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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

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Abstract The objective of the present study was to examine the functional coordination among hydraulic traits, xylem characteristics and gas exchange rates across three deciduous Euphorbiaceae tree species (*Hevea brasiliensis*, *Macaranga denticulata* and *Bischofia javanica*) and three evergreen Euphorbiaceae tree species (*Drypetes indica*, *Aleurites moluccana* and *Codiaeum variegatum*) from a seasonally tropical forest in south-western China. The deciduous tree species were more vulnerable to water stress-induced embolism than the evergreen tree species. However, the deciduous tree species generally had higher maximal rates of sapwood and leaf-specific hydraulic conductivity (K_S and K_L), respectively. Compared with the evergreen tree species, the deciduous tree species, however, possessed a lower density of sapwood and a wider diameter of xylem vessels. Regardless of leaf phenology, the hydraulic vulnerability and conductivity were significantly correlated with sapwood density and mean vessel diameter. Furthermore, the hydraulic vulnerability was positively correlated with water transport efficiency. In addition, the deciduous tree species exhibited higher maximal photosynthetic rates (A_{max}) and stomatal conductance (g_{max}), but lower water use efficiency (WUE). Interestingly, the A_{max} , g_{max} and WUE were strongly correlated with K_S and K_L across the deciduous and evergreen tree species. These results suggest that xylem structure, rather than leaf phenology, accounts for the difference in hydraulic traits between the deciduous tree species and the evergreen tree species. Meanwhile, our

results show that there is a significant trade-off between hydraulic efficiency and safety, and a strong functional correlation between the hydraulic capacity and gas exchange rates across the deciduous and evergreen tree species.

Keywords Hydraulic conductivity · Hydraulic vulnerability · Gas exchange rate · Xylem structure · Leaf phenology

Introduction

Higher plants possess a vascular system that connects their water source to the sites of evaporation in the leaf mesophyll. It is generally accepted that the hydraulic conductivity of a plant's vascular system is responsible for supplying water to leaves, and, therefore, affects the rate of transpiration and photosynthesis of the leaves it supplies. However, water transport within xylem conduits is not always effective because the hydraulic pathway is vulnerable to cavitations. Cavitation is the process where a vapour phase is introduced to the xylem water column, accordingly, creating an embolism (Choat et al. 2003). Because of its inability to transmit tension, the vapour phase limits the volume flow of water through the conduit (Meinzer et al. 2001). Once embolisms occur, the conduits no longer function to conduct water, consequently, causing a decline in hydraulic conductivity. This may impair photosynthesis and growth, which are limited by the efficiency of water supply from the soil to the leaves through the xylem conduit (Brodrribb and Field 2000; Hubbard et al. 2001).

The deciduous tree species have higher rates of water transport (Gartner et al. 1990; Sobrado 1997), but this fact alone does not imply that the hydraulic conductivity for the evergreen tree species is always inefficient (Brodrribb et al. 2003). On the other hand, previous work

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has demonstrated that the deciduous tree species were more vulnerable to water stress-induced embolism than the evergreen tree species (Choat et al. 2003). Nevertheless, there is evidence that the resistance of stem conduit to cavitations is independent of the leaf phenology (Brodribb et al. 2003; Choat et al. 2007). Therefore, it is commonly believed that the vulnerability of stem conduits to embolisms is influenced by the structure of the xylem conduit (Hacke et al. 2001; Domec and Gartner 2002). Also, the deciduous tree species have a greater vessel length and a wider vessel diameter than the evergreen tree species (Sobrado 1993; Choat et al. 2005). Different hydraulic architectures may cause the deciduous and evergreen tree species to employ different strategies to deal with the same conditions. For example, tropical deciduous tree species shed their leaves during drought season, while co-existing evergreen tree species must maintain water transport to their canopies at a rate sufficient to prevent permanent damage due to drought (Holbrook et al. 1995).

Interestingly, there is evidence of good functional coordination between gas exchange and hydraulic conductivity across tree species (Brodribb and Field 2000; Meinzer 2002). Furthermore, leaf photosynthetic traits are correlated with many of the same whole-organism traits that can be predicted by plant hydraulic conductivity (Santiago et al. 2004). Thus, we may speculate that hydraulic traits strongly affect photosynthetic rates because it influences the rate at which water can be transported to the leaves. Rather, the xylem structure, which determines the hydraulic traits, has the potential to affect the leaf water status and, consequently, to limit photosynthesis and growth (Sperry and Saliendra 1994; Brodribb and Field 2000; Santiago et al. 2004). Indeed, photosynthesis is the sole mechanism of carbon assimilation in most vascular plants, and water is likely to limit photosynthesis on some time scale, and, hereby, it is widely accepted that the primary trait directly regulated by hydraulic conductivity is stomatal conductance rather than the photosynthetic rate.

