The trade-off between safety and efficiency in hydraulic architecture in 31 woody species in a karst area

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Karst topography is a special landscape shaped by the dissolution of one or more layers of soluble bedrock, usually carbonate rock such as limestone or dolomite. Due to subterranean drainage, overland flow, extraction of water by plants and evapotranspiration, there may be very limited surface water. The hydraulic architecture that plants use to adapt to karst topography is very interesting, but few systematic reports exist. The karst area in southwestern China is unique when compared with other karst areas at similar latitudes, because of its abundant precipitation, with rainfall concentrated in the growing season. In theory, resistance to water-stress-induced cavitation via air seeding should be accompanied by decreased pore hydraulic conductivity and stem hydraulic conductivity. However, evidence for such trade-offs across species is ambiguous. We measured the hydraulic structure and foliar stable carbon isotope ratios of 31 karst woody plants at three locations in Guizhou Province, China, to evaluate the functional coordination between resistance to cavitation and specific conductivity. We also applied phylogenetically independent contrast (PIC) analysis in situations where the inter-species correlations of functional traits may be biased on the potential similarity of closely related species. The average xylem tension measurement, at which 50% of hydraulic conductivity of the plants was lost ($\Psi_{50}$), was only −1.27 MPa. Stem $\Psi_{50}$ was positively associated with specific conductance ($K_s$) ($P < 0.05$) and leaf specific conductance ($K_l$) ($P < 0.05$). However, the PIC correlation for both relationships was not statistically significant. $\delta^{13}$C was positively related to $K_l$ in both the traditional cross-species correlation analysis and the corresponding PIC correlations ($P < 0.05$). The Huber value (sapwood area:leaf area ratio) was negatively correlated with $K_s$ in both the traditional cross-species correlation and the corresponding PIC correlations ($P < 0.01$). The characteristics of hydraulic architecture measured in this study showed that karst plants in China are not highly cavitation-resistant species. This study also supports the idea that there may not be an evolutionary trade-off between resistance to cavitation and specific conductivity in woody plants. Whole-plant hydraulic adjustment may decouple the trade-off relationship between safety and efficiency at the branch level.

Keywords: correlated evolution, foliar stable carbon isotope ratio, hydraulic architecture, karst plants, karst topography.

Introduction

‘Hydraulic failure’ and associated other downstream physiological processes have been regarded as critical for woody plants unable to cope with the challenge of supplying enough water to their leaves under restrictions they experience at different time scales (Maseda and Fernández 2006, McDowell et al. 2008). Negative tension as a result of low water potentials of the intact water column could make the entire water transport pathway susceptible to cavitation, due to the seeding of air bubbles through pit membranes and into the water column under stress conditions. Embolized xylem cells subsequently reduced hydraulic conductivity and greatly retarded photosynthesis and
growth. A more severe catastrophic hydraulic failure will lead to the death of plants in extreme cases in the absence of feedback of limiting transpiration.

Although many reports have shown a functional coordination between hydraulic structure and other functional traits among and within species (Brodribb et al. 2002, Meinzer 2002, Maherali et al. 2006), our knowledge of the association between variation in cavitation resistance (safety) and water transport capacity (efficiency) among plants is ambiguous. Some studies showed a trade-off of varying degrees of significance and others showed no relationship at all (Sperry and Saliendra 1994, Tyree et al. 1994, Wagner et al. 1998, Pockman and Sperry 2000, Martinez-Vilalta et al. 2002, Maherali et al. 2006, Sperry et al. 2008, Meiner et al. 2010). Furthermore, if data were collected on a larger scale across many vegetation types (Maherali et al. 2004), or if phylogenetically independent contrast (PIC) analysis was applied (Maherali et al. 2006), there might be a weak or even insignificant evolutionary trade-off between resistance to cavitation and specific conductivity in woody plants.

Comprehensive investigation of such trade-offs across a broad range of taxonomic groups can be problematical, primarily due to both a lack of control of data gathered across seasons and years (Jacobsen et al. 2007) and the utilization of different methods (van Ieperen 2007). Phylogenetically independent contrast analysis within a few woody species (<10) may also suffer from statistical ‘funnel effects’ described previously (Wright et al. 2005). Furthermore, according to the Ohm’s law analogy, the xylem tension range determined the relationship between flow resistance and flow rate (Tyree and Ewers 1991). Therefore, only under a similar xylem tension range there may be functional coordination between safety and efficiency. Hence, although Maherali et al. (2004) previously studied the adaptive significance of variation in cavitation resistance and water transport capacity across a broad range of taxonomic groups, we believe it is necessary to investigate this issue in other specialized vegetation with a similar xylem tension range in different climate zones across the world for a more comprehensive understanding of the role of such trade-offs in the adaptation of woody plants to the local environment (Sperry et al. 2008).

