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Research paper

# Different hydraulic traits of woody plants from tropical forests with contrasting soil water availability

Shi-Dan Zhu[1,3,†], Ya-Jun Chen[2,†], Pei-Li Fu[2] and Kun-Fang Cao[1,3]

[1]Guangxi Key Laboratory of Forest Ecology and Conservation, State Key Laboratory for Conservation and Utilization of Subtropical Agro-bioresources, College of Forestry, Guangxi University, Nanning 530004, Guangxi, China; [2]Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, Yunnan, China; [3]Corresponding authors (zhushidan@gxu.edu.cn; kunfangcao@gxu.edu.cn)

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**In southwestern China, tropical karst forests (KF) and non-karst rain forests (NKF) have different species composition and forest structure owing to contrasting soil water availability, but with a few species that occur in both forests. Plant hydraulic traits are important for understanding the species' distribution patterns in these two forest types, but related studies are rare. In this study, we investigated hydraulic conductivity, vulnerability to drought-induced cavitation and wood anatomy of 23 abundant and typical woody species from a KF and a neighboring NKF, as well as two *Bauhinia* liana species common to both forests. We found that the KF species tended to have higher sapwood density, smaller vessel diameter, lower specific hydraulic conductivity ($k_s$) and leaf to sapwood area ratio, and were more resistant to cavitation than NKF species. Across the 23 species distinctly occurring in either KF or NKF, there was a significant tradeoff between hydraulic efficiency and safety, which might be an underlying mechanism for distributions of these species across the two forests. Interestingly, by possessing rather large and long vessels, the two *Bauhinia* liana species had extremely high $k_s$ but were also high resistance to cavitation (escaping hydraulic tradeoff). This might be partially due to their distinctly dimorphic vessels, but contribute to their wide occurrence in both forests.**

***Keywords***: cavitation, hydraulic conductivity, liana, sapwood density, tradeoff, vessel diameter.

## Introduction

Water availability is a key factor in determining plant species distribution, community structure and diversity in many tropical forests (Engelbrecht et al. 2007, Poorter and Markesteijn 2008). For example, clear patterns in species distribution along the moisture gradient have been observed in many tropical regions such as the Cerrado-Amazonian forest transition zone in central Brazil (Tuomisto et al. 2003) and across the Kangar-Pattani Line in Southeast Asia (Baltzer et al. 2007). The association between water availability and community composition has been amply documented (Comita and Engelbrecht 2009, Fortunel et al. 2014). Recent studies have reported that plant hydraulic architecture is a key mechanistic trait determining the species distribution along a soil moisture gradient (Baltzer et al. 2008, Kursar et al. 2009, Zhu et al. 2013, Pineda-Garcia et al. 2016).

Xylem hydraulic architecture describes the ability of xylem to supply water to distal leaves and to tolerate drought-induced cavitation (Tyree and Ewers 1991, Pratt et al. 2008). These characteristics are determined by xylem anatomy (Hacke and Sperry 2001), and are related to plant performance such as growth (Zhang and Cao 2009, Poorter et al. 2010) and drought tolerance (Lopez et al. 2005, Canham et al. 2009). Many studies have reported the hydraulic efficiency–safety tradeoff: the capacity for xylem to transport water vs the ability to resist embolism formation and spread (Sperry et al. 1994, Hacke et al. 2006, Litvak et al. 2012). This tradeoff has been suggested to

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[†]These authors contributed equally.

explain hydraulic adaptation in plants growing in environments with various water availabilities, e.g., species from dry habitats tend to have narrower vessels, more dense wood, and thus greater resistance to drought-induced cavitation but lower hydraulic conductivity compared with those from wet habitats (Pockman and Sperry 2000, Canham et al. 2009). By contrast, such a tradeoff is not found in nine *Cordia* species growing in three tropical rain forests (Choat et al. 2007), or is rather weak in global data meta-analysis (Gleason et al. 2016).

Southwest China covers one of the world's largest continuous karst zone, with a total karst land area of 550 000 km$^2$ (Yuan 1992). The forests in this karst zone host a high richness of total and endemic plant species (Zhu et al. 1998). The habitats of karst areas are characterized by large rock outcrops, shallow and patchy soils, and rapid subterranean drainage and overland flow (Yuan 1992, Zhang et al. 2011). Therefore, karst plants frequently experience drought because of low soil water availability, particularly in the dry season (Fu et al. 2012, 2015). Previous forest surveys have reported that tropical karst forests (KF) differ significantly in species composition from adjacent non-karst rain forests (NKF; Zhu et al. 1998, 2003). However, a few species can be found commonly in both forests (Zhu et al. 1998), for example, two *Bauhinia* liana species, *Bauhinia tenuiflora* (Watt ex C.B. Clarke) and *Bauhinia touranensis* Gagnep. Plant hydraulic traits might be an underlying mechanisms governing species distribution patterns in these two forests, but related studies are rare.

Lianas are climbing plants that produce little wood for mechanical support (Gerwing et al. 2006), and are an important component of tropical forests (Schnitzer and Bongers 2002). It is generally assumed that lianas possess high water transport efficiency due to large and long vessels (Ewer and Fisher 1991, Jacobsen et al. 2012), but are highly susceptible to drought-induced cavitation (Zhu and Cao 2009, Van der Sande et al. 2013). However, several liana species from either arid or humid regions have been reported to be highly resistant to cavitation (Choat et al. 2010, Vergeynst et al. 2014, Carvalho et al. 2015). In a previous study, Baas et al. (2004) indicated that lianas possessing both large and small vessels in the wood might achieve both hydraulic efficiency and safety. This speculation has not been closely tested.

In the present study, we investigated the hydraulic conductivity, vulnerability to cavitation and wood anatomy of 23 abundant and typical tree and liana species from a KF and an adjacent NKF, as well as the two *Bauhinia* liana species common to both forests. We hypothesized that the KF species would have lower hydraulic conductivity with smaller vessels but higher resistance to cavitation than the NKF species. In addition, we expected that the two *Bauhinia* liana species might deviate from the hydraulic tradeoff and represented both high hydraulic efficiency and low vulnerability to cavitation, which might provide an explanation for their common occurrence in both forests.