In the present study, we examined the hydraulic architecture and photosynthetic traits in three deciduous tree species (*Hevea brasiliensis*, *Macaranga denticulata* and *Bischofia javanica*) and three evergreen tree species (*Drypetes indica*, *Aleurites moluccana* and *Codiaeum variegatum*) coexisting in a seasonally tropical forest in south-western China. All of the six tree species belong to a single family (Euphorbiaceae) and, thus, the experimental results largely ruled out the impact of differences due to phylogeny. We hypothesized that there exists a trade-off between hydraulic efficiency and safety such that the deciduous tree species have a more efficient water transport system, but are more vulnerable to water stress-induced embolism than the evergreen tree species and such a difference will reflect more in the xylem structure than leaf phenology, and that the variation in hydraulic traits can interpret the variation in leaf photosynthetic traits across the deciduous and evergreen tree species.

Materials and methods

Study site

The study was carried out at the Xishuangbanna Tropical Botanical Garden (21°41'N, 101°25'E and 570 m a.s.l.), The Chinese Academy of Sciences, in south-western Yunnan, China. The mean annual air temperature is about 21.7°C and the annual precipitation is about 1,560 mm. However, it has a strong seasonality such that more than 85% of precipitation occurs between the months of May and October, thereby, resulting in a pronounced rainy season from May to October, and a well-defined dry season from November to April. All measurements in the present study were performed in the middle of the rainy season between July and August.

Plant material

Six tree species of Euphorbiaceae (*H. brasiliensis*, *M. denticulata*, *B. javanica*, *D. indica*, *A. moluccana* and *C. variegatum*) were selected for our study. *H. brasiliensis* is an evergreen tree in its native habitat of South America, but, interestingly, it is deciduous in the present region; it sheds all of its leaves at the end of February, and new leaves flush in early March. *M. denticulata* and *B. javanica* are native deciduous tree species. Correspondingly, *D. indica*, *A. moluccana* and *C. variegatum* are evergreen tree species. The tree height and the diameter at breast height for *C. variegatum* is 2–3 m and 3–4 cm, respectively. The tree height for the remaining tree species are 5–7 m and the diameter at breast height are 15–20 cm. All of the sampled tree species selected in our study are fully exposed to sunlight and three to five mature individuals were located for each of the target species. All of the samplings and measurements were conducted at the near-top canopy.

Hydraulic vulnerability curves

Stem hydraulic vulnerability curves were determined by the bench drying method on detached branches (Sperry and Tyree 1988). Large (about 1.5-m) branches from three to five individuals of each species were collected early in the morning, immediately sealed in plastic bags and then transported to the laboratory. In the laboratory, these branches were allowed to dehydrate for different periods of time to reach a large variety of water potential. The branches were then sealed into double layers of black plastic bags with wet paper towels for at least 2 h to equilibrate between different parts of the stems. A series of measurements was then made on the branch tissue using tubing apparatus to assess the percentage loss of hydraulic conductivity (PLC) as a result of embolism. The xylem tension of

branch segments was assessed by measuring the water potential of three to five leaves distal to the stem segment. A stem segment (15–20-cm) was then cut under water and connected to the hydraulic apparatus. For a fixed pressure head, the hydraulic conductivity (K_h) is proportional to the volumetric flow rate (J_v) of water through the stem segments, and, thus, in practice, the calculations of PLC were based on J_v rather than K_h . After the initial measurement of flow rate (J_i), the segments were flushed using filtered, 10 mmol oxalic acid solution under a constant pressure of 0.15–0.18 MPa for 10–30 min to remove embolisms until stable readings of flow rate were reached. Then, the maximum flow rate (J_{max}) was measured by using the same pressure head as before. The PLC was then calculated as: $PLC = 100(J_{max} - J_i)/J_{max}$. For each branch, three to five segments were selected for measurement, and the total number of measurements for each species was between 50 and 100. The vulnerability curves were generated for each species by fitting curves for the PLC against xylem tension (Pammenter and Vander Willigen 1998): $PLC = 100/[1 + \exp(a(\Psi - b))]$, where Ψ is the xylem tension, a is the slope of the line and b is the xylem tension at which 50% loss of conductivity occurs (Ψ_{P50}). In addition, Ψ_{P12} and Ψ_{P88} were calculated from the fitted curves. The value of Ψ_{P12} , termed the air entry point (Sparks and Black 1999), is an estimate of the xylem tension at which the runaway cavitations and embolisms begin when the resistance to the air entry of pit membranes within the conducting xylem is overcome (Sperry and Tyree 1988). Likewise, Ψ_{P88} is the full embolism point, interpreted as approximating the actual tension of the xylem before it becomes non-conductive (Domec and Gartner 2001). In our study, Ψ_{P88-12} (Ψ_{P88} subtracted from Ψ_{P12}) was defined as the capacities for maintaining xylem conductivity. The more negative the Ψ_{P88-12} values, the higher the capacities for maintaining xylem hydraulic conductivity.