Karst topography is a special landscape shaped by the dissolution of one or more layers of soluble bedrock, usually carbonate rock such as limestone or dolomite. Subterranean drainage, overland flow, plant extraction and evaportranspiration lead to low levels of water available to plants in the shallow soils in many karst landscapes. The hydraulic architecture that plants use to adapt to karst topography is very interesting, but few systematic reports exist. The few existing studies focusing on hydraulic structure, which looked at several woody species in karst topography in the Mediterranean area and the Edwards Plateau of central Texas, have shown that most of the species studied are highly cavitation-resistant (Tognetti et al. 1998, Martinez-Vilalta et al. 2002, Maherali et al. 2004, McElrone et al. 2004). However, this may not be conclusive, because a diversity of karst environments and vegetation are distributed worldwide, such as Madagascar’s dry deciduous forest (Fowler et al. 1989), Vietnam’s tropical forest (Tuyet 2001) and Slovakia’s spruce forest (Oszlanyi 1997).

The karst area in southwestern China is unique when compared with other karst areas at similar latitudes, because of its abundant precipitation, with rainfall concentrated in the growing season (Wu et al. 2003), mainly due to the rise in elevation of the Qinghai-Tibet Plateau. Meteorological data show that two consecutive rainfall events normally occur 7–10 days apart during the growing season (Li et al. 2008). Eco-physiological field investigations report that woody plants in this area experienced similar midday leaf water potentials during the growing season (Yu et al. 2002) (C.C. Liu, unpublished data), suggesting a similar terminal xylem tension control across a variety of taxa. All these characteristics make karst areas in China an ideal platform on which to investigate the issues mentioned above. Furthermore, investigation of hydraulic acclimation in this area is of practical importance in assessing the hydrological imbalance, as well as associated land degradation issues due to current over-exploitation by intensive agro-economic activities.

In this study, first we measured the hydraulic architecture of 31 karst woody species at three locations in Guizhou Province, China, and conducted a comparison based on the global database of hydraulic architecture of woody plants (Maherali et al. 2004). Second, by using information on phylogenetic relationships among seed plants, we calculated PICs to evaluate the strength of the relationship between vulnerability to xylem cavitation and xylem transport capacity in woody species of karst habitats in China. We focus on two specific questions: (i) what are the characteristics of hydraulic architecture of woody species of karst habitats in China? (ii) is there a significant coordination between the evolutionary aspects of vulnerability to xylem cavitation and xylem transport capacity among woody species in karst habitats?

Materials and methods

Study site and plant materials

The study was conducted at three sites in Guizhou Province, southwestern China. These sites, the Huajiang site (HJ, 25°42′N, 105°35′E), the Puding site (PD, 26°15′N, 105°44′E) and the Libo site (LB, 25°26′N, 108°05′E), are located in the southwestern, western and southern parts of Guizhou Province, at altitudes of ~900, 1200 and 800 m, respectively.

The HJ site has a warm temperate climate, a mean annual temperature of 18.4 °C (Wu et al. 2003) and a mean annual precipitation (MAP) of 1100 mm, of which 83% falls during the
The polygenetic relationship among studied species is shown in Figure 1. D, winter deciduous; E, evergreen; HJ, Huajiang site; PD, Puding site; LB, Libo site. DP, diffuse-porous; RP, ring-porous; sRP, semi-ring-porous; number in parentheses: range of vessel length variation in micrometers.

our species was incomplete (Table 1), so some vessels of investigated species may have been open.

Hydraulic conductance ($K_h$) was measured as described by Sperry and Saliendra (1994) in an air-conditioned laboratory (26 °C). Segments were cleared of air emboli by perfusing them at high pressure with filtered (0.2 μm) distilled water for 30 min at 110 kPa. Water conducted through the segments at ~8 kPa of hydrostatic pressure was collected in a vial on a 0.0001 g balance (Satorius, Germany) connected to a computer to record efflux weight changes every 30 s. Measurements were not initiated until ~2 min, when the flow rates stabilized. Hydraulic conductivity ($K_h$; kg m MPa^-1 s^-1) was expressed as the flow rate divided by the pressure gradient. Specific conductivity ($K_s$; kg m^-1 MPa^-1 s^-1) was calculated by dividing $K_h$ by the segment’s sapwood cross-sectional area. Stem sapwood cross-sectional area was determined by measuring the maximum and minimum diameter of the acropetal end of each branch segment using a digital micrometer. Pith area was subtracted from gross cross-sectional area after measuring its dimension under a dissecting microscope equipped with a stage micrometer. Leaf specific conductivity ($K_s$; kg m^-1 MPa^-1 s^-1) was calculated by dividing $K_h$ by the leaf area distal to the measured sample. Sampled leaves were first scanned with a scanner (Epson, Japan), and then each leaf sample’s area was calculated using WinFOLIA software (Regent, Canada). The Huber value was calculated as the ratio of wood cross section per unit leaf area attached.