## Materials and methods

### Study sites and plant materials

The present study was carried out in the tropical NKF and the tropical KF, which are attached to the Xishuangbanna Tropical Botanical Garden (XTBG; 21°54′N, 101°46′E) in southern Yunnan, China. This region is profoundly influenced by the Indian Ocean monsoon and thus has a distinct dry season from November to April. Mean annual precipitation is ~1600 mm, of which ~80% occurs in the wet season between May and October. The mean annual temperature is 22.7 °C, with monthly temperatures ranging from 14.8 °C in January to 25.5 °C in July. The tropical NKF has a total area of 100 ha, at an altitude of 570 m. This forest has multiple tree layers, with an average canopy height of 20 m. The soil has a shallow water table. The tropical KF grows in a limestone hill close by XTBG (300 ha), at altitudes of 650–700 m. The hill top is rocky without soil, and the slope is covered by shallow soil with many karst outcrops. The depth of the water table was estimated to be at least lower than 10 m (Liu et al. 2013). This forest has two distinctive tree layers, with the upper layer standing 15 m tall on average (Zhu et al. 1998). According to Chen et al. (2015), the soil water potential (0–30 cm) of NKF and KF is −0.26 and −0.24 MPa, respectively, in the wet season, and −0.9 and −3.2 MPa, respectively, at the peak of a dry season.

In this study, we selected a total of 23 abundant and typical tree and liana species from the KF (10 species) and the NKF (13 species), as well as two *Bauhinia* liana species (*B. tenuiflora* and *B. touranensis*) common to both forests (Table 1). All the plants were mature and the liana species reached the forest canopy; all the tree species sampled were not covered by any lianas. We measured all the hydraulic traits during the wet season. Terminal branches carrying new, fully expanded, healthy sun-exposed leaves were harvested from the canopy crowns using a tree pruner attached to a long pole. Five individuals per species were sampled.

### Hydraulic conductivity

Maximum vessel length (MVL) for each species was measured using the air infiltration technique (Ewers and Fisher 1989). Long branches were collected and low air pressure (60 kPa) was applied to the distal end of the branch segment. The proximal end of the branch was trimmed at 1 cm intervals in water until the first air bubble emerged from cut end. The MVL was determined as the length of remaining segment plus 0.5 cm (data shown in Table S1 available as Supplementary Data at *Tree Physiology* Online).

A total of 10 long leaf-bearing sun-exposed branches from five mature individuals for each species were harvested before sunrise, sealed in black plastic bags with moist towels, and immediately transported to the laboratory. The targeted segments were re-cut under water and trimmed with a sharp razor

Table 1. The 25 liana and tree species investigated in this study. The two *Bauhinia* liana species are common to both tropical forests.

| Species | Family | Code | Life form |
|---|---|---|---|
| Tropical non-karst rain forest | | | |
| *Bauhinia purpurea* L. | Fabaceae | Bp | Tree |
| *Bauhinia variegate* L. | Fabaceae | Bv | Tree |
| *Bischofia javanica* BL. | Euphorbiaceae | Bj | Tree |
| *Castanopsis indica* (Roxb.) Miq. | Fagaceae | Ci | Tree |
| *Lagerstroemia tomentosa* Presl | Lythraceae | Lt | Tree |
| *Millettia cubitti* Dunn | Fabaceae | Mc | Tree |
| *Millettia leptobotrya* Dunn | Fabaceae | Ml | Tree |
| *Syzygium cumini* (L.) Skeels | Myrtaceae | Sc | Tree |
| *Syzygium latilimbum* Merr. et Perry | Myrtaceae | Sl | Tree |
| *Syzygium szemaoense* Merr. et Perry | Myrtaceae | Ss | Tree |
| *Byttneria integrifolia* Lace | Sterculiaceae | Bi | Liana |
| *Millettia pachycarpa* Benth. | Fabaceae | Mp | Liana |
| *Uncaria macrophylla* Wall. | Rubiaceae | Um | Liana |
| Tropical karst forest | | | |
| *Alphonsea monogyna* Merr. et Chun | Annonaceae | Am | Tree |
| *Celtis philippensis* Blanco | Ulmaceae | Cp | Tree |
| *Cipadessa baccifera* (Roth.) Miq. | Meliaceae | Cb | Tree |
| *Cleistanthus sumatranus* (Miq.) Muell. Arg. | Euphorbiaceae | Cs | Tree |
| *Croton crassifolius* Geisel. | Euphorbiaceae | Cc | Tree |
| *Lasiococca comberi* Haines | Euphorbiaceae | Lc | Tree |
| *Pistacia weinmannifolia* J. Poisson ex Franch. | Anacardiaceae | Pw | Tree |
| *Turpinia pomifera* (Roxb.) DC. | Staphyleaceae | Tp | Tree |
| *Combretum latifolium* Bl. | Combretaceae | Cl | Liana |
| *Ventilago calyculata* Tulasne | Rhamnaceae | Vc | Liana |
| *Bauhinia* liana species | | | |
| *Bauhinia tenuiflora* (Watt ex C.B. Clarke) | Fabaceae | Bte | Liana |
| *Bauhinia touranensis* Gagnep. | Fabaceae | Bto | Liana |

