerance between stems and leaves.

Key words: Tropical dry forest, karst, leaf habit, hydraulic conductivity, cavitation resistance, leaf water-stress tolerance, wood density, leaf density, phylogenetic independent contrasts.

INTRODUCTION

Evergreen and deciduous tree species often co-occur in the tropical seasonally dry forests (Reich, 1995; Eamus, 1999). The deciduous species shed their leaves in the dry season to avoid transpiration, while co-occurring evergreen species need to maintain water transport to their canopy year-round. It has been suggested that the two groups differ in the strategies of carbon gain and water use, with the deciduous trees having greater photosynthetic capacity and higher transpiration demand while the evergreen trees possessing lower photosynthetic capacity but more conservative water use (Chabot and Hicks, 1982; Kikuzawa, 1991; Eamus, 1999). However, there is no agreement over the differences in stem hydraulic traits between the two groups. Some studies have found that the deciduous trees have greater hydraulic efficiency (Sobrado, 1993; Choat *et al.*, 2005; Chen *et al.*, 2009; Fan *et al.*, 2011; Markesteijn *et al.*, 2011a), while other studies have found overlapping hydraulic efficiency between the two groups

(Brodribb *et al.*, 2002; Ishida *et al.*, 2010), and Goldstein *et al.* (1989) even found the evergreen tree species had higher stem hydraulic efficiency.

Xylem embolism (cavitation) occurs when the water potential in the vessels is negative enough to aspirate air into vessels through pit membranes (Zimmerman, 1983; Sperry and Tyree, 1988). The vulnerability to xylem embolism is correlated with pit area per conduit and pit structure as well as the dimension of the conduits (Wheeler *et al.*, 2005; Hacke *et al.*, 2006; Choat *et al.*, 2008; Cai and Tyree, 2010; Lens *et al.*, 2011). Cavitation resistance is particularly important for evergreen species since they need to maintain water transport to the leaves in the driest period of the year. Some studies have found that the evergreen trees have higher cavitation resistance (Choat *et al.*, 2003; Chen *et al.*, 2009; Fan *et al.*, 2011); however, overlapping cavitation resistance between evergreen and deciduous trees has also been found (Sobrado, 1997; Brodribb *et al.*, 2003; Markesteijn *et al.*, 2011b). More comparative studies are needed before a comprehensive conclusion

can be drawn on the relationships between leaf habits and stem hydraulic traits.

Leaf life span (LLS) is an important functional trait that differentiates evergreen and deciduous tree species (Chabot and Hicks, 1982; Kikuzawa, 1991). It is generally correlated with leaf carbon-fixation capacity and plant-growth strategies: the species with a short LLS having high photosynthetic capacity and a fast growth rate and vice versa (Reich et al., 1992; Selaya and Anten, 2010). More recently, Simonin et al. (2012) found that LLS was negatively correlated with leaf hydraulic conductance across species. However, there is little knowledge about the relationship between LLS and stem hydraulic traits (but see Sobrado, 1993).

Leaf water status is largely mediated by stem hydraulic characteristics. Across species, there are closely correlations between leaf minimum water potential and both stem hydraulic efficiency and sapwood capacitance (Ackerly, 2004; Scholz et al., 2007; Zhang and Cao, 2009). When facing water deficit, maintaining a positive leaf turgor is important for stomatal regulation and cell growth (Levitt, 1980; Brodribb et al., 2003), and leaf turgor maintenance capacity is closely correlated with the drought tolerance of tree species (Lenz et al., 2006; Baltzer et al., 2008). Plants could maintain their leaf turgor through the accumulation of osmotically active compounds and changing cell wall elasticity (Kozłowski and Pallardy, 2002). Further, it is important for both leaf and stem to have good water-stress tolerance to maintain function under water deficit; thus there would be co-ordinated development in drought tolerance between leaf and stem across species.

One limitation of using traditional trait correlations to examine the functional trade-offs or correlated evolution is that these correlations may be biased by the potential similarity of closely correlated species (Felsenstein, 1985). Accounting for the effect of phylogeny can avoid the problem of species non-independence; and the phylogenetic independent contrasts (PICs) can be used to examine correlated evolution between traits among taxa (Felsenstein, 1985; Garland et al., 1992). Thus, it is important to investigate the functional trade-offs and adaptation of traits in a phylogenetic framework (Maherali et al., 2004; Jacobsen et al., 2007).

Karst habitats account for 10–15 % of the land in the world and 1/7 of that in China, with an extensive distribution in south-west China (Yuan, 1991; Ford and Williams, 2007). The karst forests have great plant species diversity and are rich in endemic species (Zhu et al., 2003; Clements et al., 2006); however, there is little knowledge about the hydraulic traits of the tree species therein (but see Tognetti et al., 1998; McElrone et al., 2004; Fan et al., 2011). The karst habitats are characterized by shallow soil and highly porous bedrock that leaves little water-storage capacity for the rooting area; plants therein would suffer from great water deficit, especially in the dry season. The severe water deficit of the karst habitats could put a great selective pressure on the water-use strategies of tree species; hence the co-occurring evergreen and deciduous trees may differ in their stem hydraulic traits and leaf water relationships.

In the present study, we compared the stem hydraulic conductivity, xylem-cavitation resistance, wood anatomy, LLS, leaf pressure–volume characteristics and gas exchange of six

evergreen and six deciduous tree species co-occurring in a tropical dry karst forest in south-west China. We hypothesize that different leaf habits represent different water-use strategies that the co-occurring evergreen and deciduous species differ in stem hydraulic traits and leaf water relationships; specifically, the deciduous tree species have higher stem hydraulic efficiency, and the evergreen tree species have greater xylem-cavitation resistance and greater water-stress tolerance. We used PICs to test the correlated evolution between LLS and hydraulic traits as well as the evolutionary relationships between leaf water-stress tolerance and stem traits.

MATERIALS AND METHODS

Study site and species

The present study was carried out in a karst forest that was located approx. 3 km from the Xishuangbanna Tropical Botanical Garden (21°54'N, 101°46'E, 580 m a.s.l.), southern Yunnan, China. This region has a distinct dry season from November to April. According to the climatic record by the Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies at the site close to the present study site, the average annual rainfall in the past 50 years (1959–2009) is approx. 1500 mm, of which 84 % occurs in the wet season from May to October, and the mean annual temperature is 21.8 °C. The soil is a brown calcareous soil with coarse texture and pH of approx. 7.3 (Zhang, 2006). Six evergreen and six deciduous tree species were selected for the present study. They are the main components of the forest in the present study site. The evergreen species are *Cleistanthus sumatranus* (Euphorbiaceae), *Lasiococca comberi* (Euphorbiaceae), *Celtis philippensis* (Ulmaceae), *Turpinia pomifera* (Staphyleaceae), *Alphonsea mollis* (Annonaceae) and *Pistacia weinmannifolia* (Anacardiaceae). The deciduous species are *Bauhinia variegata* (Fabaceae), *Lagerstroemia tomentosa* (Lythraceae), *Croton yanhuii* (Euphorbiaceae), *Cipadessa baccifera* (Meliaceae), *Millettia cubittii* (Fabaceae) and *Ficus pisocarpa* (Moraceae). All the species have diffuse-porous wood except *P. weinmannifolia* which has a ring-porous wood. *Ficus pisocarpa* sheds leaves at the beginning of the dry season (December). The other five deciduous tree species shed leaves in the middle of dry season (February to March), and then after 1 month or so flush leaves, which become mature in the late dry season (April to early May). All the evergreen tree species flush leaves from March to April except *T. pomifera*, which flushes leaves in the middle of the wet season (July to August), and *P. weinmannifolia*, which flushes leaves three or four times every year.