The vulnerability of xylem to cavitation was characterized using a vulnerability curve constructed by the method described by Sperry and Saliendra (1994). After measuring the maximum hydraulic conductivity ($K_h$), stems were inserted and sealed into a collar with both ends protruding. Air was then injected into the collar to the desired air injection pressure, which was maintained for 15 min. Two shallow (0.5 mm deep) notches into the collar to the desired air injection pressure, which was maintained for 15 min. Two shallow (0.5 mm deep) notches were cut into opposite sides of the xylem ~0.05 m apart at the midpoint of the segment. These cuts ensured entry of air into the xylem inside the pressure chamber. The air injection pressure used is equivalent to the negative value of water potential in the xylem (Cochard et al. 1992, Sperry and Saliendra 1994). The pressure in the collar was then slowly released down to 0.5 MPa until hydration. The pressure in the chamber was calculated as PLC = 100 × ((Ψ_c−Ψ_0)/ $K_h$), where $K_h$ is the hydraulic conductivity of the sample measured after each chamber pressurization. Vulnerability curves were fitted with an exponential sigmoidal equation (Pammenter and Vander 1998):

$$PLC = \frac{100}{1 + \exp(a \times (\Psi - b))} \quad (1)$$

where $\Psi$ is the negative of the injection pressure, $a$ is a measure of the steepness of the response of conductivity to injection pressure or tension (curve slope) and $b$ represents the $\Psi$ at which a 50% loss in conductivity occurs ($\Psi_{50}$ or curve displacement along the x-axis). Coefficients $a$ and $b$ were estimated using the non-linear regression procedure in SPSS 10.0 (SPSS, Evanston, IL, USA).

Foliar carbon isotope discrimination

After measurement of leaf area, leaves distal to the measured samples were oven-dried at 70 °C for 48 h and finely ground. Specific leaf area (SLA) was calculated by dividing leaf size by leaf mass. A sub-sample of 1 mg of powdered leaf material was combusted and analyzed for $^{13}$C composition using an isotope ratio mass spectrometer (Finnigan MAT Delta V advantage, ThermoFinnigan, USA). Leaf carbon isotope composition ($\delta^{13}C$) was calculated as

$$\delta^{13}C = \frac{R_{is} - R_{st}}{R_{st}} \times 1000 \quad (2)$$

where $R_{is}$ and $R_{st}$ are the $^{13}C/^{12}C$ ratios in the sample and in the conventional Pee Dee Belemnite standard, respectively.

Since only sunlit leaves were sampled, atmospheric CO$_2$ concentration ($C_a$) and carbon isotope composition ($\delta^{13}C_a$) at close sites can be considered as constant (Buchmann et al. 1997). In fact, we sampled atmospheric CO$_2$ at these three sites and found no significant difference. We corrected the $\delta^{13}C$ for elevation by a method based on Hultine and Marshall (2000) and Marshall and Zhang (1994) to obtain rigorous data. All $\delta^{13}C$ data were normalized to the elevation of 800 m.

Phylogenetically independent contrasts and statistical analyses

As the cross-species correlations may be biased by a lack of statistical independence between data points of closely related species with shared evolutionary history, PICs were applied in this study. We first constructed the phylogenies for our species with the program Phylomatic (Webb et al. 2008), using a maximally resolved seed plant tree (Phylomatic tree version: R20040402) based on the Angiosperm Phylogeny Group supertree (Hilu et al. 2003). The Phylomatic program, however, was unable to fully resolve the trees to the species level, resulting in four species-level polytomies within the phylogeny, which could theoretically create >2000 fully resolved trees.

As a fully bifurcated tree is the premise for the calculation of independent contrasts, we found several papers (Chase et al. 1993, Wurdack et al. 2005, Tokuoka 2007) to resolve these polytomies to reduce the number of resolved trees. We were unable to find support for resolution below the level of genus Mallotus, resulting in one polytomy within the phylogeny. Resolving it to create fully bifurcated trees resulted in three possible trees. Because we combined several trees to create
our final trees, our phylogenies lacked branch length information; therefore, all analyses were run assuming equal branch lengths. This is a conservative approach that minimizes the Type I error rate (Ackerly 2000).

Phylogenetically independent contrasts were calculated to test for patterns of correlated evolutionary change between traits (Felsenstein 1985) using COMPAR E, version 4.6b (Martins 2004). Contrasts were calculated for all three fully resolved trees. For the five species co-occurring at two sites, mean values were used in the analyses. Phylogenetically independent contrast Pearson correlation analyses between traits were conducted through the point of coordinates (0, 0), because of the arbitrary sign of an independent contrast. Because the PIC correlations calculated over the three alternate phylogenies were similar, only the PIC results for phylogeny in Figure 1 are presented in this study.