blade. The remaining segments used for hydraulic measurement were ~6–10 mm in diameter and ~10% longer than MVL for each species. Segments were flushed with a filtered (0.2 μm) 20 mM KCl solution at a pressure of 0.1 MPa for ~20–30 min to remove air embolisms. Each segment was then connected to an apparatus for hydraulic conductivity measurement (Sperry et al. 1988). An elevated water reservoir supplied the same flush solution to the segment with a head pressure of ~5.5 kPa. Water flow through the segment was allowed to equilibrate for ~5–10 min, after which the mass flow through the segment over time was measured. Maximum hydraulic conductivity of the segment ($k_h$) was calculated as $k_h = FL/\Delta P$, where $F$ is the flow rate (kg $s^{-1}$), $\Delta P$ is the pressure gradient (MPa) through the segment and $L$ is the length of the segment (m). Sapwood specific hydraulic conductivity ($k_s$, kg $m^{-1}$ $s^{-1}$ $MPa^{-1}$) is calculated by dividing $k_h$ by the cross-sectional sapwood area in the middle of segment ($A_S$). Leaf specific hydraulic conductivity ($k_l$, $\times 10^{-4}$ kg $m^{-1}$ $s^{-1}$ $MPa^{-1}$) was calculated as the ratio of $k_h$ to the total area of leaves distal to the stem segment ($A_L$, $m^2$). Leaf to sapwood area ratio ($A_L/A_S$) was calculated by dividing $A_L$ by $A_S$.

### *Vulnerability curves*

The air-injection method was used to establish xylem vulnerability curves (Cochard et al. 1992). To avoid the potential sample length 'artifact' (Choat et al. 2010), the segment length for each species used in the air-injection measurements was higher than the sum of MVL plus chamber length (Ennajeh et al. 2011). Each segment flushed to achieve maximum hydraulic conductivity (as described for above hydraulic measurements) was placed into a pressure sleeve (10 cm) connected to a pressure tank (PMS 1000, Corvallis, OR, USA). Cavitation was induced by applying a series of increasing pressures on the same segment for 10–15 min. After each pressurization treatment, the pressure was released and the stable hydraulic conductance ($k_i$) was measured. The percent loss of conductivity (PLC, %) was calculated as $PLC = 100 \times (k_{max} - k_i)/k_{max}$. The vulnerability curves were plotted using PLC as a function of xylem tension (equals the negative value of applied pressure), and were fitted using a three-parameter sigmoid model in SigmaPlot 12.5 (Systat Software Inc., San Jose, CA, USA). Xylem tension causing 50% loss of hydraulic conductivity (P50, MPa) was used to describe vulnerability to drought-induced cavitation. Five branch segments for each species were used to determine the xylem vulnerability curves.

### *Sapwood density and wood anatomy*

After hydraulic conductivity measurements, the remaining segments were used for wood trait analyses. The bark and pith were removed from the samples and the volume of fresh sapwood was determined by the water-displacement method, and dry mass was subsequently determined after oven drying the samples at 70 °C for 48 h. The sapwood density (WD, g $cm^{-3}$) was calculated as the ratio of dry mass to fresh volume. Transverse sections of tissue were obtained from the sapwood with a sliding microtome (SM2010R, Leica, Wetzlar, Germany). Images of the slides were scanned by a light microscope equipped with an ocular micrometer (DM2500, Leica, Wetzlar, Germany) and were analyzed with ImageJ software (version 1.44; http://rsb.info.nih.gov/ij/). We counted the number of vessels per unit transection (average counts from 15 fields), and measured their diameters ($d$). The hydraulically weighted vessel diameter ($D_H$, μm) was calculated as $D_H = \sum d^5 / \sum d^4$.

### *Statistical analysis*

We used linear mixed-effects models (LMM) to analyze the effects of site (KF or NKF) and group (liana or tree) on variances of hydraulic traits, with species as a random factor. Because the outlier nature of the trait values of the two common liana *Bauhinia* species strongly affected the analyses, we next tried to exclude them from the analyses. However, without common species between each fixed factor (site or group), species could not be pointed as a random factor and LMM could not be applied. So a two-way ANOVA was also conducted for the remaining 23 species. Meanwhile, we compared traits of the two *Bauhinia* species between the two sites using *t*-tests. To homogenize variance, all the data were log-transformed before analysis. Models were conducted using the *lme4* package in R (R Development Core Team 2013), to assess statistical significance of fixed factors by Type III ANOVA with Satterthwaite's approximation of denominator degrees of freedom, and of random factors using likelihood ratio tests in the *lmerTest* package. The relationships between P50 and other hydraulic traits ($k_s$, $D_H$ and WD) were analyzed using exponential growth equation or linear function from a plotting program (SigmaPlot version 12.5, Systat Software Inc.).

## Results

Based on the linear mixed-effects models, both the site and plant group, and the interaction of site and group had significant effects on most of the six hydraulic traits, except that only group effect was non-significant for $A_L/A_S$, and only site and interactive factors were non-significant for P50 (Table 2). Species as a random factor could explain a high proportions of the random residuals (Table 2). Without the two common *Bauhinia* liana species, there were no longer interactive effects of site and group, while site and group still showed significant effects on the six hydraulic traits, except that only group effect was non-significant for $k_l$ (see Table S2a available as Supplementary Data at *Tree Physiology* Online). However, all the six traits of the two common *Bauhinia* species showed no differences between the two sites ($P > 0.05$; see Table S2b available as Supplementary Data at *Tree Physiology* Online). Thus, the interactive effects were mainly brought by the two common liana species, with extremely large or small trait values compared with other species from both sites.

Compared with NKF species, KF species tended to have a lower $k_s$, $k_l$ and $A_L/A_S$. The two *Bauhinia* liana species, *B. tenuiflora* and *B. touranensis* common to both forests, had exceptionally high values of $k_s$ (92.13 and 104.50 kg $m^{-1}$ $s^{-1}$ $MPa^{-1}$, respectively) and $A_L/A_S$ (7.99 and 9.62 $m^2$ $cm^{-2}$, respectively) among species (Figure 1 and see Table S1 available as Supplementary Data at *Tree Physiology* Online). Compared with NKF species, KF species tended to have higher WD, smaller $D_H$ and more negative P50 values (Figure 2). The two common *Bauhinia* liana species showed the lowest WD (0.33 and 0.35 g $cm^{-3}$, respectively) and the largest $D_H$ (310 and 344 μm, respectively), but were relatively less vulnerable to cavitation among species in this study (Figure 2). Unlike other tree and liana species, cross-sections of branch xylem of the two *Bauhinia* liana species were composed of extremely large vessels (>400 μm) as well as many small vessels (<50 μm; see Figure S2 available as Supplementary Data at *Tree Physiology* Online).