Stem hydraulic conductivity

Stem K_h was measured on three to five branches per species, taken from three to five different individuals. Branches of about 1.5 m in length were collected early in the morning, recut immediately under water and then returned to the laboratory shortly. Branch segments of more than 30 cm in length and 7–9 mm in diameter were cut under water, trimmed with a fresh razor blade and connected to the hydraulic apparatus. Segments were perfused with filtered, 10 mmol oxalic acid solution. The perfusing solution was supplied from a reservoir raised above the flow meter to generate a gravity-induced pressure head of approximately 5 kPa. The segment was perfused with solution until a steady-state flow was attained, at which point, the hydraulic conductivity of the segment was calculated as $K_h = FL/\Delta P$, where F is the flow rate (kg s^{-1}), ΔP is the

pressure drop (MPa) along the stem segment and L is the length of the stem segment (m). Upon completion of the measurement, the segment was perfused with 0.01% Safranin dye to determine the conductive sapwood area. The leaf surface area distal to the stem segment was measured using a leaf area meter (LI-Cor, Lincoln, NE). The sapwood and leaf areas were used to calculate K_S and K_L , respectively. The sapwood-specific hydraulic conductivity (K_S , $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) and leaf-specific hydraulic conductivity (K_L , $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) were calculated as K_h divided by the sapwood and leaf areas, respectively.

Stem xylem anatomy and sapwood density

The vessel diameters were measured from transverse sections of xylem tissue. Transverse sections of the branch were made, and at least 50–70 vessels were measured in each of the samples. The sapwood density (g cm^{-3}) was determined for each sample that was tested hydraulically. Sapwood with both bark and pith removed was immersed in tap water overnight to saturate the samples. After the surface was wiped dry, the volume of sapwood was measured immediately using the water displacement method. Sapwood density = M_d/V_f , where M_d is the oven dry mass (dried at 80°C for 72 h) and V_f is the fresh volume.

Gas exchange

Leaf gas exchange rates were measured with a portable photosynthesis apparatus (LI-6400, Li-Cor, Lincoln, NE). All measurements were performed between 09:30 and 11:00 hours to avoid the midday depression in photosynthesis. We measured sun-exposed, fully expanded and apparently non-senescent leaves at the near-top canopy by dint of a mobile platform. The relationship between the photosynthetic photon flux density (PPFD) and the carbon assimilation rate was determined for leaves in three stems per species, taken from three to five different individuals. The PPFD, CO_2 concentration and temperature in the chamber were 0–1,500 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$, 360 $\mu\text{mol mol}^{-1}$ and 30°C, respectively. The PPFD was controlled by an internal LED light source (LI-6400-2B). The PPFD was increased stepwise to a maximum of 1,500 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$, which was sufficient to induce light-saturate photosynthesis. Measurements were logged once the rates of gas exchange became stable, which took 5–15 min at each point, depending on the preceding conditions. The light response of photosynthesis was fitted to a nonrectangular hyperbola (Webb et al. 1974):

$A(\text{PPFD}) = A_{max} - C_o e^{-b \cdot \text{PPFD}}$, where A_{max} is the maximum net photosynthesis rate at light saturation.

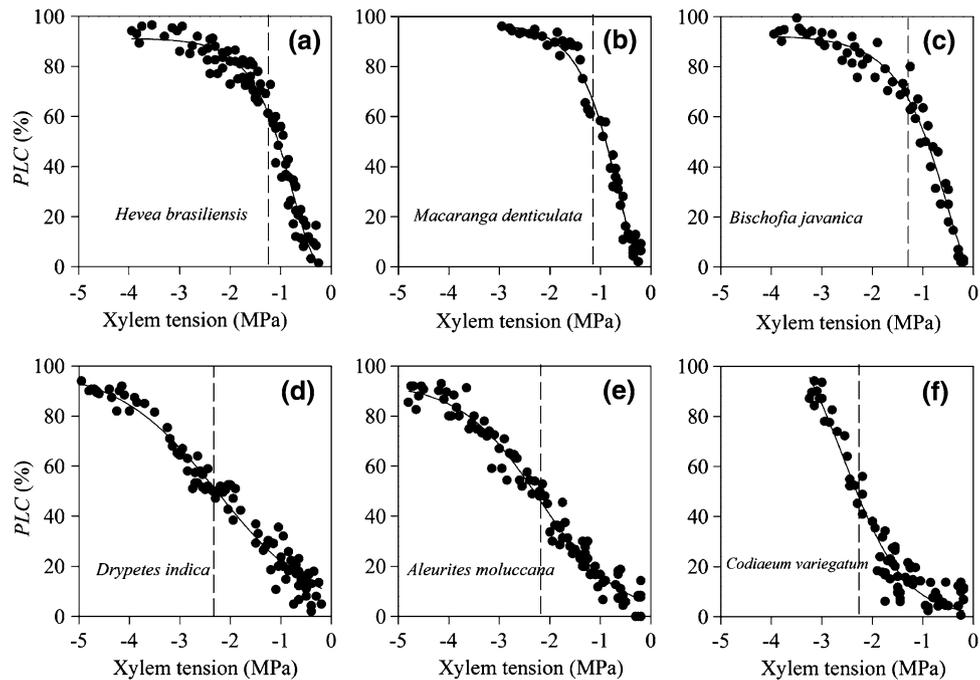


Fig. 1 Vulnerability to water stress-induced embolism in six tree species; *Hevea brasiliensis*, *Macaranga denticulata*, *Bischofia javanica*, *Drypetes indica*, *Aleurites moluccana* and *Codiaeum variegatum*. Percentage loss of hydraulic conductivity (PLC) is

plotted against xylem tension for each tree species. The vertical dashed lines indicate the xylem tension at which 50% loss of hydraulic conductivity occurs

In addition, the maximum stomatal conductance (g_{\max}) and instantaneous water use efficiency (WUE, A/g) were calculated from the above-measured data.