Analysis of variance was applied to test the difference among sites and between leaf phenologies separately. Pearson correlation analysis was conducted among investigated traits. For the cross-species correlation analysis, all data were log 10-transformed prior to analysis, because previously described non-linear relationships exist between some trait sets (Pockman and Sperry 2000, Martínez-Vilalta et al. 2002, McElrone et al. 2004). To facilitate log transformation and analysis, ΔΨ50 and δ13C data were converted from negative to positive values.

Results

There were wide variations in hydraulic architecture across investigated species (Table 2; Figure 2). Stachyurus obovatus, an evergreen species at the PD site, was the most resistant species to xylem cavitation with a ΔΨ50 of −4.31 MPa. This was about eightfold more negative than the species most vulnerable to xylem cavitation, Broussonetia papyrifera (L.) L'Hér. ex Vent., a deciduous-leaved species at HJ site (Figure 2). The mean value of resistance to xylem cavitation of the 31 studied woody species was only −1.27 MPa (Table 2). Similarly, Ks and Kl also showed wide inter-specific variations. For example, Ks ranged from 0.29 of Ilex chinensis Sims, an evergreen species at the PD site, to 7.52 kg m−1 MPa−1 s−1 of Alangium chinense (Loureiro) Harms, a deciduous species at HJ site. In addition, species with low stem ΔΨ50 also had low hydraulic conductance, and vice versa (Table 2).

In the three sites, hydraulic architecture and foliar carbon isotope discrimination were significantly different between the two types of leaf phenology (Table 3). Deciduous woody species displayed higher Ks, Kl and ΔΨ50, a less negative δ13C, higher SLA and lower Huber value than evergreen woody species. There was no significant difference in hydraulic architecture and leaf carbon isotope discrimination between the HJ and LB sites. However, both sites contrasted significantly with the PD site. This might be due to the different leaf phenology of the investigated species, as the species studied at the HJ site included 14 deciduous (D) and one evergreen (E) species (Table 1). The three sites had D and E species as follows: HJ (14D/1E), LB (6D/4E) and PD (4D/7E). No significant difference in ΔΨ50, Kl, SLA and Huber value was found among the three sites for the deciduous species. Within the evergreen species, there was no significant difference in hydraulic structure and δ13C between the PD and LB sites (data not shown). The HJ site was excluded, as it had only one evergreen species.

Three species co-occurred at the LB and HJ sites and two species co-occurred at the LB and PD sites. Alangium chinense, Mallotus philippensis (Lam.) Müll. and Vernicia fordii (Hemsley) Airy Shaw at the HJ site had significantly higher δ13C than that at the LB site; meanwhile, the former two species had higher Ks (P < 0.05) and the latter one had lower ΔΨ50 (P < 0.05) at the HJ site (Figure 3). There were no significant differences in hydraulic structure and δ13C of Platycarya longipes Wu and Lindera communis Hemsley between the LB and PD sites, except that Platycarya longipes had higher Ks (P < 0.001) at the LB site (Figure 3).

In the cross-species analysis, our results show that resistance to water-stress-induced xylem cavitation (ΔΨ50) increased significantly with decreasing Ks (Figure 4, P = 0.042) and Kl (Figure 4, P = 0.039). However, these relationships were not supported by the PIC correlation (Figure 4). Only Kl increased with increasing δ13C in the cross-species comparison and PICs (Figure 5). Nevertheless, there was no association between

[Figure 1. One of three alternative phylogenetic trees showing the relationships among the species used in this study. It was first constructed using the program Phylomatic, and then modified manually based on the literature, and re-drawn using TreeViewX (version 5.0). The unresolved polytomy is shown in the inset.]
Table 2. Summary of stem $K'$ (specific conductivity, kg m$^{-1}$ MPa$^{-1}$ s$^{-1}$), $K_0$ (leaf specific conductivity, kg m$^{-1}$ MPa$^{-1}$ s$^{-1}$), $\Psi_{50}$ (MPa), SLA (g cm$^{-2}$) and leaf isotope discrimination $\delta^{13}C$ (‰) for each species at the three sites in the study.