Stem hydraulic conductivity

Stem hydraulic conductivity was measured in the wet season following the method of Sperry et al. (1988). Two branches were cut from each of four or five individuals per species early in the morning. Then the cut ends were wrapped with wet tissue paper and put into black plastic bags and immediately taken into the laboratory. Maximum vessel length (MVL, cm) was determined by the air injection method from four to six branches per species (Brodribb and Field, 2000). Segments longer than the MVL were used for hydraulic

conductivity measurement for all the species except *C. philippensis*, *T. pomifera* and *L. tomentosa*, which had MVL of 83.7 cm, 119.2 cm and 93.8 cm, respectively (Supplementary Data Table S2). Segments with lengths about 50 cm were used in these three species for hydraulic conductivity measurement owing to the great variations in their shoot morphologies. The hydraulic conductivity of these three species might be somewhat overestimated due to the existence of open vessels. Bark was removed from both ends (about 1 cm) of the segments, and then the segments were connected to a hydraulic conductivity-measurement apparatus which contained a reservoir container and tubes connected to the segments. Since *F. pisocarpa* produced latex from its bark and pith, this material was removed from both ends of the segments without damaging the sapwood. The gaps in the centre of the segments resulting from removing the pith were filled with rubber clay to stop the flow of latex from the inner part of the pith. A head pressure of about 6 kPa was induced by gravity. A degassed and filtered solution of 10 mmol L⁻¹ oxalic acid was used to prevent the decline in conductivity caused by microbial growth within the vessels (Sperry *et al.*, 1988). The hydraulic conductivity (K_h , kg m s⁻¹ MPa⁻¹) was calculated from $K_h = F/(\Delta P/L)$, where F (kg s⁻¹) is flow rate and ΔP (MPa) is pressure drop along the length of the segment (L , m). Afterwards the sapwood of the segment was flushed with a methyl blue solution and the sapwood area (A_s , cm²) on the traverse section of the middle part of the stem segment was measured. Sapwood-specific hydraulic conductivity (K_s , kg m⁻¹ s⁻¹ MPa⁻¹) was calculated from $K_s = K_h/A_s$. The distal leaf area (A_L , cm²) of the branch was measured with a leaf area meter (LI-3000A; Licor, Lincoln, NE, USA) and leaf-specific conductivity (K_L , kg m⁻¹ s⁻¹ MPa⁻¹) was calculated from $K_L = K_h/A_L$. The Huber value (HV) was calculated from $HV = A_s/A_L$.

Stem vulnerability curve

Stem vulnerability curves were measured following the bench drying method (Sperry *et al.*, 1988). Branches from four or five individuals were bench dried and then were wrapped with plastic bags for 1–2 h to equilibrate the water potential between leaves and stems. Two leaves from each branch were used to measure the water potential with a pressure chamber (PMS, Corvallis, OR, USA); the average of which was assumed to be the xylem water potential. A segment 15–20 cm long was then cut from the branch and connected to the hydraulic-measurement apparatus to determine the volumetric flow rate (J_v). As K_h is proportional to J_v through the segment under a fixed pressure gradient, calculation of the percentage loss of hydraulic conductivity (PLC %) was based on J_v rather than K_h . The initial volumetric flow rate (J_i) of the segment was measured when connected to the hydraulic-measurement apparatus. The segment was then flushed with 10 mmol L⁻¹ oxalic acid solution under 0.15 MPa pressure for 15–30 min, and the maximum volumetric flow rate (J_{max}) was measured. PLC % of the segment was calculated from $PLC \% = 100 \times (J_{max} - J_i)/J_{max}$. With different time of branch drying, different levels of PLC % were obtained. The vulnerability curves were plotted using PLC %

as a function of the xylem water potential and fitted by an exponential sigmoid function (Pammenter and Van der Willigen, 1998): $PLC \% = 100/[1 + \exp[a(\Psi_x - b)]]$, where Ψ_x is the xylem water potential, a is the maximum slope of the curve and b is xylem water potential at 50 % loss of hydraulic conductivity (P_{50}). P_{50} was used to assess the xylem-cavitation resistance of different tree species.

Wood density and xylem anatomy

The segments used for hydraulic conductivity measurement were taken to measure the sapwood density (WD, g cm⁻³) and xylem anatomy characteristics. Bark and pith material was removed from the 4- to 5-cm-long segments, and the water displacement method was used to measure the volume of the fresh sapwood. The sapwood sample was dried out in an oven in 70 °C for 72 h and then the dry mass was measured and used for determination of WD. Segments about 4–5 cm in length from each of three individuals per species were stored in 1 : 1 (v/v) ethanol and glycerol solutions for anatomical measurements. Traverse sections about 20 µm thick were made with a microtome and the vessel diameters measured under a microscope. At least 30 vessels for each sample were randomly chosen from the latest growth sapwood and the vessel diameter was measured. The hydraulically weighted vessel diameter (D_h , µm) was calculated from $D_h = (\sum D^4/N)^{1/4}$, where N was the number of vessels (Tyree and Zimmermann, 2002). The number of vessels per square millimetre sapwood area (VN, no. mm⁻²) was also measured.

Minimum leaf water potential

In the late dry season of 2008 (19–21 April), when there were several continuously sunny days, minimum leaf water potentials (Ψ_L) were measured at midday (1200–1400 h). The newly produced leaves were used to determine Ψ_L for both evergreen and deciduous species. Two leaves or leafy twigs from each of four to six individuals per species were cut from the trees and sealed in plastic bags and taken into the laboratory. The water potentials were measured in a pressure chamber, and all the measurements were completed within 1 h.

Leaf pressure–volume curve

In the wet season (June to August) and late dry season (April to early May), leaves or leafy twigs were sampled from each of four to six individuals per species early in the morning. In the laboratory the petioles or stems were re-cut under water and inserted in the water for 2–4 h to get full re-hydration. The leaf pressure–volume curves were measured following the bench drying technique (Turner, 1988). The leaves or twigs were dried out on the bench, and the water potentials and fresh weights were measured periodically. We stopped measuring when the water potentials stopped decreasing or even increased, and then the leaves or twigs were dried in an oven at 70 °C for 24 h to determine the dry weights. Leaf water potential at turgor-loss point (π_0) and osmotic potential at full turgor (π_{100}) were estimated according to the method of Schulte and Hinckley (1985). The bulk modulus of elasticity (ϵ) was calculated following Lenz *et al.* (2006).

Leaf gas exchange measurement

Maximum leaf area-based photosynthetic rate (A_a) and maximum stomatal conductance (g_s) were measured between 0900 h and 1200 h in the wet season of 2008 using a portable photosynthetic gas exchange system (LI-6400; Licor), with ambient CO_2 concentration (about $400 \mu\text{mol m}^{-2} \text{s}^{-1}$) and photosynthetic photon flux density of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ provided by the LED light source. Two sunlit leaves from each of three to five individuals per species were chosen. The leaf to air vapour pressure deficit was <1.6 kPa and the average temperature was 29.5°C . Photosynthetic water-use efficiency (WUE, $\mu\text{mol mol}^{-1}$) was calculated from $\text{WUE} = (A_a/g_s)$.

Leaf structure and nutrients

In the wet season, four or five leaves or leaflets from each of three to five individuals per species were sampled and taken into the laboratory; in the case of *P. weinmannifolia*, 20 leaflets from each individual were used because of the small size. Leaf area was determined by a leaf area meter, and the leaves were then dried in an oven at 70°C for 24 h and dry mass was determined. The leaf dry mass per area (LMA, g m^{-2}) was calculated. Leaf maximum mass-based photosynthetic rate (A_m , $\text{nmol g}^{-1} \text{s}^{-1}$) was calculated from $A_m = A_a/\text{LMA}$. Leaf thickness (T_{leaf} , μm) was measured using a microscope for two leaves or leaflets from each of three to five individuals per species, and leaf density (ρ_{leaf} , g cm^{-3}) was calculated from $\rho_{\text{leaf}} = \text{LMA}/T_{\text{leaf}}$.