Statistical analysis

Statistical and regression analyses were performed with the SPSS software package (Chicago, IL). Except for Ψ_{P12} , Ψ_{P88} and Ψ_{P50} , calculated from the fitted curves, which are shown as means, the other variables are given as mean \pm SD. The significance of the relationships between traits was evaluated by one-way analysis of variance (ANOVA). Correlations between two variables were also examined by linear or nonlinear regression analyses. Differences between relationships were accepted as significant if P was ≤ 0.05 .

Results

Vulnerability to embolisms

The xylem tension at which 50% loss of hydraulic conductivity occurred was more negative in the evergreen tree species (Fig. 1). Of the evergreen tree species, Ψ_{P50} was -2.32 , -2.17 and -2.23 MPa for *D. indica*, *A. moluccana* and *C. variegatum*, respectively. Correspondingly, Ψ_{P50}

occurred at -1.27 , -1.14 and -1.27 MPa for *H. brasiliensis*, *M. denticulata* and *B. javanica*, respectively. Ψ_{P12} and Ψ_{P88} were also more negative in the evergreen tree species (Table 1). Ψ_{P12} for the deciduous tree species were less negative than -0.5 MPa (e.g. the maximum value of Ψ_{P12} attained -0.10 MPa in *B. javanica*), while Ψ_{P12} for the evergreen tree species were more negative than -0.5 MPa. Ψ_{P88} for the deciduous tree species ranged from -1.86 to -2.40 MPa, whereas Ψ_{P88} for the evergreen tree species fluctuated between -3.27 and -4.00 MPa. Compared to the deciduous tree species, the evergreen tree species generally have higher capacities for maintaining xylem conductivity (Ψ_{P88-12} , Table 1).

Hydraulic traits

In general, the deciduous tree species exhibited clearly higher values of K_L and K_S than the evergreen tree species (Table 1). Nevertheless, higher values of K_L and K_S were also observed in the evergreen tree species of *A. moluccana*, and its K_L value of $4.27 \pm 1.55 \times 10^{-4}$ $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ even exceeded that of $3.64 \pm 1.38 \times 10^{-4}$ $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ for the deciduous tree species of *M. denticulata*. Indeed, the values of K_L for the three deciduous tree species were between 2 and 8 times greater than those for the remaining two evergreen tree species of *D. indica* and *C. variegatum*, and, correspondingly, the values of K_S were between 5 and 10 times greater.

Table 1 Photosynthetic and hydraulic traits in six study tree species: *Hevea brasiliensis*, *Macaranga denticulata*, *Bischofia javanica*, *Drypetes indica*, *Aleurites moluccana* and *Cordia alliodora*

Tree species	Leaf phenology	A_{\max}	g_{\max}	WUE	K_L	K_S	$\Psi_{P_{12}}$	$\Psi_{P_{88}}$	$\Psi_{P_{88-12}}$	$\Psi_{P_{50}}$	ρ	D_{m-v}
<i>H. brasiliensis</i>	Deciduous	14.18 ± 1.29	0.34 ± 0.01	50 ± 3.11	4.08 ± 1.02	4.38 ± 1.28	-0.16	-2.38	-2.23	-1.27	0.48 ± 0.04	80.9 ± 12.6
<i>M. denticulata</i>	Deciduous	16.72 ± 1.26	0.29 ± 0.02	54 ± 2.42	3.64 ± 1.38	4.41 ± 1.14	-0.42	-1.86	-1.45	-1.14	0.41 ± 0.03	97.3 ± 10.9
<i>B. javanica</i>	Deciduous	14.35 ± 1.42	0.28 ± 0.02	50 ± 3.28	4.50 ± 1.12	6.16 ± 1.58	-0.10	-2.40	-2.35	-1.27	0.43 ± 0.04	85.4 ± 13.9
<i>D. indica</i>	Evergreen	4.29 ± 0.62	0.09 ± 0.01	58 ± 2.16	0.56 ± 0.26	0.60 ± 0.46	-0.64	-4.00	-3.35	-2.32	0.67 ± 0.04	33.6 ± 4.5
<i>A. moluccana</i>	Evergreen	11.79 ± 1.20	0.20 ± 0.01	54 ± 3.67	4.27 ± 1.55	3.57 ± 1.33	-0.59	-3.74	-3.15	-2.17	0.52 ± 0.03	49.2 ± 3.2
<i>C. variegatum</i>	Evergreen	7.22 ± 0.72	0.13 ± 0.01	56 ± 2.09	1.71 ± 0.92	0.86 ± 0.48	-1.20	-3.27	-2.07	-2.23	0.49 ± 0.05	38.0 ± 5.6