Out of the 25 species in this study, P50 values of 16 species in the same study sites were previously determined by using the bench-drying method, and the results from these two methods were similar (see Figure S1 available as Supplementary Data at *Tree Physiology* Online), indicating the validity of P50 data of this study. We found that P50 was positively correlated with $k_s$ and $D_H$, but was negatively correlated with WD across the 23 typical KF and NKF species (Figure 3), indicating a significant hydraulic efficiency–safety tradeoff among these species. Remarkably, *B. tenuiflora* and *B. touranensis* were found to escape from such a tradeoff, with both high hydraulic efficiency and safety (Figure 3).

## Discussion

### *Different hydraulic traits between tropical KF and NKF*

Our results showed that woody plant species from KF tended to have higher sapwood density, narrower vessel diameter, lower hydraulic conductivity, and were more resistant to drought-induced cavitation than those from NKF (Figures 1 and 2). Previous studies at the same study sites have demonstrated that water availability differed significantly between the two forests (Fu et al. 2015, Chen et al. 2016). For example, at the peak of a dry season, soil water potential in the KF could decline to less than −3.0 MPa, while adjacent NKF remains well above −1.0 MPa (Chen et al. 2015). A principal mechanism by which drought leads to tree mortality is the loss of xylem hydraulic conductivity, and some plants appear to be at higher risk of mortality when PLC exceeds 80% (Kursar et al. 2009, Anderegg et al. 2016). One important feature for woody plants to adapt to drought is to possess highly cavitation-resistant xylem to prevent hydraulic failure (Maherali et al. 2004, Pratt et al. 2007, Barigah et al. 2013, Pfautsch et al.

Table 2. The results of linear mixed-effected models with hydraulic traits of all the species as response variables. Site (karst or non-karst forest) and group (liana or tree) are fixed factors and species is the random factor. Sampling sizes (*n*), degrees of freedom (*df*), *F* values, *P* (*ns*, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$) and residual variance of random effect are reported. Abbreviation: $k_s$, sapwood specific hydraulic conductivity; $k_l$, leaf specific hydraulic conductivity; $A_L/A_S$, leaf area to sapwood area ratio; WD, sapwood density; P50, xylem water potential at 50% loss of hydraulic conductivity; $D_H$, hydraulically weighted vessel diameter.

| Traits | *n* | Fixed effects (*df*) | | | Random effect (*df*) | |
|---|---|---|---|---|---|---|
| | | Site (1) | Group (1) | Site × Group (1) | Residual variance (1) | Residual error (22) |
| $k_s$ | 27 | 7.18* | 16.50*** | 7.04* | 0.534 | 0.000 |
| $k_l$ | 27 | 4.50* | 4.80* | 6.88* | 0.194 | 0.001 |
| $A_L/A_S$ | 27 | 3.98 *ns* | 17.83*** | 1.83 *ns* | 0.246 | 0.006 |
| WD | 27 | 6.53* | 18.65*** | 7.01* | 0.024 | 0.000 |
| $D_H$ | 27 | 10.91** | 47.53*** | 12.70** | 0.888 | 0.001 |
| P50 | 27 | 17.35*** | 3.11 *ns* | 22.04*** | 0.074 | 0.000 |

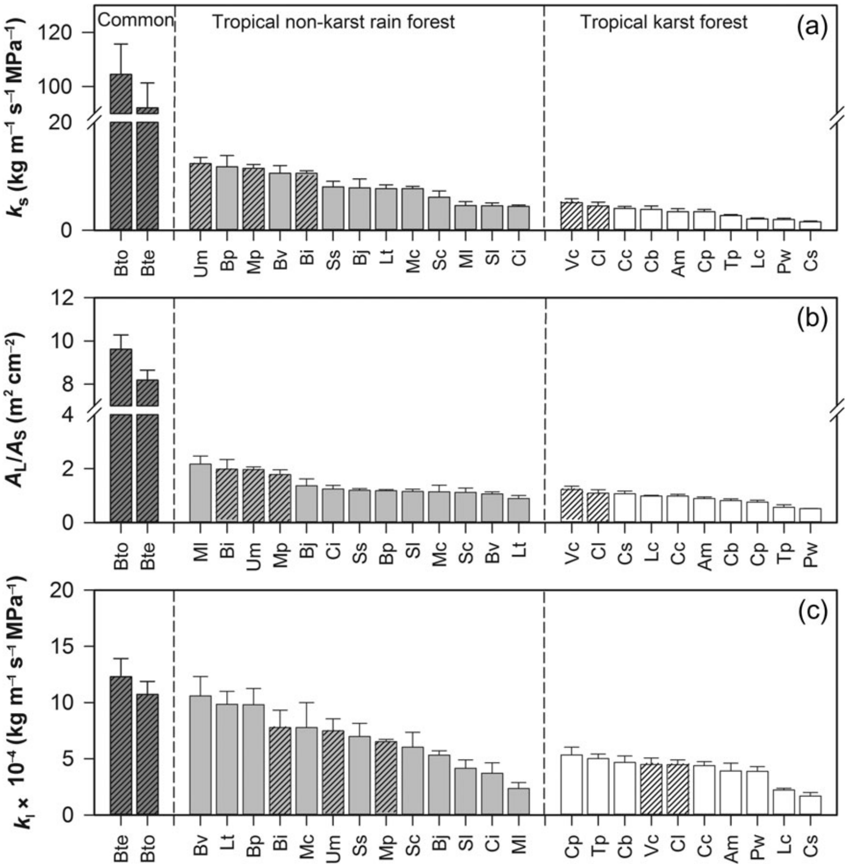

Figure 1. (a) Sapwood specific hydraulic conductivity ($k_s$), (b) leaf area to sapwood area ratio ($A_L/A_S$) and (c) leaf specific hydraulic conductivity ($k_l$) of the 25 woody species. Symbols: dark gray bars, the two *Bauhinia* liana species (common to both forest); light gray bars, tree and liana species from tropical non-karst rain forest; white bars, tree and liana species from tropical karst forest. Note that no significant differences in these traits was found between sites for the two *Bauhinia* liana species (see Table S2 available as Supplementary Data at *Tree Physiology* Online), so we showed the mean values of each trait calculated from all the replicates. The bars of lianas are cross-hatched. Species abbreviations follow Table 1. Data are means + 1SE.