The nitrogen and phosphorus concentrations of leaves were analysed by the Biogeochemistry Laboratory of Xishuangbanna Tropical Botanical Garden. The total leaf mass-based nitrogen concentration (N_m) was analysed using a CN elemental analyser (Vario MAX CN; Elementar Analysensysteme GmbH, Germany) and total leaf mass-based phosphorus concentration (P_m) was measured using an inductively coupled plasma atomic-emission spectrometer (IRIS Advantage-ER; Thermo Jarrell Ash Corporation, USA) after the samples were digested with $\text{HNO}_3\text{--HClO}_4$ solutions. Photosynthetic nitrogen use efficiency (PNUE) and phosphorus-use efficiency (PPUE) were calculated as maximum A_m divided by N_m and P_m , respectively.

LLS

For all the deciduous tree species and the two evergreen tree species, *A. mollis* and *P. weinmannifolia*, which have LLS shorter or slightly longer than 1 year, the LLS was measured by labelling 30–50 newly produced leaves from three individuals per species in April 2009. The leaf loss number was counted every 4 weeks in the growing season and every 2 weeks in the leaf shedding season. LLS was calculated from the period between leaf produced and leaf lost. For the other four evergreen tree species which had LLS longer than 1 year, the LLS was measured following the method of King (1994). In April 2009, eight to ten twigs from three individuals per species were labelled, and the leaves on the twigs were marked with a marker pen. The numbers of the attached leaves, newly produced leaves as well as lost leaves were counted in April 2010 and May 2011. The LLS was calculated

from $\text{LLS} = 2N_m/(r_P + r_L)$ where N_m is the mean attached leaf number on the shoot and r_P and r_L are the yearly leaf production and loss rate, respectively (King, 1994).

Construction of the phylogenetic tree

A phylogenetic tree at family level was constructed using PHYLOMATIC, which is based on Angiosperm Phylogeny group III classification of angiosperm (APG III; <http://www.phylodiversity.net/phyloomatic/>). There were three species from Euphorbiaceae (*Cleistanthus sumatranus*, *Croton yanhui* and *Lasiococca comberi*) in the present study, forming a polytomy. The genus-level phylogeny of this family was constructed by using the ITS, *rbcL* and *matK* DNA sequences. The DNA sequences of the species from *Croton* and *Cleistanthus* were downloaded from GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>; Supplementary Data Table S1). While the ITS, *rbcL* and *matK* DNA sequences of *L. comberi* were analysed by a DNA Barcoding Project of the Xishuangbanna Tropical Botanical Garden (XQ Ci, XTBG, Yunnan, China, unpubl. res.). The sequences were concatenated and the alignment was calculated with ClustalW included in MEGA 5.05 (Tamura et al., 2011). The phylogenetic tree was constructed using the maximum likelihood method based on the Tamura–Nei model (Tamura and Nei, 1993). The final phylogenetic tree included all the 12 species (Supplementary Data Fig. S1). Equal branch length was assumed in the present study to minimize type I error rates (Ackerly, 2000).

Statistics and phylogenetic comparative methods

To meet the assumptions of parametric statistics, all the original data were $\log_{10}$ -transformed prior to analysis. The values of P_{50} , $\pi_{0,\text{wet}}$, $\pi_{100,\text{wet}}$, $\pi_{0,\text{dry}}$, $\pi_{100,\text{dry}}$ and Ψ_L were converted from negative to positive for facilitating the log transformation. However, for consistency the data of these traits were presented and interpreted as usual negative values, e.g. more negative P_{50} indicated greater cavitation resistance. Differences in the eco-physiological traits between evergreen and deciduous tree species were compared by using independent-samples *t*-test in SPSS 16.0 (SPSS Inc., Chicago, IL, USA). We tested the phylogenetic signal using the *K*-statistic and a randomization test implemented via PICs (Blomberg et al., 2003) with R package (v2.14.1, R Development Core Team, 2008). The Pearson's correlation coefficients between pairs of continuous traits were analysed by using SPSS 16.0. The PICs correlation coefficients and the significance levels were determined using CATUS 1.13 (Schwikl and Ackerly, 2001).

RESULTS

Eco-physiological differences between the evergreen and deciduous trees

There were great variations in the stem and leaf traits across the 12 species. The values of K_S ranged from 1.96 to $3.67 \text{ kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ among the evergreen species (*Celtis philippensis* and *Alphonsea mollis*) and ranged from 3.65 to

8.85 kg m⁻¹ s⁻¹ MPa⁻¹ among the deciduous species (*Cipadessa baccifera* and *Bauhinia variegata*; Supplementary Data Table S2). Xylem water potential at 50 % loss of hydraulic conductivity (P_{50}) varied from -0.74 MPa (*Millettia cubitti*) to -3.98 MPa (*Pistacia weinmannifolia*) among all the 12 species. The slope of the vulnerability curves ranged from 0.60 to 1.43 among the evergreen species (*P. weinmannifolia* and *C. philippensis*) and ranged from 0.88 to 3.57 among the deciduous species (*C. baccifera* and *Ficus pisocarpa*; Supplementary Data Fig. S2). The deciduous tree *C. baccifera* had the lowest P_{50} (-2.45 MPa; Supplementary Data Table S2), the smallest D_h (54.4 µm) and the largest number of vessels per sapwood area (with VN of 108.7 mm⁻²) among the deciduous species (one-way ANOVA followed by the Turkey test). A_m ranged from 59 to 152 nmol g⁻¹ s⁻¹ among the evergreen species (*C. philippensis* and *Cleistanthus sumatranus*) and ranged from 132 to 291 nmol g⁻¹ s⁻¹ among the deciduous species (*Lagerstroemia tomentosa* and *C. baccifera*). LLS varied from 10.5 to 37.0 months among the evergreen species (*P. weinmannifolia* and *C. sumatranus*, respectively) and varied from 5.1 to 10.9 months among the deciduous species (*F. pisocarpa* and *M. cubitti*, respectively). Leaf density

(ρ_{leaf}) ranged from 0.31 g cm⁻³ (*F. pisocarpa*) to 0.64 g cm⁻³ (*P. weinmannifolia*) across the species.

Compared with the evergreen species, the deciduous species as a group had significantly higher K_S , P_{50} , D_{mv} , A_m , g_s and P_m , and higher VI with marginal significance (0.05 ≤ P ≤ 0.10) (Table 1). The evergreen species as a group had significantly higher LMA, LLS, WUE and ρ_{leaf} , and higher WD with marginal significance than those of the deciduous species. Compared with the deciduous species, the evergreen species as a group had significantly lower $\pi_{100,\text{wet}}$, $\pi_{100,\text{dry}}$ and $\pi_{0,\text{dry}}$, and higher ε_{wet} and ε_{dry} than those of the deciduous species. These indicate higher leaf water-stress tolerance in the evergreen trees than the deciduous trees. Both the evergreen species (e.g. *C. sumatranus*, *Lasiococca comberi* and *C. philippensis*) and deciduous species (e.g. *Bauhinia variegata*, *L. tomentosa* and *Croton yanhuii*) tended to lose their leaf turgor in the midday of late dry season because the minimum leaf water potentials of these species were lower than their $\pi_{0,\text{dry}}$ (Supplementary Table S2). However, there were no significant differences in HV, VN, MVL, T_{leaf} , A_a , N_m , PNUE, PPUE and $\pi_{0,\text{wet}}$ between the evergreen and deciduous groups.

TABLE 1. Comparison of stem and leaf traits between the six evergreen and six deciduous tree species (values are means ± s.e.)