A_{\max} = maximum net photosynthetic rates ($\mu\text{mol m}^{-2} \text{s}^{-1}$); g_{\max} = maximum stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$); WUE = instantaneous water use efficiency ($\mu\text{mol mol}^{-1}$); K_L = leaf area specific hydraulic conductivity ($10^{-4} \text{ kg m}^{-1} \text{ s}^{-1} \text{ Mpa}^{-1}$); K_S = sapwood area specific hydraulic conductivity ($\text{kg m}^{-1} \text{ s}^{-1} \text{ Mpa}^{-1}$); $\Psi_{P_{12}}$ = xylem tension at which the runaway cavitations and embolisms begin (MPa); $\Psi_{P_{88}}$ = xylem tension at which the xylem becomes non-conductive (MPa); $\Psi_{P_{88-12}}$ = $\Psi_{P_{88}}$ subtracted from $\Psi_{P_{12}}$ (MPa); $\Psi_{P_{50}}$ = xylem tension at 50% loss of hydraulic conductivity (MPa); ρ = sapwood density (g cm^{-3}); D_{m-v} = mean vessel diameter (μm)

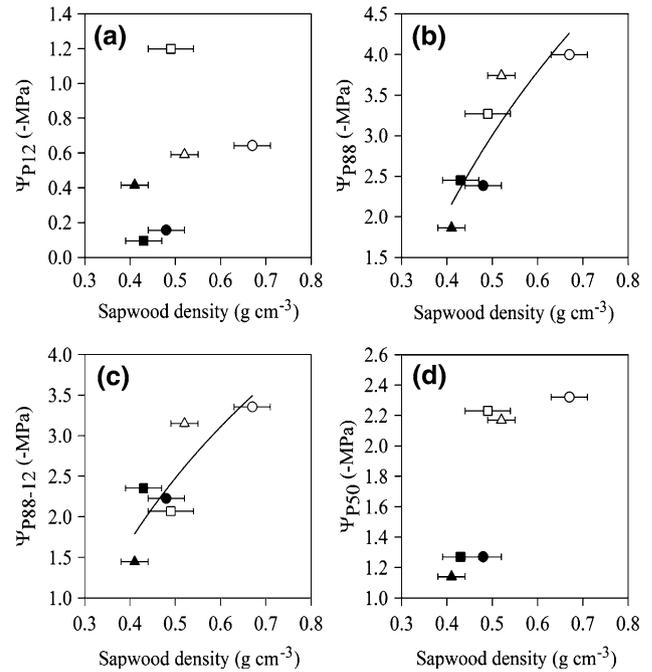


Fig. 2 Correlations between hydraulic traits and sapwood density across the deciduous and evergreen Euphorbiaceae tree species. The deciduous tree species: *H. brasiliensis* (filled circles), *M. denticulata* (filled triangles) and *B. javanica* (filled squares). The evergreen tree species: *D. indica* (open circles), *A. moluccana* (open triangles) and *C. variegatum* (open squares). $\Psi_{P_{12}}$ = xylem tension at which the runaway cavitations and embolisms begin; $\Psi_{P_{88}}$ = xylem tension at which the xylem becomes non-conductive; $\Psi_{P_{88-12}}$ = $\Psi_{P_{88}}$ subtracted from $\Psi_{P_{12}}$; $\Psi_{P_{50}}$ = xylem tension at 50% loss of hydraulic conductivity. The values are species means. The mean \pm SD ($n = 3-5$) is shown for each point. The solid lines represent the best-fit linear and non-linear regressions

Xylem traits

The mean vessel diameters (D_{m-v}) were considerably narrower in the evergreen tree species than in the deciduous tree species (Table 1). In brief, the values of D_{m-v} for the deciduous tree species were between 2 and 3 times larger than those for the evergreen tree species. In addition, the evergreen tree species generally exhibited higher values of sapwood density (ρ) than the deciduous tree species (Table 1).

Photosynthetic traits

As shown in Table 1, A_{\max} in the three deciduous tree species were greater than $14.0 \mu\text{mol m}^{-2} \text{s}^{-1}$, whereas A_{\max} in the three evergreen tree species were less than $12.0 \mu\text{mol m}^{-2} \text{s}^{-1}$. Correspondingly, g_{\max} in the three deciduous tree species ranged from 0.28 ± 0.02 to $0.34 \pm 0.01 \text{ mol m}^{-2} \text{s}^{-1}$, while g_{\max} in the evergreen tree species were $\leq 0.20 \pm 0.01 \text{ mol m}^{-2} \text{s}^{-1}$. The lowest g_{\max} was observed in *D. indica*, which was accompanied by the lowest A_{\max} . In general, the higher WUE values were observed in the evergreen tree species (Table 1).