2016). Therefore, compared with NKF tree species, the hydraulic characteristics of KF tree species indicated a better adaptation to water-stressed environment. A similar pattern was also found in lianas, with the two typical KF liana species (*Combretum latifolium* and *Ventilago calyculata*) being relatively more resistant to cavitation than three typical NKF liana species (*Millettia pachycarpa*, *Uncaria macrophylla* and *Byttneria integrifolia*; Figure 2 and see Table S1 available as Supplementary Data at *Tree Physiology* Online). Despite strong differences in hydraulic traits between the two forests, there were significant relationships between P50 and WD, $D_H$ and $k_s$ across the 23 typical KF and NKF species (Figure 3). Our results supported the hydraulic efficiency–safety

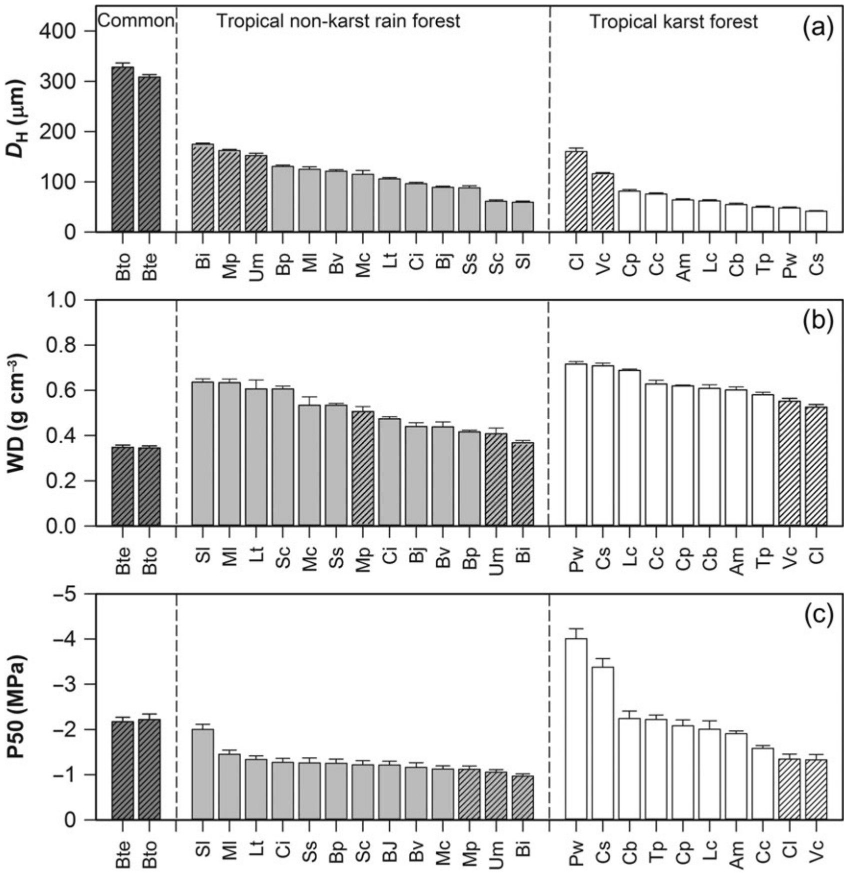

Figure 2. (a) Hydraulically weighted vessel diameter ($D_H$), (b) sapwood density (WD) and (c) xylem water potential at 50% loss of hydraulic conductivity (P50) of the 25 woody species. The symbols and species abbreviations are shown in Figure 1 and Table 1, respectively. Note that no significant differences in these traits was found between sites for the two *Bauhinia* liana species (see Table S2 available as Supplementary Data at *Tree Physiology* Online), so we showed the mean values of each trait calculated from all the replicates. Data are means + 1SE.

tradeoff for these forest communities, which might be an important eco-physiological mechanism underlying species distribution across the two forests with different soil water availability.

Compared with NKF species, KF species tended to have a lower value of $A_L/A_S$ (Figure 1b). An effective adaptation for woody plant to cope with drought is to reduce the leaf to sapwood area ratio (Drake and Franks 2003). In a previous study, Carter and White (2009) also reported that *Eucalyptus kochii*, a common tree species in southwestern Australia, had a significantly lower $A_L/A_S$ when growing in a dry site than in a wet site. In another study, Martinez-Vilalta et al. (2009) found a significantly negative relationship between $A_L/A_S$ and climate aridity index across 12 Scots pine populations grown in a wide range of environmental conditions. The authors concluded that modification of $A_L/A_S$ was an important hydraulic adjustment in response to local climatic conditions. This is due to the fact that reduction in leaf to sapwood area ratio can avoid excessive transpirational water loss and promote leaf-level water supply, resulting in a low risk of hydraulic failure (Gotsch et al. 2010).