Trait	Unit	Evergreen	Deciduous	<i>P</i>
K_L	$\times 10^{-4}$ kg m ⁻¹ s ⁻¹ MPa ⁻¹	3.70 ± 0.48	6.28 ± 1.37	0.114
K_S	kg m ⁻¹ s ⁻¹ MPa ⁻¹	2.76 ± 0.23	5.98 ± 0.86	0.001
HV	—	1.41 ± 0.21	1.06 ± 0.15	0.238
WD	g cm ⁻³	0.63 ± 0.03	0.56 ± 0.03	0.074
P_{50}	MPa	-2.37 ± 0.40	-1.27 ± 0.26	0.025
D_h	µm	59.6 ± 8.7	94.7 ± 10.1	0.026
VN	no. mm ⁻²	82.0 ± 30.5	30.5 ± 15.9	0.125
VI	—	2.55 ± 1.55	8.49 ± 3.70	0.082
MVL	cm	67.3 ± 13.3	55.3 ± 12.7	0.460
LMA	g m ⁻²	94.3 ± 17.6	53.4 ± 6.5	0.027
LLS	months	23.3 ± 5.3	7.8 ± 1.0	0.001
T_{leaf}	µm	184.4 ± 25.9	152.6 ± 22.2	0.302
ρ_{leaf}	g cm ⁻³	0.50 ± 0.04	0.36 ± 0.02	0.009
A_a	µmol CO ₂ m ⁻² s ⁻¹	10.4 ± 0.6	11.64 ± 1.4	0.562
A_m	nmol CO ₂ g ⁻¹ s ⁻¹	125 ± 14	225 ± 23	0.009
g_s	mol H ₂ O m ⁻² s ⁻¹	0.17 ± 0.02	0.25 ± 0.03	0.047
WUE	µmol mol ⁻¹	66.7 ± 4.9	49.7 ± 2.0	0.009
N_m	mg g ⁻¹	21.4 ± 1.9	27.4 ± 3.0	0.117
P_m	mg g ⁻¹	1.35 ± 0.14	2.02 ± 0.14	0.006
PNUE	µmol mol ⁻¹ s ⁻¹	84.6 ± 11.4	120.9 ± 16.5	0.132
PPUE	mmol mol ⁻¹ s ⁻¹	2.94 ± 0.38	3.58 ± 0.46	0.389
$\pi_{0,\text{wet}}$	MPa	-2.22 ± 0.29	-1.64 ± 0.09	0.107
$\pi_{100,\text{wet}}$	MPa	-1.91 ± 0.21	-1.37 ± 0.07	0.037
ε_{wet}	MPa	26.64 ± 2.22	16.19 ± 1.76	0.005
$\pi_{0,\text{dry}}$	MPa	-2.82 ± 0.32	-1.65 ± 0.12	0.007
$\pi_{100,\text{dry}}$	MPa	-2.39 ± 0.26	-1.47 ± 0.10	0.009
ε_{dry}	MPa	23.87 ± 2.24	14.94 ± 2.42	0.022
Ψ_L	MPa	-2.81 ± 0.58	-1.87 ± 0.28	0.324

Means of the two phenological groups were compared using independent-samples *t*-test. *P*-values < 0.05 are shown in boldface.

K_L , Leaf-specific hydraulic conductivity; K_S , sapwood-specific hydraulic conductivity; HV, Huber value; WD, sapwood density; P_{50} , xylem water potential at 50 % loss of hydraulic conductivity; D_h , hydraulically weighted vessel diameter; VN, vessel numbers per square millimetre sapwood; VI, vulnerability index (D_h/VN); MVL, maximum vessel length; LMA, leaf dry mass per area; LLS, leaf life span; T_{leaf} , leaf thickness; ρ_{leaf} , leaf density; A_a , maximum leaf area-based photosynthesis rate; A_m , maximum leaf mass-based photosynthetic rate; g_s , maximum stomata conductance; WUE, photosynthetic water-use efficiency; N_m , leaf mass-based nitrogen content; P_m , leaf mass-based phosphorus content; PNUE, photosynthetic nitrogen use efficiency; PPUE, photosynthetic phosphorus-use efficiency; $\pi_{0,\text{wet}}$, leaf water potential at turgor-loss point in wet season; $\pi_{100,\text{wet}}$, leaf saturate osmotic potential in wet season; ε_{wet} , bulk modulus of elasticity in wet season; $\pi_{0,\text{dry}}$, leaf water potential at turgor-loss point in dry season; $\pi_{100,\text{dry}}$, leaf saturate osmotic potential in dry season; ε_{dry} , bulk modulus of elasticity in dry season; Ψ_L , minimum leaf water potential.

Principal component analysis

In the principal component analysis (PCA), the PC axis 1 was loaded by LMA, WD, P_{50} , LLS, ρ_{leaf} and leaf pressure–volume curve derived parameters on the positive side, and by A_m and K_S on the negative side (Fig. 1A). PC axis 2 was loaded by A_a , HV, VN, PPUE, PNUE and g_s on the positive side, and by D_h , VI, N_m and P_m on the negative side (Fig. 1A). The evergreen and deciduous tree species can be divided into two groups along the PC axis 1 (Fig. 1B). The patterns of the phylogenetic PCA were generally consistent with the conventional PCA; however, the PC axis 2 of phylogenetic PCA was loaded by D_h and VI on the positive side, and by VN and PPUE on the negative side (Fig. 1C).

Phylogenetic signal

Most of the eco-physiological traits had weak phylogenetic signal with the Blomberg K values <1 , and no significant signal for these traits was found using the randomization test (Supplementary Data Table S3). However, a relatively strong and significant phylogenetic signal was found in VI, VN, D_h , P_{50} and HV.

Traditional and PICs correlations

The traditional and PICs correlations were mostly consistent in the present study (Supplementary Data Table S4). LLS was significantly and negatively correlated with K_L , K_S , A_m and $\pi_{0,\text{dry}}$, and positively correlated with WUE by both Pearson's and PICs methods (Fig. 2). However, no correlation was found between LLS and P_{50} by either method. There were significant correlations between P_{50} and D_h , K_S and VN across species; however, when the phylogenetic relationship was taken into account, the magnitude of these correlation coefficients decreased and the correlation between P_{50} and VN became insignificant (Fig. 3). There was significantly positive correlation between P_{50} and $\pi_{0,\text{dry}}$ for both Pearson's and PICs methods. Wood density was significantly correlated with ρ_{leaf} and leaf water-stress tolerance ($\pi_{100,\text{wet}}$, $\pi_{0,\text{wet}}$, $\pi_{100,\text{dry}}$, $\pi_{0,\text{dry}}$ and Ψ_L) by both Pearson's and PICs methods (Table 2). There was significantly negative correlation between WD and P_{50} by Pearson's method, and the correlation was insignificant by PICs method. The correlation between WD and A_m was insignificant across species; however, it became significant when the phylogeny was taken into account. Leaf density was significantly correlated with P_{50} , A_m , as well as leaf water-stress tolerance by both Pearson's and PICs methods.