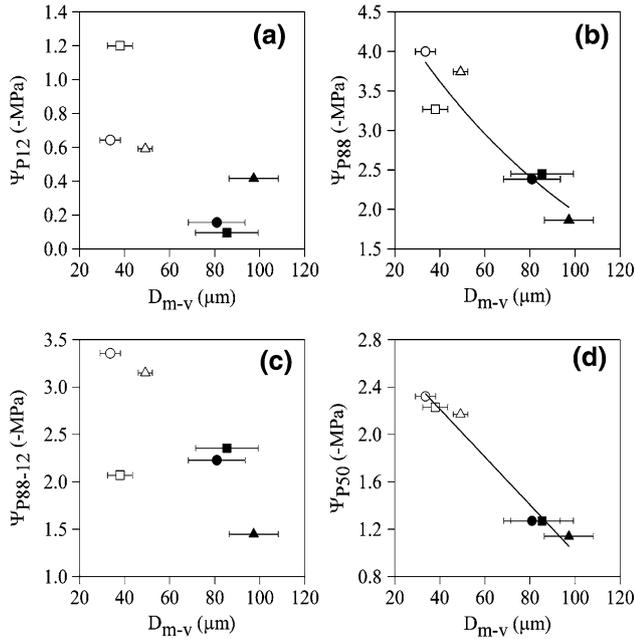


Fig. 3 Correlations between hydraulic traits and the mean vessel diameter (D_{m-v}) across the deciduous and evergreen Euphorbiaceae tree species. See Fig. 2 for a description of the figure annotations

Relationships between traits

Negative correlations of Ψ_{P12} ($R^2 = 0.20$, $P = 0.37$), Ψ_{P88} ($R^2 = 0.78$, $P < 0.05$), Ψ_{P88-12} ($R^2 = 0.72$, $P < 0.05$) and Ψ_{P50} ($R^2 = 0.63$, $P = 0.06$) with sapwood density were obtained across the six tree species (Fig. 2). Conversely, there were positive relationships between Ψ_{P12} ($R^2 = 0.59$, $P = 0.07$), Ψ_{P88} ($R^2 = 0.90$, $P < 0.01$), Ψ_{P88-12} ($R^2 = 0.49$, $P = 0.12$), Ψ_{P50} ($R^2 = 0.97$, $P < 0.01$) and D_{m-v} (Fig. 3). As shown in Fig. 4, the K_S values were positively related to Ψ_{P12} ($R^2 = 0.75$, $P < 0.05$), Ψ_{P88} ($R^2 = 0.53$, $P < 0.1$) and Ψ_{P50} ($R^2 = 0.73$, $P < 0.05$). In addition, there were negative correlations of K_L ($R^2 = 0.62$, $P = 0.07$) and K_S ($R^2 = 0.73$, $P < 0.05$) with sapwood density (Fig. 5a, b), while the positive relationships between K_L and D_{m-v} ($R^2 = 0.83$, $P < 0.05$) and between K_S and D_{m-v} ($R^2 = 0.64$, $P = 0.05$) were observed across the six tree species (Fig. 5c, d). Also, there were significantly positive relationships between K_L , K_S and A_{max} , and between K_L , K_S and g_{max} (Fig. 6a–d). In contrast, there were significantly negative correlations of the WUE values with K_L and K_S (Fig. 6e, f).

Discussion

The vulnerability curves indicated that the three deciduous tree species were more vulnerable to water stress-induced embolism than the three evergreen tree species. This is consistent with the previously reported results that the deciduous tree species, *Brachychiton australis* and *Cochlospermum gillivaii*, were more susceptible to

water stress-induced embolism than the coexisting evergreen tree species, *Alphitonia excelsa* and *Austromyrtus bidwillii* (Choat et al. 2003). Meanwhile, the less negative Ψ_{P12} and Ψ_{P88} values for the deciduous tree species further indicates that the deciduous tree species are more sensitive to water stress-induced embolism. On the other hand, it should be noted that the value of Ψ_{P88-12} for the evergreen tree species of *C. variegatum* was less negative than that for the deciduous tree species of *H. brasiliensis* and *B. javanica*. However, the Ψ_{P12} value for *C. variegatum* was the most negative among the study six tree species, and this possibly compensates for the less negative Ψ_{P88-12} value of *C. variegatum*. Overall, the evergreen tree species are more resistant to water stress-induced embolism, and have a higher capacity for maintaining the stem hydraulic conductivity.

However, it has been proposed that the structure of xylem vessels should be seen as an important factor in determining the occurrence of water stress-induced embolism (Zimmermann 1983), and that the vulnerability of xylem to water stress-induced embolism is more closely related to the porosity of inter-vessel pit membranes (Choat et al. 2003). The characteristics of inter-vessel pit membranes have not been checked, but the vessel analysed in our study demonstrated that there were considerable differences in the vessel diameter between different leaf phenologies, but not among identical leaf phenologies. This characteristic agrees with the above-mentioned hydraulic traits that there were substantial differences in the resistance to water stress-induced embolisms between different leaf phenologies, but not among identical leaf phenologies. Indeed, the differences in the vessel diameters cannot fully explain the differences in the resistance to embolisms.

The wood density in many tree species from different ecosystems is correlated with a variety of hydraulic related traits, such as the capacity of stem water storage, the efficiency of xylem water transport, the regulation of leaf water status and the avoidance of turgor loss (Meinzer 2003; Bucci et al. 2004; Gartner and Meinzer 2005). Xylem becomes more resistant to water stress-induced embolism with increasing wood density (Hacke et al. 2001; Hao et al. 2008). It is important to note that, in our study, the resistance to embolism was more strongly correlated to D_{m-v} than the sapwood density. More recently, there has been evidence of a strongly positive correlation between Ψ_{P12} and the xylem conduit diameter and tracheid length (Rosner et al. 2007) and between Ψ_{P50} and the mean hydraulically weighted conduit diameter (Maherali et al. 2006). In addition, our analysis of the data of Choat et al. (2003) also demonstrated that Ψ_{P50} was significantly related to the mean vessel diameter. Therefore, the resistance of xylem conduit to embolisms may be related to a series of sapwood characteristics, such as the diameter and length of the vessels, porosity, strength and durability of the pit membrane, and the wood density.