There was a larger variation in P50 values in the KF than that in the lowland rain forest, i.e., coefficient of variation was 38% for KF, but 19% for NKF. This might be partially due to the large spatial differentiation in micro-habitats in the karst hill (Zhu et al. 1998, Zhang et al. 2011), which leads to spatial distributions of plant species that are potentially determined by differential resistance to drought (Baltzer et al. 2008). For example, two karst tree species *Cleistanthus sumatranus* and *Pistacia weinmannifolia*, which occurred in the middle to top of karst hill that is mostly rocky without soils (Zhu et al. 1998), showed the highest resistance to cavitation among species (P50 values were −3.4 and −4.1 MPa, respectively). Meanwhile, another two karst tree species *Lasiococca comberi* and *Celtis philippensis*, which dominated in the lower slopes with a certain amount of soil and less outcrops, were relatively less resistant to cavitation (P50 values were −2.0 and −2.1 MPa, respectively) among the karst tree species in this study (Figure 2 and see Table S1 available as Supplementary Data at *Tree Physiology* Online).

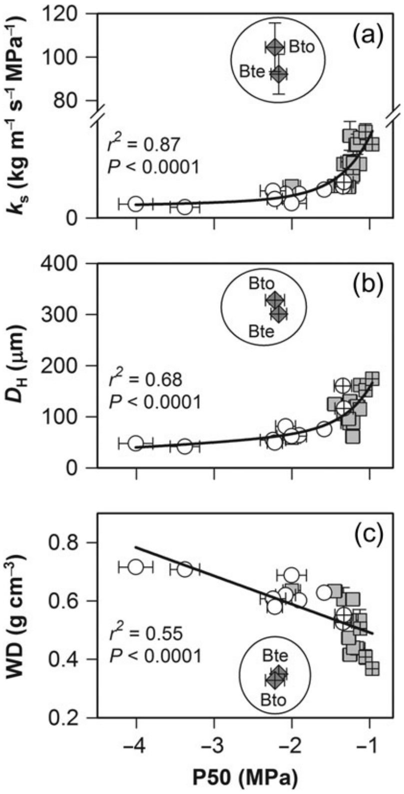

Figure 3. Relationships between xylem water potential at 50% loss of hydraulic conductivity (P50) and (a) sapwood specific hydraulic conductivity ($k_s$), (b) hydraulically weighted vessel diameter ($D_H$) and (c) sapwood density (WD) across 23 woody species. Symbols: dark gray diamonds, two common *Bauhinia* liana species (Bto and Bte); gray squares, species from tropical non-karst rain forest; white circles, species from tropical karst forest. The symbols of lianas are crossed. No significant differences in these traits was found between sites for the two *Bauhinia* liana species (see Table S2 available as Supplementary Data at *Tree Physiology* Online), so we showed the mean values of each trait calculated from all the replicates. Note that Bto and Bte surrounded with an ellipse are excluded from the regression lines. Error bars represent the standard errors.

### *Hydraulic traits of the two* Bauhinia *liana species common to both forests*

The two *Bauhinia* liana species showed extraordinary high $k_s$ compared with the other species (Figure 1 and see Table S1 available as Supplementary Data at *Tree Physiology* Online). Such high $k_s$ values have been also reported in some other tropical liana species, such as *Entadopsis polystachya* (Gartner et al. 1990) and *Maripa panamensis* (Van der Sande et al. 2013). Undoubtedly, the high $k_s$ of the two *Bauhinia* species was primarily due to their extremely wide and long vessels (Figure 2 and see Table S1 available as Supplementary Data at *Tree Physiology* Online), given that hydraulic efficiency is proportional to vessel diameter to the fourth power (Tyree and Zimmermann 2002), and is less limited by end wall resistances in long vessels (Jacobsen et al. 2012). In contrast to the general view that lianas tend to maximize their hydraulic efficiency at the expense of hydraulic safety, which is called a 'sacrificial strategy' (Hacke et al. 2006), the two *Bauhinia* species were highly resistant to cavitation (Figure 3). Similar results were also found in a large-vesseled grapevine species *Vitis vinifera*, with a P50 value less than −2 MPa based on both air-injection and NMR imaging measurements (Choat et al. 2010).

What could be the causes for high cavitation-resistance in the two *Bauhinia* liana species? It was found that their xylem showed distinctive dimorphic vessels (see Figure S2 available as Supplementary Data at *Tree Physiology* Online), which is particularly evident in *Bauhinia* liana species (Ewers et al. 1990). The extremely large vessels allow for a high hydraulic efficiency, while the many small vessels provide a high resistance auxiliary transport system (Carlquist 1985, Rosell and Olson 2014). This xylem dimorphism may assure both hydraulic efficiency and safety (Baas et al. 2004, Gutierrez et al. 2009, Carvalho et al. 2015). In addition, considering that smaller pit pores are more resistant to the air spread from adjacent embolized conduits (the pit area hypothesis; Wheeler et al. 2005, Hacke et al. 2006), great cavitation resistance in the two species might be associated with their intervessel pit structure (e.g., pit size, pit density and membrane thickness), but further studies are needed to evaluate this. Therefore, the two *Bauhinia* species were capable of escaping the hydraulic tradeoff (Figure 3), which might be a reason for their common occurrence in the two tropical forests with contrasting soil water conditions. Similarly, Choat et al. (2007) investigated hydraulic traits of nine *Cordia* species from three tropical forests differing in precipitation, with one species (*Cordia allidora*) that could establish across the three sites. They found no hydraulic tradeoff as well, and a combination of high conductivity and low vulnerability in the widespread species.

## Conclusions

Our results provide evidence of a significant tradeoff between hydraulic efficiency and safety across the dominant and typical woody species from a tropical KF and a NKF. Species from KF tend to show higher sapwood density, smaller vessels, lower specific hydraulic conductivity and leaf to sapwood area ratio, and are more resistant to cavitation than those from NKF. This indicated a hydraulic adaptation in the karst woody species to the water-stressed environment. We suggest that the hydraulic tradeoff would be an important underlying mechanism governing species distribution across tropical forests with different soil water availabilities. In addition, we also find that two *Bauhinia* liana species show a distinct hydraulic combination of fast hydraulic efficiency and great resistant to cavitation. They can escape from the hydraulic tradeoff, which might explain their distributions across wide water availability gradients in tropical forests. More investigations involving a broader range of species are needed to evaluate the unusual hydraulic characteristics, which would substantially improve our understanding on the diversity of plant hydraulics.