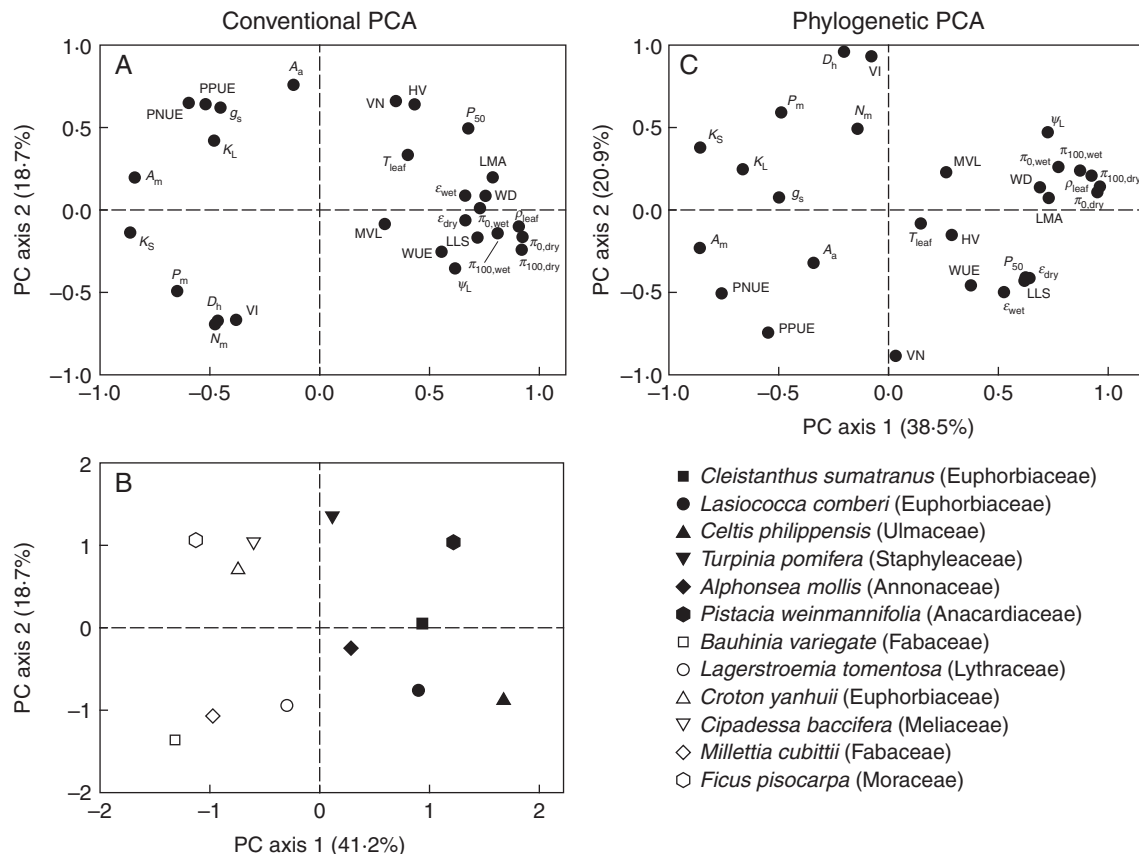


FIG. 1. Arrangement of the 28 stem and leaf traits along the first two principal component axes constructed based on (A) species traits means and (C) phylogenetic independent contrasts (PICs). The factor loadings of species along PC axis 1 and axis 2 are shown in (B). Note that all the original data were $\log_{10}$ -transformed prior to analysis, and the values of P_{50} , $\pi_{0,\text{wet}}$, $\pi_{100,\text{wet}}$, $\pi_{0,\text{dry}}$, $\pi_{100,\text{dry}}$ and Ψ_L were converted from negative to positive values for facilitating the log transformation. The abbreviations for the traits are as in Table 1.

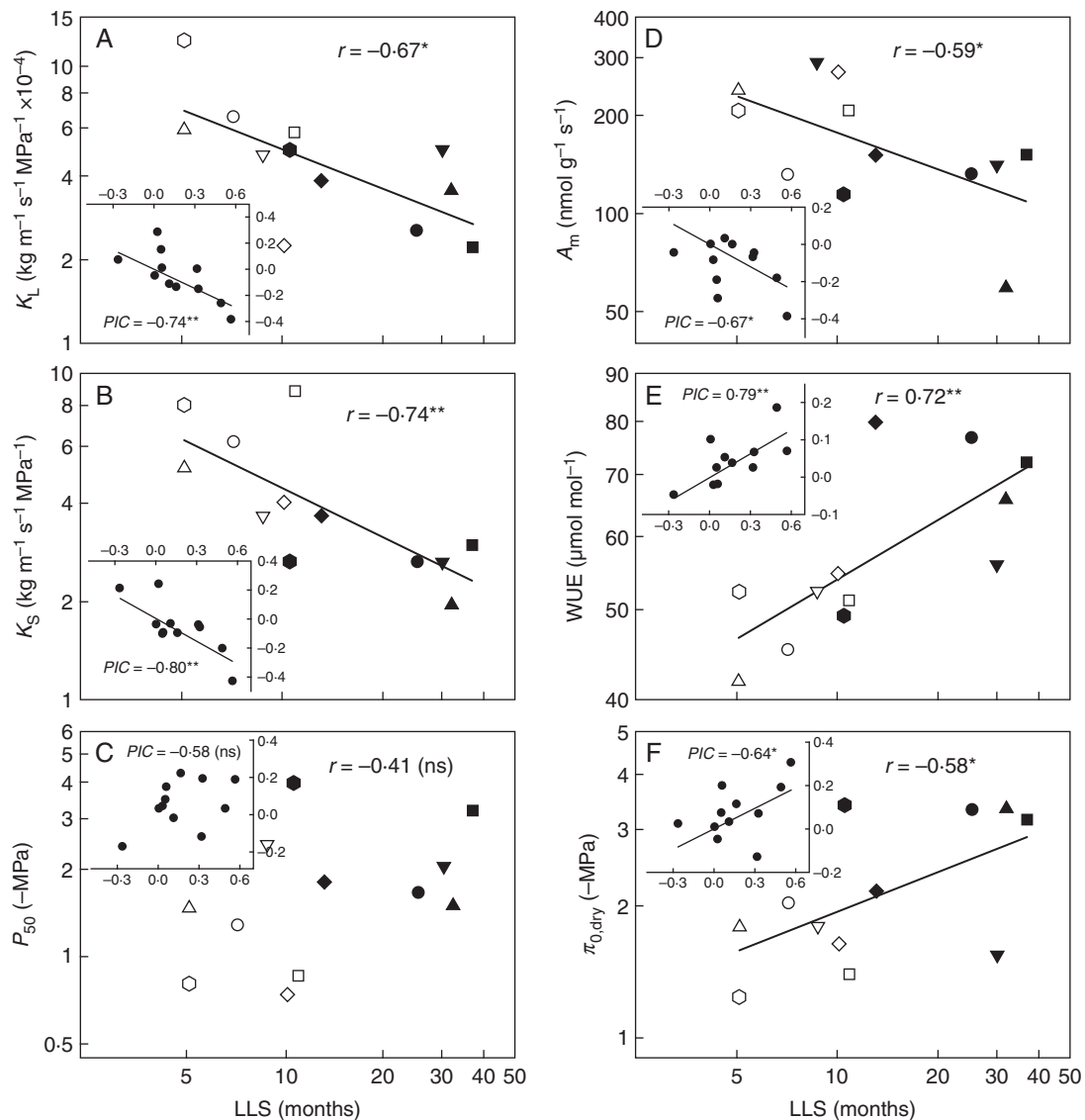


FIG. 2. Traditional and phylogenetic independent contrasts (PICs) correlations between leaf life span (LLS) and (A) leaf specific hydraulic conductivity (K_L), (B) sapwood specific hydraulic conductivity (K_S), (C) xylem water potential at 50% loss of hydraulic conductivity (P_{50}), (D) leaf mass-based maximum photosynthesis rate (A_m), (E) photosynthetic water-use efficiency (WUE) and (F) dry season leaf turgor-loss point water potential ($\Pi_{0,dry}$). Note that in each panel the data were plotted on logarithmic scale, and the straight lines describe the logarithmic equations fitted to the species mean values. Pearson correlation coefficients (r) and the significance levels are shown in each panel. Evergreen and deciduous species are distinguished by closed and open symbols, respectively; each species has a different symbol as defined in Fig. 1. The PICs correlations for each pair of traits and the corresponding correlation coefficients as well as significance levels are shown in the insets. *, $P < 0.05$; **, $P < 0.01$.

DISCUSSION

The above results showed that there were clear distinctions in stem hydraulic traits and water-stress tolerance between the evergreen and deciduous trees (Table 1 and Fig. 1B) although the continuous variations across species (Supplementary Data Table S2). The deciduous trees had significantly higher stem hydraulic efficiency while the evergreen trees had greater xylem-cavitation resistance. The results of the present study are consistent with findings of other studies in seasonally dry forests in Venezuela (Sobrado, 1993), Australia (Choat *et al.*, 2005) and China (Chen *et al.*, 2009); however, the results contrast with those of studies from Costa Rica (Brodribb *et al.*,

2002, 2003) and Bolivia (Markesteijn *et al.*, 2011b). The clear distinctions in hydraulic traits of the two groups in the present study could be driven by the severe selection pressure of water deficit due to the long dry season (6 months) and leaking rocky substrate of karst habitat; and thus the co-occurring evergreen and deciduous species use contrasting water-use strategies to adapt to the dry habitat.