Higher hydraulic vulnerability is associated with higher hydraulic conductivity within (Gartner 1995;

Fig. 4 Correlations of the sapwood area specific hydraulic conductivity (K_S) with Ψ_{P12} , Ψ_{P88} and Ψ_{P50} across the deciduous and evergreen Euphorbiaceae tree species. See Fig. 2 for a description of the figure annotations

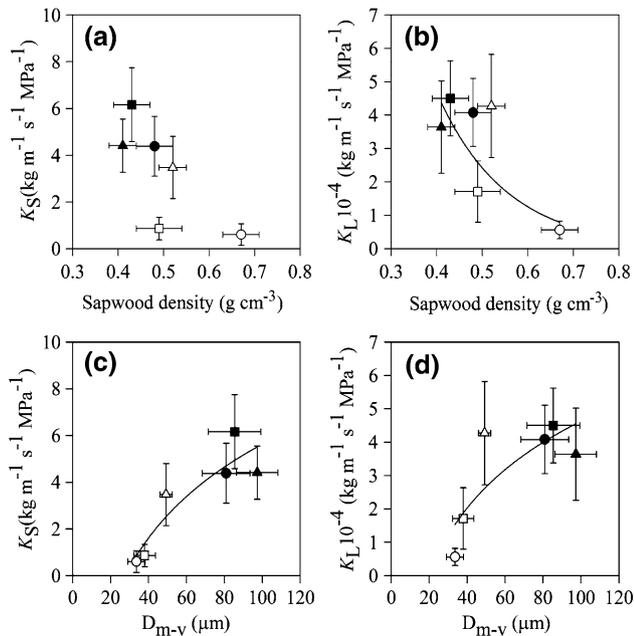
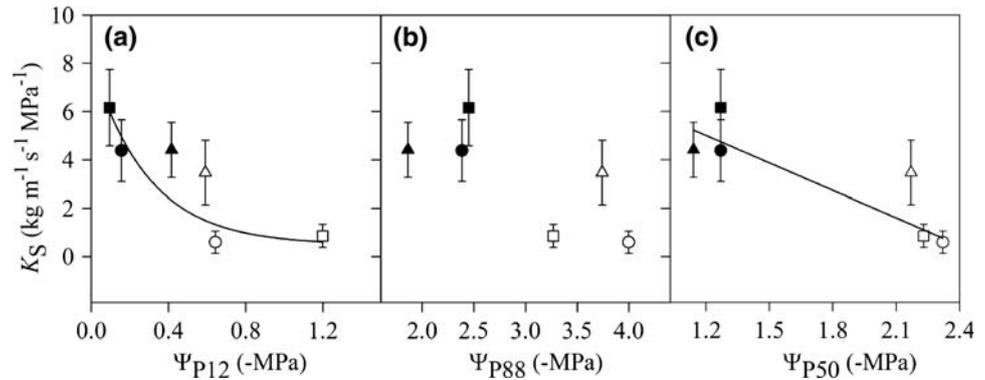


Fig. 5 Hydraulic conductivity as a function of sapwood density and mean vessel diameter (D_{m-v}) across the deciduous and evergreen Euphorbiaceae tree species. K_S = sapwood area specific hydraulic conductivity; K_L = leaf area specific hydraulic conductivity. See Fig. 2 for a description of the figure annotations