<table>
<thead>
<tr>
<th>Species</th>
<th>$K_s$</th>
<th>$K_0$ (x10$^{-4}$)</th>
<th>SLA</th>
<th>$\Psi_{50}$</th>
<th>$\delta^{13}C$ (‰)</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ss</td>
<td>4.58 ± 0.62</td>
<td>4.52 ± 0.82</td>
<td>209.35 ± 56.41</td>
<td>−0.65 ± 0.08</td>
<td>−27.72 ± 0.24</td>
<td>HJ</td>
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<td>Ma</td>
<td>6.08 ± 1.51</td>
<td>8.09 ± 3.49</td>
<td>191.49 ± 106.06</td>
<td>−1.11 ± 0.23</td>
<td>−26.92 ± 0.05</td>
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<tr>
<td>Mp</td>
<td>3.73 ± 0.76</td>
<td>2.86 ± 0.73</td>
<td>181.63 ± 8.96</td>
<td>−0.68 ± 0.10</td>
<td>−27.62 ± 0.44</td>
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<tr>
<td>Mp</td>
<td>1.22 ± 0.37</td>
<td>2.00 ± 0.71</td>
<td>103.10 ± 5.75</td>
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<td>−29.14 ± 0.07</td>
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<td>Vf</td>
<td>3.50 ± 0.79</td>
<td>4.10 ± 1.03</td>
<td>116.79 ± 13.70</td>
<td>−1.23 ± 0.22</td>
<td>−25.07 ± 0.22</td>
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<td>Vf</td>
<td>4.82 ± 0.66</td>
<td>5.37 ± 0.74</td>
<td>113.02 ± 1.95</td>
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<td>Vf</td>
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<td>5.70 ± 2.10</td>
<td>188.74 ± 7.92</td>
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<tr>
<td>Bj</td>
<td>1.22 ± 0.37</td>
<td>2.00 ± 0.71</td>
<td>103.10 ± 5.75</td>
<td>−0.64 ± 0.12</td>
<td>−29.14 ± 0.07</td>
<td>HJ</td>
</tr>
</tbody>
</table>

$^1$Abbreviations indicate genus and species, as listed in Table 1.

$^2$Data were normalized to the elevation of 800 m, according to the method of Hultine and Marshall (2000) and Marshall and Zhang (1994).

other hydraulic traits and $\delta^{13}C$ across all taxa in PICs (Figure 5). The cross-species relationship between $\Psi_{50}$ and $\delta^{13}C$ was also insignificant in PIC analysis.

Specific leaf area had a strong positive correlation with hydraulic conductance ($K_s$ and $K_0$) and a negative association with the Huber value in both the raw values and PIC co-relationship analyses (Figure 5, Table 4), suggesting adaptive association among these functional traits. In contrast, SLA was not associated with $\Psi_{50}$ in the PIC co-relationship analysis (Figure 5, Table 4). The Huber value was negatively correlated with hydraulic conductance ($K_s$ and $K_0$), but only showed a significant positive correlation with $K_s$ in the PIC co-relationship analysis.

Discussion

Karst plants in China are not highly cavitation-resistant species

The average value of $\Psi_{50}$ of 31 karst woody species in Guizhou Province, China, was only $-1.27$ MPa. This value can be compared with $\Psi_{50}$ values of other ecosystem types. Our species $\Psi_{50}$ values fall between those of tropical rain forest ($-0.77$ MPa) and tropical dry forest ($-2.42$ MPa), and show that the 31 species in this study are much more vulnerable to xylem cavitation than Mediterranean ($-5.31$ MPa) or desert vegetation ($-4.48$ MPa) (Maherali et al. 2004). Since high cavitation resistance is a key component of drought tolerance
(Maherali et al. 2004, but see Jacobsen et al. 2008), the present study does not support the idea that karst plants are long-term drought-tolerant species. In fact, in 2010 we observed widespread mortality of woody species in study areas, due to a lack of rainfall for 6 weeks in the 2009 growing season (C.C. Liu, field observation).

Meteorological data showed that the annual rainfall in Guizhou Province ranged between 1100 and 1500 mm, close to that reported for rain forest in Xishuangbanna in southern China (Qu et al. 2001, Tan et al. 2008). Critically, >80% of annual rainfall occurred in the growing season, from April to October (Wu et al. 2003), suggesting the lack of a high water deficit for local vegetation during the growing season. Since MAP is the main environmental stimulus that determines $\Psi_{50}$ (Maherali et al. 2004), we hypothesized that the unique abundant rainfall in summer in this karst area of China, combined with other biological characteristics, such as the deep root system of woody karst plants (Jackson et al. 1999, Bleby et al. 2010), will alleviate the plant's water deficit caused by the very limited surface soil water capacity of this karst topography. This may be one reason why well-developed primary and secondary evergreen and deciduous forests occur in this region, compared with arid vegetation in other karst areas at similar latitudes globally.

A site's effect on the hydraulic architecture of the investigated species was partially attributed to the different leaf pheno-logy composition of these species. Evergreen-leaved species had developed more resistance to xylem cavitation and lower hydraulic conductance when compared with co-occurring deciduous species (Table 3), in agreement with previous reports (Choat et al. 2004, Chen et al. 2009). Higher hydraulic conductance and lower water transport safety of deciduous species might guarantee sufficient acquisition of water when water is abundant during the growing season, and reflected the balance between carbon gain and water transport capacity through stomatal regulation in favor of fast growth closely associated with a higher photosynthetic rate (Santiago et al.