The evergreen trees had greater xylem-cavitation resistance so that could maintain water transport to leaves under the water-deficit condition in a dry season. The leaves of the evergreen trees also had greater leaf turgor maintenance capacity and higher bulk modulus of elasticity (ϵ) in both wet and

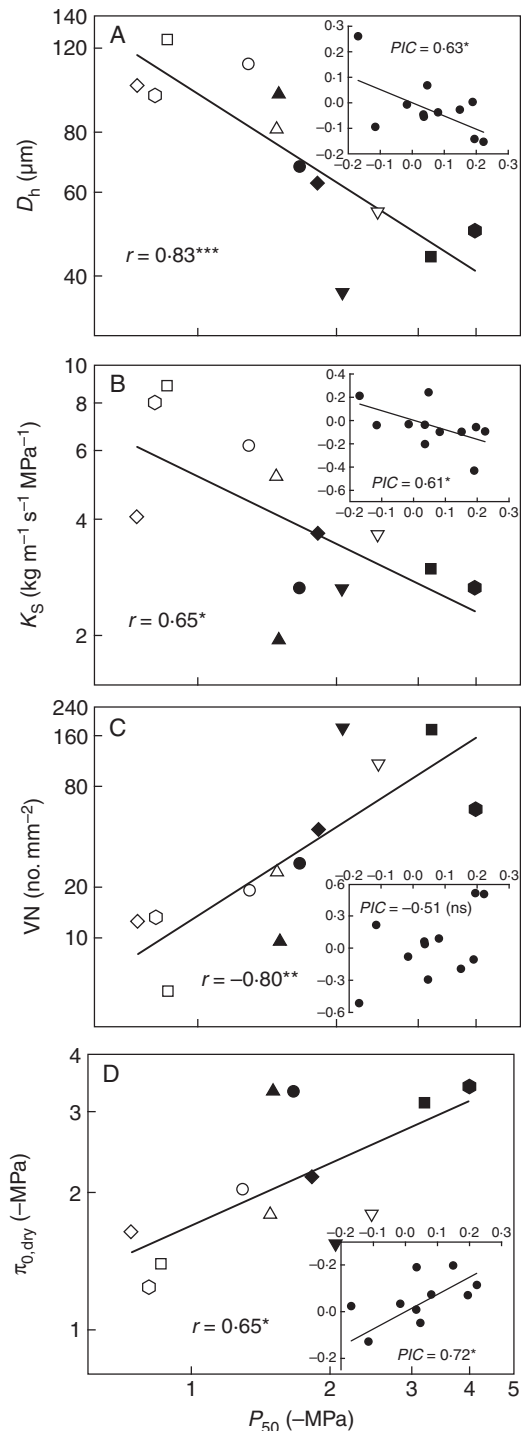


FIG. 3. Traditional and phylogenetic independent contrasts (PICs) correlations of xylem water potential at 50 % loss of hydraulic conductivity (P_{50}) and (A) hydraulically weighted vessel diameter (D_h), (B) sapwood-specific hydraulic conductivity (K_S), (C) vessel density (VN) and (D) leaf turgor-loss point water potential in dry season ($\pi_{0,dry}$). Note that in each panel the data were plotted on logarithmic scale, and the straight lines describe the logarithmic equations fitted to the species mean values. Pearson correlation coefficients (r) and the significance levels are shown in each panel. Evergreen and deciduous species are distinguished by closed and open symbols; each species has a different symbol as defined in Fig. 1. The PICs correlations for each pair of traits and the corresponding correlation coefficients as well as the significance levels are shown in the insets. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

TABLE 2. The traditional and phylogenetic independent contrasts (PICs) correlations of wood density and leaf density with stem and leaf traits

	Pearson's correlation		PICs correlation	
	WD	ρ_{leaf}	WD	ρ_{leaf}
WD	—	0.83***	—	0.84**
P_{50}	-0.66*	-0.61*	-0.60	-0.61*
ρ_{leaf}	0.83***	—	0.84**	—
A_m	-0.53	-0.79**	-0.65*	-0.89***
PNUE	-0.23	-0.56	-0.53	-0.80**
PPUE	-0.43	-0.63*	-0.56	-0.75**
$\pi_{0,wet}$	-0.70*	-0.78**	-0.78**	-0.81**
$\pi_{100,wet}$	-0.62*	-0.80**	-0.77**	-0.89***
ε_{wet}	0.25	0.43	0.33	0.54
$\pi_{0,dry}$	-0.84***	-0.92***	-0.84**	-0.94***
$\pi_{100,dry}$	-0.82**	-0.92***	-0.83**	-0.94***
ε_{dry}	0.37	0.47	0.53	0.59
Ψ_L	-0.68*	-0.74**	-0.74**	-0.82**

Values in boldface are statistically significant. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.
The abbreviations for traits are as in Table 1.

dry seasons (Table 1), which are important for the leaves to be physiologically functional at low water availability (Kozłowski and Pallardy, 2002). The evergreen trees compensate for their lower stem hydraulic efficiency and photosynthetic capacity by maintaining functioning leaves all year round. There is no significant difference in A_a between the evergreen and deciduous species; however, the deciduous species had thinner leaves (lower LMA) and thus significantly higher A_m than the evergreen species. These results are consistent with the findings of other studies from tropical dry forests (Goldstein *et al.*, 1989; Choat *et al.*, 2006). Thus the deciduous trees have higher water transport efficiency and greater photosynthetic rate in the wet season; and their leaves drop in the dry season to avoid excess water loss. The leaf shedding of deciduous tree species may be caused by xylem embolism in the stems (Brodribb *et al.*, 2002; Salleo *et al.*, 2002) or leaves (Brodribb and Holbrook, 2003).

The present study shows the trade-offs between drought tolerance and both xylem water transport and leaf photosynthetic capacity (Fig. 1). Traits related to water transport (K_L , K_S) and photosynthetic capacity (A_m , g_s , PNUE, PPUE) clustered together on the negative side of PC axis 1, while traits related to drought tolerance (WD, Ψ_L , P_{50} , LMA, ρ_{leaf} and leaf pressure-volume-deprived traits) clustered together on the positive site. The evolutionary correlation between stem hydraulic efficiency and leaf gas exchange found in the present study (Fig. 1C) was consistent with the plant hydraulic-photosynthetic co-ordination model (Brodribb *et al.*, 2002; Hao *et al.*, 2011). Higher water transport efficiency and higher photosynthetic capacity enable plant to have a higher growth rate (Zhang and Cao, 2009), but at the cost of lower drought tolerance (Markesteijn *et al.*, 2011a; Hao *et al.*, 2010). The divergence of evergreen and deciduous species in the present study was primarily due to their differences in stem hydraulic capacity, photosynthetic traits, and leaf water-stress tolerance (Fig. 1).

The present study reveals that there is correlated evolution between leaf longevity and stem water-transport capacity (Fig. 2A, B). Trees with shorter LLS had higher stem hydraulic efficiency and higher photosynthetic capacity and thus could achieve greater carbon gain in a shorter time. However, there was no significant correlation between LLS and cavitation resistance (Fig. 2C), indicating that leaf longevity might be determined by the stem hydraulic efficiency rather than safety. Another exception is the evergreen tree *P. weinmannifolia*, which had LLS <1 year (10.5 months) but had the greatest cavitation resistance among all the species (Supplementary Data Table S2). This tree compensates for its short LLS by flushing leaves three or four times during the year, and the high cavitation-resistant stems could assure the water transport to leaves in the driest period of the year. The species with greater LLS also had a lower A_m , but higher photosynthetic WUE and greater water-stress tolerance (Fig. 2D–F).