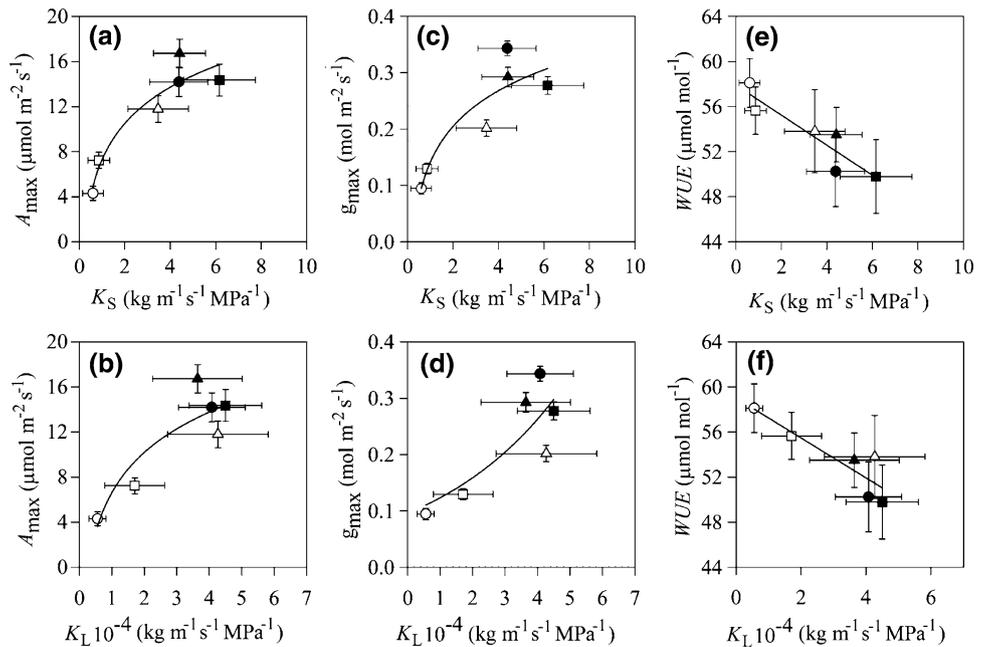
Kavanagh et al. 1999; Domec and Gartner 2002; Rosner et al. 2006) and across species (Piñol and Sala 2000; Maherali et al. 2004). In general, trees with higher hydraulic conductivity have wider vessel diameters, and such a vessel structure is more susceptible to water stress-induced embolisms. This line of reasoning is confirmed by our results that the hydraulic conductivity was positively related to D_{m-v} , while the resistance of xylem conduit to embolisms was negatively correlated with D_{m-v} . Actually, this indicates that trees exhibit different strategies for acquiring water resource based on a trade-off between hydraulic safety and efficiency. Higher hydraulic conductivity might guarantee the sufficient acquisition of water resource for trees with higher hydraulic vulnerability before embolism occurs, while a low hydraulic vulnerability would ensure trees with low hydraulic conductivity the sufficient acquisition of water resource by delaying the occurrence of embolisms.

In general, the deciduous tree species had higher hydraulic conductivity, especially K_S (Table 1). These results are similar to those reported for the evergreen and deciduous tree species from a seasonally dry forest in Venezuela, in which K_L was 2–4 times lower and K_S was 2–6 times lower in the evergreen tree species (Sobrado 1993). In contrast, Goldstein et al. (1989) demonstrated that two evergreen tree species from a Venezuelan tropical savanna had higher K_L and K_S values than two co-existing deciduous tree species. More recently, Brodrribb et al. (2002) observed that the values of K_S overlapped substantially for a range of evergreen and deciduous tree species from a dry forest in Costa Rica, although the highest values recorded were for two deciduous species. Similarly, in our study, K_L for the evergreen tree species of *A. moluccana* was higher than the deciduous tree species of *H. brasiliensis* and *M. denticulata*, and K_S for the former also approached that for the latter. These results strongly suggest that the differences in both K_L and K_S values between the evergreen and deciduous tree species possibly rely on xylem structure characteristics. From the Hagen–Poiseuille law, it is predicted that the wider vessels of tree species would result in higher flow rates for a given pressure gradient. This is confirmed by our results that K_L and K_S were positively correlated with D_{m-v} .

On the other hand, the deciduous tree species exhibited higher A_{max} and g_{max} values. This is consistent with previously reported results (Reich et al. 1992; Villar et al. 1995; Cornelissen et al. 1996). Furthermore, A_{max} and g_{max} were positively correlated with K_L and K_S across the evergreen and deciduous tree species. The relationship between photosynthetic and hydraulic traits may reflect a balance between carbon gain and water transport capacity, thus, the primary features regulated by hydraulic conductivity are probably stomatal conductance and, in turn, intercellular CO_2 . Therefore, the relationship between photosynthetic rates and hydraulic conductivity is mediated by stomata to meet the demand for photosynthetic CO_2 assimilation while controlling water loss from leaves in a manner that minimises embolisms in the plant hydraulic system (Katul et al. 2003; Santiago et al. 2004).

Trees with lower photosynthetic rates and hydraulic conductivity showed evidence of higher WUE, and the

Fig. 6 Correlations between hydraulic and photosynthetic traits across the deciduous and evergreen Euphorbiaceae tree species. K_S = sapwood area specific hydraulic conductivity; K_L = leaf area specific hydraulic conductivity, A_{max} = maximum photosynthetic rates; g_{max} = maximum stomatal conductance; WUE = instantaneous water use efficiency. See Fig. 2 for a description of the figure annotations



WUE value was negatively related to K_L and K_S across the evergreen and deciduous tree species. This suggests that trees with lower efficiency in water transport systems preferentially use the limited water resources to enhance photosynthetic capacity, consequently resulting in higher WUE, while trees with higher efficiency in water transport systems are not readily restricted by water resources, and, thus, possibly show a preference for using other limited resources to enhance photosynthetic capacity. The results obtained here are consistent with previously reported results. For example, Santiago et al. (2004) reported that trees with high K_L would exhibit correspondingly low WUE, consequently resulting in a higher photosynthetic rate per unit nitrogen.

In conclusion, the deciduous tree species was more vulnerable to water stress-induced embolism and had higher hydraulic conductivity. However, such differences in hydraulic traits between the deciduous and evergreen tree species should be attributed more to the xylem structure than leaf phenology. Meanwhile, our study showed that the differences in the hydraulic conductivity and vulnerability lead to a significant trade-off between hydraulic efficiency and safety, and that there was a strong functional correlation between the hydraulic capacity and gas exchange rates across the deciduous and evergreen tree species.

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