Figure 2. Percentage loss in hydraulic conductivity as a function of pressure for stems of 31 karst woody species in this study. Curves were fitted using all data; only means ($\pm$ 1 SE) are presented.
Table 3. Analysis of variance performed to test the site and leaf phenology effect on hydraulic architecture and leaf isotope discrimination.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>$K_s$</th>
<th>$K_l$ (x10^{-4})</th>
<th>SLA</th>
<th>$\Psi_{50}$</th>
<th>$\delta^{13}C$</th>
<th>Huber value (x10^{-4})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>$P = 0.003$</td>
<td>$P = 0.003$</td>
<td>$P = 0.003$</td>
<td>$P &lt; 0.001$</td>
<td>$P &lt; 0.001$</td>
<td>$P = 0.009$</td>
</tr>
<tr>
<td>HJ</td>
<td>$3.94 \pm 0.30^a$</td>
<td>$4.36 \pm 0.35^a$</td>
<td>$155.68 \pm 10.5^a$</td>
<td>$-0.95 \pm 0.06^a$</td>
<td>$-27.23 \pm 0.16^a$</td>
<td>$1.10 \pm 0.06^a$</td>
</tr>
<tr>
<td>LB</td>
<td>$3.06 \pm 0.38^a$</td>
<td>$3.10 \pm 0.36^a$</td>
<td>$120.50 \pm 4.06^a$</td>
<td>$-0.97 \pm 0.08^a$</td>
<td>$-28.14 \pm 0.22^a$</td>
<td>$1.18 \pm 0.08^a$</td>
</tr>
<tr>
<td>PD</td>
<td>$2.12 \pm 0.48^b$</td>
<td>$2.50 \pm 0.51^b$</td>
<td>$116.94 \pm 6.63^b$</td>
<td>$-2.11 \pm 0.24^b$</td>
<td>$-28.63 \pm 0.24^b$</td>
<td>$1.52 \pm 0.16^b$</td>
</tr>
<tr>
<td>Leaf phenology</td>
<td>$P &lt; 0.001$</td>
<td>$P &lt; 0.001$</td>
<td>$P = 0.013$</td>
<td>$P &lt; 0.001$</td>
<td>$P = 0.005$</td>
<td>$P &lt; 0.001$</td>
</tr>
<tr>
<td>D</td>
<td>$4.18 \pm 0.26$</td>
<td>$4.53 \pm 0.29$</td>
<td>$150.60 \pm 7.68$</td>
<td>$-1.05 \pm 0.06$</td>
<td>$-27.60 \pm 0.18$</td>
<td>$1.13 \pm 0.05$</td>
</tr>
<tr>
<td>E</td>
<td>$1.25 \pm 0.18$</td>
<td>$1.48 \pm 0.17$</td>
<td>$106.48 \pm 3.51$</td>
<td>$-1.70 \pm 0.22$</td>
<td>$-28.35 \pm 0.25$</td>
<td>$1.45 \pm 0.08$</td>
</tr>
</tbody>
</table>

D, winter deciduous; E, evergreen. $K_s$, stem specific conductivity (kg m^{-1} MPa^{-1} s^{-1}); $K_l$, leaf specific conductivity (kg m^{-1} MPa^{-1} s^{-1}); $\Psi_{50}$, xylem tension at 50% cavitation (MPa); SLA (g cm^{-2}); $\delta^{13}C$, leaf isotope discrimination (%); Huber value, the ratio of wood cross-section invested per unit leaf area attached. Means followed by the same letter were not statistically different at $P < 0.05$.

Figure 3. Specific conductivity ($K_s$), xylem tension at 50% cavitation ($\Psi_{50}$) and leaf isotope discrimination ($\delta^{13}C$) for five co-occurring woody species at different sites in this study. Means followed by the same letter were not statistically different at $P < 0.05$. 
The trade-off between vulnerability to xylem cavitation and xylem transport capacity

Previous studies and our investigation of the daily leaf minimum water potential ($\Psi_{\min}$) have shown that woody species had $\Psi_{\min}$ values of $-1.51 \pm 0.04$ MPa at the PD site (C.C. Liu, unpublished data) and $-1.43 \pm 0.12$ MPa at the LB site (Yu et al. 2002), suggesting that a relatively similar daily xylem tension range was experienced by the species investigated in this study. Based on this, and while taking phylogeny into account, we investigated the trade-off between hydraulic safety and efficiency among 31 karst woody species in China, with the same method and similar xylem tension range during the same growing season.

On the surface, the traditional cross-species correlation $r$ was significant for the trade-off between hydraulic safety and efficiency in the present study, confirming previous reports (Pockman and Sperry 2000, Martínez-Vilalta et al. 2002) in other ecosystems, and the investigation of the trade-off relationship between efficiency and vulnerability to cavitation across stem, shallow roots and deep roots of two woody karst species in the Edwards Plateau of central Texas (McElrone et al. 2004). However, when phylogenetic information was included using PICs, the correlation was weakened to an insignificant level, further supporting the idea that there may not be an evolutionary trade-off between resistance to cavitation and specific conductivity in woody plants (Maherali et al. 2004, 2006).