Our study showed that stem hydraulic efficiency was evolutionarily correlated with xylem-cavitation resistance (Fig. 3B), which is consistent with the hydraulic efficiency and safety trade-off hypothesis (Martínez-Vilalta et al., 2002), but is in contrast to the results of other studies (Maherali et al., 2004; Jacobsen et al., 2007; Fan et al., 2011). However, the stem hydraulic trade-off found in the present study could not be scaled to whole-plant level, because mechanisms such as sapwood water storage, dynamics of water transport and architectural adjustments may compensate the whole-plant hydraulic safety (Meinzer et al., 2010). The present study found that the magnitude of correlation coefficients between xylem-cavitation resistance and vessel characteristics decreased and even became insignificant when phylogeny was considered, as also found by another study (Jacobsen et al., 2007). This might be due to the fact that the vessel characteristics had relatively high phylogenetic signal in the present study (Supplementary Data Table S3). The correlations between xylem-cavitation resistance and vessel characteristics may be casual, because the xylem-cavitation resistance is more directly determined by the inter-vessel pit properties, such as pit number and pit area per vessel as well as pit structure (Wheeler et al., 2005; Hacke et al., 2006; Choat et al., 2008; Lens et al., 2011).

We found close correlation between xylem-cavitation resistance and the dry-season leaf turgor-maintenance capacity, by both Pearson's and PICs methods (Fig. 2), indicating the correlated evolution in drought tolerance between stems and leaves across the evergreen and deciduous tree species. We also found wood density was evolutionarily correlated with leaf water-stress tolerance (Table 2). Previous studies showed that species with higher wood density usually had more negative minimum leaf water potential (Ackerly, 2004; Bucci et al., 2004); thus, greater leaf water stress tolerance is important for the higher wood density species. The stem–leaf co-ordination in drought tolerance also has been suggested by other studies from dry habitats; e.g. Ishida et al. (2008) found that the wood density was negatively correlated with turgor-loss point water potential among the woody species at the range site in Bonin Island, and Markesteijn et al. (2011b) found a close correlation of xylem-cavitation resistance with leaf dry

matter content in a seasonally dry forest in Bolivia. The stem–leaf co-ordination in drought tolerance is highly adaptive in dry habitats, allowing plants to maintain physiological function under water stress.

The present study showed that higher leaf density was evolutionarily correlated with lower photosynthetic capacity and higher leaf water-stress tolerance (Table 2). The negative correlation between ρ_{leaf} and photosynthetic capacity is likely due to the tendency that higher ρ_{leaf} leaves have less photosynthetic tissue and a greater gas-phase transfer resistance (Niinemets, 1999). Leaves with higher ρ_{leaf} also tend to have higher ε (Niinemets, 2001); and thus have greater capacity to adjust water potential with a small change in water content (Kozłowski and Pallardy, 2002). Moreover, we found strongly evolutionary correlations between leaf density and both leaf osmotic potential and turgor-loss point water potential (Table 2). Higher leaf density enables plants to be more tolerant of water stress at the cost of reduced photosynthetic capacity (Witkowski and Lamont, 1991; Niinemets, 2001; Alvarez-Clare and Kitajima, 2007). The above findings point to an important application of leaf density as an easily measured and important functional trait for water-stress tolerance and leaf photosynthetic capacity in tropical dry forests.

In conclusion, the co-occurring evergreen and deciduous species of tropical dry karst forest differed in their stem hydraulic traits and leaf water-stress tolerance as well as leaf photosynthetic capacity. The evergreen tree species had higher cavitation resistance and greater leaf water-stress tolerance so that could maintain their stem and leaf function in the dry season, while the deciduous species had greater hydraulic efficiency and higher photosynthetic capacity in the wet season. There was correlated evolution between LLS and xylem water transport capacity, leaf photosynthetic capacity and leaf water-stress tolerance. The strategies for plants to utilize water during drought stress require the correlated evolution among leaf and stem traits. Wood density and leaf density which are important and easily measured functional traits can be used as indicators of water-stress tolerance and leaf photosynthetic capacity in a tropical dry forest. The different hydraulic strategies between the co-occurring evergreen and deciduous trees may contribute to the maintenance of water balance of a dry karst forest ecosystem and, consequently, species co-existence and diversity.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Table S1: DNA sequences used for the phylogeny polytomy resolution within Euphorbiaceae. Table S2: means of the stem and leaf traits of the six evergreen and six deciduous angiosperm tree species. Table S3: the phylogenetic signal tests for the eco-physiological traits among the 12 species studied. Table S4: traditional and phylogenetic independent contrasts (PICs) correlations between the leaf and stem traits. Figure S1: phylogenetic relationships of the 12 species studied. Figure S2: stem vulnerability curves for the six evergreen and six deciduous tree species.

ACKNOWLEDGEMENTS

We thank Hong Ma, Yin-Bin Yang and Ting-Fa Dong for field assistance, Yun-Hong Tan for identification of plant specimens, Ze-Xin Fan and Jian-Li Zhao for data analysis, and Yong-Jiang Zhang and Megan Bartlett for useful comments on the manuscript. The Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies (XSTRE) provided the climate data, and the Biogeochemistry Laboratory of Xishuangbanna Tropical Botanical Garden analysed the leaf nutrients. This work was supported by a major '973' project from the Chinese Ministry of Science and Technology (2006CB403207).