## Supplementary Data

Supplementary Data for this article are available at *Tree Physiology* Online.

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## Conflict of interest statement

None declared.

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## References

Anderegg WRL, Klein T, Bartlett M, Sack L, Adam FA, Pellegrini AFA, Choat B, Jansen S (2016) Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. Proc Natl Acad Sci USA 113:5024–5029.

Baas P, Ewers FW, Davis SD, Wheeler EA (2004) Evolution of xylem physiology. In: Hemsley AR, Poole I (eds) The evolution of plant physiology. Elsevier Academic Press, London, UK, pp 273–295.

Baltzer JL, Davies SJ, Noor NSM (2007) Geographical distributions in tropical trees: can geographical range predict performance and habitat association in co-occurring tree species? J Biogeogr 90:2755–2765.

Baltzer JL, Davies SJ, Bunyavejchewin S, Noor NSM (2008) The role of desiccation tolerance in determining tree species distributions along the Malay-Thai Peninsula. Funct Ecol 22:221–231.

Barigah TS, Charrier O, Douris M, Bonhomme M, Herbette S, Ameglio T, Fichot R, Brignolas F, Cochard H (2013) Water stress-induced xylem hydraulic failure is a causal factor of tree mortality in beech and poplar. Ann Bot 112:431–1437.

Canham CA, Froend RH, Stock WD (2009) Water stress vulnerability of four *Banksia* species in contrasting ecohydrological habitats on the Gnangara Mound, Western Australia. Plant Cell Environ 32:64–72.

Carlquist S (1985) Observations on functional wood histology of vines and lianas: vessel dimorphism, tracheids, vasicentric tracheids, narrow vessels, and parenchyma. Aliso 11:139–157.

Carter JL, White DA (2009) Plasticity in the Huber value contributes to homeostasis in leaf water relations of a mallee Eucalypt with variation to groundwater depth. Tree Physiol 29:1407–1418.

Carvalho ECD, Martins FR, Soares AA, Oliveira RS, Muniz CR, Araujo FS (2015) Hydraulic architecture of lianas in a semiarid climate: efficiency or safety? Acta Bot Bras 29:198–206.

Chen YJ, Cao KF, Schnitzer SA, Fan ZX, Zhang JL, Bongers F (2015) Water-use advantage for lianas over trees in tropical seasonal forests. New Phytol 205:128–136.

Chen YJ, Bongers F, Tomlinson K, Fan ZX, Lin H, Zhang SB, Zheng YL, Li YP, Cao KF, Zhang JL (2016) Time lags between crown and basal sap flows in tropical lianas and co-occurring trees. Tree Physiol 36: 736–747.

Choat B, Sack L, Holbrook NM (2007) Diversity of hydraulic traits in nine *Cordia* species growing in tropical forest with contrasting precipitation. New Phytol 175:686–698.

Choat B, Drayton WM, Brodersen C, Matthews MA, Shackel KA, Wade H, Mcelrone AJ (2010) Measurement of vulnerability to water stress-induced cavitation in grapevine: a comparison of four techniques applied to a long-vesseled species. Plant Cell Environ 33: 1502–1512.

Cochard H, Cruiziat P, Tyree MT (1992) Use of positive pressure to establish vulnerability curves. Further support for the air-seeding hypothesis and implications for pressure-volume analysis. Plant Physiol 100:205–209.

Comita LS, Engelbrecht BMJ (2009) Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. Ecology 90:2755–2765.

Drake PL, Franks PJ (2003) Water resource partitioning, stem xylem hydraulic properties, and plant water use strategies in a seasonally dry riparian tropical rainforest. Oecologia 137:321–329.

Engelbrecht BMJ, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP (2007) Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447:80–83.

Ennajeh M, Simoes F, Khemira H, Cochard H (2011) How reliable is the double-ended pressure sleeve technique for assessing xylem vulnerability to cavitation in woody angiosperms? Physiol Plant 142: 205–210.

Ewers FW, Fisher JB (1989) Techniques for measuring vessel lengths and diameters in stems of woody-plants. Am J Bot 76:645–656.

Ewers FW, Fisher JB (1991) Why vines have narrow stems: histological trends in *Bauhinia* (Fabaceae). Oecologia 88:233–237.

Ewers FW, Fisher JB, Chiu S (1990) A survey of vessel dimensions in stems of tropical lianas and other growth forms. Oecologia 84: 544–552.

Fortunel C, Paine CET, Fine PVA, Kraft NJB, Baraloto C (2014) Environmental factors predict community functional composition in Amazonian forests. J Ecol 102:123–136.

Fu PL, Jiang YJ, Wang AY, Brodribb TJ, Zhang JL, Zhu SD, Cao KF (2012) 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. Ann Bot 110:189–199.

Fu PL, Liu WJ, Fan ZX, Cao KF (2015) Is fog an important water source for woody plants in an Asian tropical karst forest during the dry season? Ecohydrology 9:964–972.

Gartner BL, Bullock SH, Mooney HA, Brown VB, Whitbeck JL (1990) Water transport properties of vine and tree stems in a tropical deciduous forest. Am J Bot 77:742–749.

Gerwing JJ, Schnitzer SA, Burnham RJ et al. (2006) A standard protocol for liana censuses. Biotropica 38:256–261.

Gleason SM, Westoby M, Jansen S et al. (2016) Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. New Phytol 209:80–83.

Gotsch SG, Geiger EL, Franco AC, Goldstein G, Meinzer FC, Hoffmann WA (2010) Allocation to leaf area and sapwood area affects water relations of co-occurring savanna and forest trees. Oecologia 163: 291–301.