The absence of an evolutionary correlation between stem $\Psi_{50}$ and $K_l$ among woody angiosperm species in karst ecosystems may be attributable to differences in other xylem traits across sampled taxonomic species, such as vessel conductivity compensation by length (Sperry and Hacke 2004), the embolus refilling process (Bucci et al. 2003) and mitigation of tension fluctuation by xylem capacitance (Sperry et al. 2007, Meinzner et al. 2009). Plants can develop alternative functional designs with different hydraulic trait combinations, leading to approximately equivalent fitness in a specific habitat (Jacobsen et al. 2009). For example, in the present study, the sapwood area to leaf area ratio ($A_s$/$A_l$, Huber value) was negatively associated with $K_s$ if PICs were applied (Table 4), suggesting adaptive significance between the stem water transport capacity and the plant’s architectural adjustment (Maherali and DeLucia 2001). Given that the canopy conductivity is proportional to the product of $A_s$/$A_l$, the water potential gradient, $\Psi_{\min}$, and the inverse of tree height ($\text{Schäfer et al. 2000}$), an increase of $A_s$/$A_l$ and a decrease of $K_s$ under a similar xylem tension range and tree height may result in similar canopy conductivities across the studied species. On the other hand, adjustments of $A_s$/$A_l$ did not correspond to changes in vulnerability to cavitation in stems (Table 4, PIC coefficient). The most likely explanation for this observation is that mean conduit diameter (proportional to $\sqrt{A_s}$) (Martinez-Vilalta et al. 2002) and the size of the largest pit pore (inversely proportional to $\Psi_{\min}$) in a conduit did not hold a constant relationship across species (Martinez-Vilalta et al. 2002, 2004; Butler et al. 2009).

Looking more closely at the differences in hydraulic structure of co-occurring species at the three sites, species at the HJ site tended to have more resistance to xylem cavitation, lower water use efficiency (indicated by higher $\delta^{13}$C) and higher hydraulic conductance than the LB site (Figure 3). The HJ site has the most historic human disturbance of the three sites studied (Li et al. 2008). At any site, serious human disturbance will increase soil erosion and correspondingly decrease soil water retention capacity, thus increasing the water transport safety of local plants. It remains to be explained why HJ species inherited a higher $\delta^{13}$C and a higher hydraulic conductance than LB species, although a subsequent instantaneous water use efficiency measurement confirmed the tendency (S.R. Zhang, unpublished data).

**Figure 4.** Specific conductivity ($K_0$) and leaf specific conductivity ($K_l$) as a function of xylem tension at 50% cavitation ($\Psi_{50}$) for 31 woody species in the karst area in this study. Phylogenetically independent contrast (PIC) plots and correlation coefficients are shown in the inset in each subfigure. Note that $\Psi_{50}$ was converted to positive values for log$_{10}$ transformation. Therefore, positive correlations were represented by negative correlation coefficients. $^*P<0.05$, ns is non-significant ($P>0.05$).
Table 4. Magnitude and statistical significance of Pearson correlations and PIC data sets comprising 31 woody species in this study.

<table>
<thead>
<tr>
<th>Traits of contrast</th>
<th>$K_s$</th>
<th>$K_l\times10^{-4}$</th>
<th>SLA</th>
<th>$\Psi_{50}$</th>
<th>$\delta^{13}C$</th>
<th>Huber $\times10^{-4}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$K_s$</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$K_l$</td>
<td>0.939**</td>
<td>0.907** (PICs)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SLA</td>
<td>0.665**</td>
<td>0.597**</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\Psi_{50}$</td>
<td>-0.315*</td>
<td>-0.322*</td>
<td>-0.310*</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\delta^{13}C$</td>
<td>-0.278</td>
<td>-0.373*</td>
<td>0.049</td>
<td>0.175</td>
<td>-0.165</td>
<td>1</td>
</tr>
<tr>
<td>Huber</td>
<td>-0.617**</td>
<td>-0.403*</td>
<td>-0.592**</td>
<td>0.147</td>
<td>-0.099</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.450**</td>
<td>-0.099</td>
<td>-0.501**</td>
<td>-0.003</td>
<td>-0.091</td>
<td></td>
</tr>
</tbody>
</table>

Value in the lower row in each cell: Pearson correlation coefficient based on PICs. $\Psi_{50}$ and $\delta^{13}C$ were converted to positive values for log$_{10}$ transformation. Therefore, positive correlations were represented by negative correlation coefficients.

* $P < 0.05$, ** $P < 0.01$, ns is non-significant ($P > 0.05$).