LITERATURE CITED

- Ackerly DD. 2000. Taxon sampling, correlated evolution, and independent contrasts. *Evolution* **54**: 1480–1492.
- Ackerly DD. 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs* **74**: 25–44.
- Alvarez-Clare S, Kitajima K. 2007. Physical defence traits enhance seedling survival of neotropical tree species. *Functional Ecology* **21**: 1044–1054.
- Baltzer JL, Davies SJ, Bunyavejchewin S, Noor NSM. 2008. The role of desiccation tolerance in determining tree species distributions along the Malay–Thai Peninsula. *Functional Ecology* **22**: 221–231.
- Blomberg SP, Garland T, Ives AR. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**: 717–745.
- Brodrick TJ, Field TS. 2000. Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. *Plant, Cell & Environment* **23**: 1381–1388.
- Brodrick TJ, Holbrook NM. 2003. Changes in leaf hydraulic conductance during leaf shedding in seasonally dry tropical forest. *New Phytologist* **158**: 295–303.
- Brodrick TJ, Holbrook NM, Gutierrez MV. 2002. Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. *Plant, Cell & Environment* **25**: 1435–1444.
- Brodrick TJ, Holbrook NM, Edwards EJ, Gutierrez MV. 2003. Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant, Cell & Environment* **26**: 443–450.
- Bucci SJ, Goldstein G, Meinzer FC, Scholz FG, Franco AC, Bustamante M. 2004. Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. *Tree Physiology* **24**: 891–899.
- Cai J, Tyree MT. 2010. The impact of vessel size on vulnerability curves: data and models for within-species variability in saplings of aspen, *Populus tremuloides* Michx. *Plant, Cell & Environment* **33**: 1059–1069.
- Chabot BF, Hicks DJ. 1982. The ecology of leaf life spans. *Annual Review of Ecology and Systematics* **13**: 229–259.
- Chen J-W, Zhang Q, Cao K-F. 2009. Inter-species variation of photosynthetic and xylem hydraulic traits in the deciduous and evergreen Euphorbiaceae tree species from a seasonally tropical forest in south-western China. *Ecological Research* **24**: 65–73.
- Choat B, Ball M, Luly J, Holtum J. 2003. Pit membrane porosity and water stress-induced cavitation in four co-existing dry rainforest tree species. *Plant Physiology* **131**: 41–48.
- Choat B, Ball MC, Luly JG, Holtum JAM. 2005. Hydraulic architecture of deciduous and evergreen dry rainforest tree species from north-eastern Australia. *Trees – Structure and Function* **19**: 305–311.
- Choat B, Ball MC, Luly JG, Donnelly CF, Holtum JAM. 2006. Seasonal patterns of leaf gas exchange and water relations in dry rain forest trees of contrasting leaf phenology. *Tree Physiology* **26**: 657–664.
- Choat B, Cobb AR, Jansen S. 2008. Structure and function of bordered pits: new discoveries and impacts on whole-plant hydraulic function. *New Phytologist* **177**: 608–625.
- Clements R, Sodhi NS, Schilthuizen M, Ng PKL. 2006. Limestone karsts of Southeast Asia: imperiled arks of biodiversity. *BioScience* **56**: 733–742.
- Eamus D. 1999. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends in Ecology and Evolution* **14**: 11–16.
- Fan D-Y, Jie S-L, Liu C-C, et al. 2011. The trade-off between safety and efficiency in hydraulic architecture in 31 woody species in a karst area. *Tree Physiology* **31**: 865–877.
- Felsenstein J. 1985. Phylogenies and the Comparative Method. *The American Naturalist* **125**: 1–15.
- Ford DC, Williams PW. 2007. *Karst hydrogeology and geomorphology*. Chichester, UK: Wiley.
- Garland T, Harvey PH, Ives AR. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* **41**: 18–32.
- Goldstein G, Rada F, Rundel P, Azocar A, Orozco A. 1989. Gas exchange and water relations of evergreen and deciduous tropical savanna trees. *Annales Des Sciences Forestieres* **46**: S448–S453.
- Hacke UG, Sperry JS, Wheeler JK, Castro L. 2006. Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiology* **26**: 689–701.
- Hao G-Y, Sack L, Wang A-Y, Cao K-F, Goldstein G. 2010. Differentiation of leaf water flux and drought tolerance traits in hemiepiphytic and non-hemiepiphytic *Ficus* tree species. *Functional Ecology* **24**: 731–740.
- Hao G-Y, Goldstein G, Sack L, et al. 2011. Ecology of hemiepiphytism in fig species is based on evolutionary correlation of hydraulics and carbon economy. *Ecology* **92**: 2117–2130.
- Ishida A, Nakano T, Yazaki K, et al. 2008. Co-ordination between leaf and stem traits related to leaf carbon gain and hydraulics across 32 drought-tolerant angiosperms. *Oecologia* **156**: 193–202.
- Ishida A, Harayama H, Yazaki K, et al. 2010. Seasonal variations of gas exchange and water relations in deciduous and evergreen trees in monsoonal dry forests of Thailand. *Tree Physiology* **30**: 935–945.
- Jacobsen AL, Pratt RB, Ewers FW, Davis SD. 2007. Cavitation resistance among 26 chaparral species of southern California. *Ecological Monographs* **77**: 99–115.
- Kikuzawa K. 1991. A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *The American Naturalist* **138**: 1250–1263.
- King DA. 1994. Influence of light level on the growth and morphology of saplings in a Panamanian forest. *American Journal of Botany* **81**: 948–957.
- Kozlowski T, Pallardy S. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. *The Botanical Review* **68**: 270–334.
- Lens F, Sperry JS, Christman MA, Choat B, Rabaey D, Jansen S. 2011. Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus *Acer*. *New Phytologist* **190**: 709–723.
- Lenz TI, Wright IJ, Westoby M. 2006. Interrelations among pressure–volume curve traits across species and water availability gradients. *Physiologia Plantarum* **127**: 423–433.
- Levitt J. 1980. *Responses of plants to environmental stresses*. Vol. II. *Water, radiation, salt, and other stresses*. New York, NY: Academic Press.
- McElrone AJ, Pockman WT, Martínez-Vilalta J, Jackson RB. 2004. Variation in xylem structure and function in stems and roots of trees to 20 m depth. *New Phytologist* **163**: 507–517.
- Maherali H, Pockman W, Jackson R. 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* **85**: 2184–2199.
- Marksteijn L, Poorter L, Bongers F, Paz H, Sack L. 2011a. Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. *New Phytologist* **191**: 480–495.
- Marksteijn L, Poorter L, Paz H, Sack L, Bongers F. 2011b. Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell & Environment* **34**: 137–148.
- Martínez-Vilalta J, Prat E, Oliveras I, Piñol J. 2002. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia* **133**: 19–29.
- Meinzer F, McCulloh K, Lachenbruch B, Woodruff D, Johnson D. 2010. The blind men and the elephant: the impact of context and scale in evaluating conflicts between plant hydraulic safety and efficiency. *Oecologia* **164**: 287–296.
- Niinemets Ü. 1999. Research review: components of leaf dry mass per area – thickness and density – alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytologist* **144**: 35–47.
- Niinemets Ü. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* **82**: 453–469.

- Pammenter NW, Van Der Willigen C. 1998.** A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiology* **18**: 589–593.
- R Development Core Team. 2008.** *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.r-project.org>.
- Reich PB. 1995.** Phenology of tropical forests: patterns, causes, and consequences. *Canadian Journal of Botany – Revue Canadienne De Botanique* **73**: 164–174.
- Reich PB, Walters MB, Ellsworth DS. 1992.** Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* **62**: 365–392.
- Salleo S, Nardini A, Lo Gullo MA, Ghirardelli LA. 2002.** Changes in stem and leaf hydraulics preceding leaf shedding in *Castanea sativa* L. *Biologia Plantarum* **45**: 227–234.
- Scholz FG, Bucci SJ, Goldstein G, Meinzer FC, Franco AC, Miralles-Wilhelm F. 2007.** Biophysical properties and functional significance of stem water storage tissues in Neotropical savanna trees. *Plant, Cell & Environment* **30**: 236–248.
- Schulte PJ, Hinckley TM. 1985.** A comparison of pressure-volume curve data analysis techniques. *Journal of Experimental Botany* **36**: 1590–1602.
- Schwilk DW, Ackerly DD. 2001.** Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* **94**: 326–336.
- Selaya NG, Anten NPR. 2010.** Leaves of pioneer and later-successional trees have similar lifetime carbon gain in tropical secondary forest. *Ecology* **91**: 1102–1113.
- Simonin KA, Limm EB, Dawson TE. 2012.** Hydraulic conductance of leaves correlates with leaf lifespan: implications for lifetime carbon gain. *New Phytologist* **193**: 939–947.
- Sobrado MA. 1993.** Trade-off between water transport efficiency and leaf life-span in a tropical dry forest *Oecologia* **96**: 19–23.
- Sobrado MA. 1997.** Embolism vulnerability in drought-deciduous and evergreen species of a tropical dry forest. *Acta Oecologica – International Journal of Ecology* **18**: 383–391.
- Sperry JS, Tyree MT. 1988.** Mechanism of water stress-induced xylem embolism. *Plant Physiology* **88**: 581–587.
- Sperry JS, Donnelly JR, Tyree MT. 1988.** A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell & Environment* **11**: 35–40.
- Tamura K, Nei M. 1993.** Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution* **10**: 512–526.
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S. 2011.** MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* **28**: 2731–2739.
- Tognetti R, Longobucco A, Raschi A. 1998.** Vulnerability of xylem to embolism in relation to plant hydraulic resistance in *Quercus pubescens* and *Quercus ilex* co-occurring in a Mediterranean coppice stand in central Italy. *New Phytologist* **139**: 437–447.
- Turner NC. 1988.** Measurement of plant water status by the pressure chamber technique. *Irrigation Science* **9**: 289–308.
- Tyree MT, Zimmermann MH. 2002.** *Xylem structure and the ascent of sap*. New York, NY: Springer-Verlag.
- Wheeler J, Sperry J, Hacke U, Hoang N. 2005.** Inter-vessel pitting and cavitation in woody Rosaceae and other vesselless plants: a basis for a safety versus efficiency trade-off in xylem transport. *Plant, Cell & Environment* **28**: 800–812.
- Witkowski ETF, Lamont BB. 1991.** Leaf specific mass confounds leaf density and thickness. *Oecologia* **88**: 486–493.
- Yuan D-X. 1991.** *Karst of China*. Beijing: Geological Publishing House.
- Zhang G-C. 2006.** *A research on soil principal nutrient components of typical forest communities in Xishuangbanna*. Masters Thesis, Graduate University of Chinese Academy of Sciences, China.
- 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.
- Zhu H, Wang H, Li B, Sirirugsap P. 2003.** Biogeography and floristic affinities of the limestone flora in Southern Yunnan, China. *Annals of the Missouri Botanical Garden* **90**: 444–465.
- Zimmermann M. 1983.** *Xylem structure and the ascent of sap in plants*. New York, NY: Springer.