Gutierrez M, Miguel-Chavez RS, Terrazas T (2009) Xylem conductivity and anatomical traits in diverse liana and small trees species from a tropical forest of Southwest Mexico. Int J Bot 5:279–286.

Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. Perspect Plant Ecol Evol Syst 4:97–115.

Hacke UG, Sperry JS, Wheeler JK, Castro L (2006) Scaling of angiosperm xylem structure with safety and efficiency. Tree Physiol 26:689–701.

Jacobsen AL, Pratt RB, Tobin MF, Hacke UG, Ewers FW (2012) A global analysis of xylem vessel length in woody plants. Am J Bot 99: 1583–1591.

Kursar TA, Engelbrecht BMJ, Burke A (2009) Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. Funct Ecol 23:93–102.

Li YH, Pei SJ, Xu ZF (eds) (1996) List of plants in Xishuangbanna (in Chinese). Yunnan Nationality Press, Kunming.

Litvak E, McCarthy HR, Pataki DE (2012) Transpiration sensitivity of urban trees in a semi-arid climate is constrained by xylem vulnerability to cavitation. Tree Physiol 32:373–388.

Liu WJ, Li PJ, Duan WP, Liu WY (2013) Dry-season water utilization by trees growing on thin karst soils in a seasonal tropical rainforest of Xishuangbanna, Southwest China. Ecohydrology 7:927–935.

Lopez OR, Kursar TA, Cochard H, Tyree M (2005) Interspecific variation in xylem vulnerability to cavitation among tropical tree and shrub species. Tree Physiol 25:1553–1562.

Maherali H, Pockman WT, Jackson RB (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. Ecology 85: 2184–2199.

Martinez-Vilalta J, Cochard JH, Mencuccini M et al. (2009) Hydraulic adjustment of Scots pine across Europe. New Phytol 184:353–364.

Pfautsch S, Harbusch M, Wesolowski A, Smith R, Macfarlane C, Tjoelker MG, Reich PB, Adams MA (2016) Climate determines vascular traits in the ecologically diverse genus *Eucalyptus*. Ecol Lett 19:240–248.

Pineda-Garcia F, Paz H, Meinzer FC (2016) Exploiting water versus tolerating drought: water use strategies of trees in a secondary successional tropical dry forest. Tree Physiol 36:208–217.

Pockman WT, Sperry JS (2000) Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. Am J Bot 87:1287–1299.

Poorter L, Markesteijn L (2008) Seedling traits determine drought tolerance of tropical tree species. Biotropica 40:321–331.

Poorter L, McDonald I, Alarcon A, Fichtler E, Licona J-C, Pena-Claros M, Sterck F, Villegas Z, Sass-Klaassen U (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. New Phytol 185:481–492.

Pratt RB, Jacobsen AL, Ewers FW, Davis SD (2007) Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. New Phytol 174: 787–798.

Pratt RB, Jacobsen AL, North GB, Sack L, Schenk HJ (2008) Plant hydraulics: new discoveries in the pipeline. New Phytol 179:590–593.

R Development Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Rosell JA, Olson ME (2014) Do lianas really have wide vessels? Vessel diameter–stem length scaling in non-self-supporting plants. Perspect Plant Ecol Evol Syst 16:288–295.

Schnitzer SA, Bongers F (2002) The ecology of lianas and their role in forests. Trends Ecol Evol 17:223–230.

Sperry JS, Donnelly JR, Tyree MT (1988) A method for measuring hydraulic conductivity and embolism in xylem. Plant Cell Environ 11:35–40.

Sperry JS, Nichols KL, Sullivan JEM, Eastlack SE (1994) Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. Ecology 75:1736–1752.

Tuomisto H, Ruokolainen K, Yli-Halla M (2003) Dispersal, environment, and floristic variation of western Amazonian forests. Science 299: 241–244.

Tyree MT, Ewers FW (1991) The hydraulic architecture of trees and other woody plants. New Phytol 119:345–360.

Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap. Springer, New York, NY.

Van der Sande MT, Poorter L, Schnitzer SA, Markesteijn L (2013) Are lianas more drought-tolerant than trees? A test for the role of hydraulic architecture and other stem and leaf traits. Oecologia 172:961–972.

Vergeynst LL, Dierick M, Bogaerts JAN, Cnudde V, Steppe K (2014) Cavitation: a blessing in disguise? New method to establish vulnerability curves and assess hydraulic capacitance of woody tissues. Tree Physiol 35:400–409.

Wheeler JK, Sperry JS, Hacke UG, Hoang N (2005) Intervessel pitting and cavitation in woody Rosaceae and other vesselled plants: a basis for a safety versus efficiency trade-off in xylem transport. Plant Cell Environ 28:800–812.

Yuan DX (1992) Karst in southwest China and its comparison with karst in north China. Quaternary Sci 4:352–361.

Zhang JL, Cao KF (2009) Stem hydraulics mediates leaf water status, carbon gain, nutrient use efficiencies and plant growth rates across dipterocarp species. Funct Ecol 23:658–667.

Zhang JG, Chen HS, Su YR, Kong XL, Zhang W, Shi Y, Liang HB, Shen GM (2011) Spatial variability and patterns of surface soil moisture in a field plot of karst area in southwest China. Plant Soil Environ 57: 409–417.

Zhu H, Wang H, Li B (1998) The structure, species composition and diversity of the limestone vegetation in Xishuangbanna, SW China. Gard Bull Singapore 50:5–30.

Zhu H, Wang H, Li B, Sirirugsa P (2003) Biogeography and floristic affinities of the limestone flora in southern Yunnan, China. Ann Mol Bot Gard 90:444–465.

Zhu SD, Cao KF (2009) Hydraulic properties and photosynthetic rates in co-occurring lianas and trees in a seasonal tropical rainforest in southwestern China. Plant Ecol 204:295–304.

Zhu SD, Song JJ, Li RH, Ye Q (2013) Plant hydraulics and photosynthesis of 34 woody species from different successional stages of subtropical forests. Plant Cell Environ 36:879–891.