Figure 5. Specific conductivity ($K_s$), leaf specific conductivity ($K_l$) and xylem tension at 50% cavitation ($\Psi_{50}$) as a function of leaf isotope discrimination ($\delta^{13}C$) and specific leaf area (SLA) for 31 woody species in this study. Phylogenetically independent contrast (PIC) plots and correlation coefficients are shown in the inset in each subfigure. Note that $\Psi_{50}$ was converted to positive values for log$_{10}$ transformation. Therefore, positive correlations were represented by negative correlation coefficients. ** $P < 0.01$, * $P < 0.05$, ns is non-significant ($P > 0.05$).
Therefore, whole-plant hydraulic adjustment may obscure the trade-off relationship between safety and efficiency at the organismal level, as discussed by Sperry et al. (2008) and Meinzer et al. (2010).

The maximum stomatal conductance measured at one point in time has been seen as one of the critical components of xylem tension control, and has been shown to have close physiological coordination with xylem structure (Sobrado 1993, Choat et al. 2004). However, xylem architecture is almost entirely determined by integrative long-term structural acclimation to environmental stimuli over time (Mencuccini 2003). As a consequence, the association between the average stomatal conductance over time and xylem structure will be more physiologically relevant than maximum stomatal conductance over time (Mencuccini 2003). As a consequence, the association between the average stomatal conductance over time and xylem structure will be more physiologically relevant than maximum stomatal conductance. The integrated stomatal conductance could be represented by average intercellular partial pressures of CO₂ (C), and consequently indicated by the carbon isotope discrimination (δ¹³C) (Farquhar et al. 1989, Huc et al. 1994, Bonal et al. 2001).

In this study, δ¹³C was positively correlated with K_s but not K_i (Table 4, PIC coefficient; Figure 5), suggesting that loose stomatal control (higher δ¹³C) was associated with higher leaf hydraulic conductivity, consistent with previous reports (Sobrado 1993, Choat et al. 2004). A close association between stomatal control and leaf hydraulic conductivity may guarantee similar xylem tension ranges among studied species (Yu et al. 2002), as the leaf water potential gradient was largely determined by the product of stomatal conductance and the inverse of K_i (Tyree and Ewers 1991). On the other hand, the absence of an evolutionary correlation between δ¹³C and K_i may be attributable to other factors, such as the buffering effect of stem xylem capacitance (Meinzer et al. 2009).

Specific leaf area, one of the leading dimensions of leaf trait variations related to plant carbon economy, was functionally associated with K_s and K_i (Table 4, Figure 5), which agrees with some previous reports (Mitchell et al. 2008, O’Grady et al. 2009) but does not agree with the findings of others (Tyree et al. 1999, Taylor and Eamus 2008). Such inconsistency could be explained by the idea that the relationships between SLA and other leaf traits would diverge from global patterns under low light environments (Santiago and Wright 2007). If samples experienced similar light environments at exposed sites, as in the present study, SLA would show a positive relationship with photosynthetic capacity and stomatal conductance (Santiago and Wright 2007), and be closely associated with hydraulic conductance via stomatal regulation, which was well-documented in previous reports (Santiago et al. 2004, Chen et al. 2009).

Our study, like other investigations of the hydraulic architecture of several species, has limitations. First, we could not guarantee we randomly sampled taxa in the study area, which might limit both traditional cross-species analysis and independent contrasts (Ackerly 2000). As a consequence, non-random sampling will lead to an underestimation of the true PIC correlation coefficients, and so only the significant PICs in our study should be regarded as robust. Nevertheless, this limitation must be balanced against inflated Type I error rates of non-phylogenetically corrected cross-species correlations (Ackerly 2000). Second, woody species with other growth forms were not included in this study. For example, there may be a weak evolutionary trade-off between hydraulic conductance and Ψ₅₀ in gymnosperm species (Maherali et al. 2004). Finally, intra- and inter-specific trait variations caused by different microhabitats should be taken into account both in traditional cross-species co-relationship studies and in independent contrast analysis (Santiago and Wright 2007).

Despite all this, to the best of our knowledge, data on the hydraulic architecture of woody karst species in China have not been reported in the literature previously. Therefore, our study provides a fundamental framework for the further investigation of hydraulic architecture of plants on karst topography in China. Comparative community physiology (Jacobsen et al. 2008) in water relations among karst plant communities, and between communities at karst and no-karst sites in similar climates, will be very helpful for understanding the characteristics of the hydraulic architecture of karst plants.

**Conclusion**

In conclusion, we provide the first available systematically collected data on the hydraulic architecture of woody karst species in China. We found that karst plants in China were not highly cavitation-resistant species. Our findings support the idea that there might not be an evolutionary trade-off between resistance to cavitation and specific conductivity in woody plants. The interactions between stomatal behavior, hydraulic capacity and other functional traits controlling xylem tension for maintenance of homeostatic water balance in whole plants, particularly under the highly variable daily moisture conditions in karst areas, are worthy of further study. Furthermore, such a study may also prove useful in understanding vegetation changes in karst ecosystems in response to local, regional and global changes in environmental conditions.

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